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Research paper

Siluro-Devonian vertebrate biostratigraphy and biogeography of China

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Abstract

During the past three decades, early vertebrates from the mid-Paleozoic of China have attracted extensive attention on account of their distinctive anatomical features, high diversity, early stratigraphic occurrence, and paleogeographic significance. These new findings have considerably increased our knowledge of vertebrate diversity, helped clarify the interrelationship of early fishes, and provided important data for mid-Paleozoic biostratigraphy and biogeography. In this paper, six Siluro-Devonian vertebrate faunas from China (Xiaoxiyu, Xiaoxiang, Xitun, Jiucheng, Haikou, and Zhongning faunas) and related stratigraphic problems are discussed. Biogeographically, the three main Chinese blocks (South China, North China, and Tarim blocks) constitute the "Pan-Cathaysian Galeaspid Province" during the mid-Paleozoic with highly endemic vertebrate faunas. Some major groups of early vertebrates, such as galeaspids, placoderms, and sarcopterygians, apparently originated and diversified in China. We suggest that three dispersal routes of early vertebrates (Northern Route, Southern Route, and Circum-Panthalassic Ocean Route) bridged the Chinese blocks with the adjacent continents or blocks during the mid-Paleozoic.

Keywords: Biostratigraphy; Biogeography; Early vertebrates; Siluro-Devonian; China

1. Introduction

The mid-Paleozoic fishes have long been regarded as having a special role in biogeographic studies because of their limited dispersal capabilities (Young, 1993). However, some biogeographic conclusions were difficult to reach because of incompleteness of the fossil record. In the last 40 years, detailed systematic studies in extra-European areas such as central and eastern Asia, and the southern continents, have enlarged the taxonomic database, which can be viewed from a global perspective (Young, 1993). Using this new database, Young (1981, 1993, 2003) has identified five distinctive faunal provinces for Early Devonian vertebrates, and discussed the paleogeographic relationships among Gondwana, Euramerica/Siberia, and eastern Asia continents. Ichthyofaunal distribution patterns can provide evidence of connections or barriers among different regions, as distinct from paleolatitude evidence provided by some other data sets, such as paleoclimatic or paleomagnetic data. Early vertebrates are gradually becoming a very useful tool in the study of mid-Paleozoic biogeography.

China, with a continuous mid-Paleozoic sequence, is one of the most important areas for studying early vertebrates and related stratigraphy and biogeography. Since Mansuy (1907) reported Devonian fishes in China, early vertebrates have been found from over 70 sites (Fig. 1), distributed mostly in the South China, North China, and Tarim blocks (Zhao and Zhu, 2007). During the past three decades, early vertebrates from China have attracted extensive attention on account of their distinctive anatomical features, high diversity, relatively early stratigraphic occurrence (Pan and Dineley, 1988), and paleogeographic importance (Pan and Dineley, 1988; Pan et al., 1996; Zhao, 2005; Zhu and Zhao, 2006). These new findings considerably increased our knowledge of vertebrate diversity, helped to clarify the interrelationships of early fishes (Chang and Yu, 1981, 1984; Zhu et al., 1999, 2001, 2006, 2009; Zhu and Yu, 2002; Zhu and Ahlberg, 2004), and provided important data for mid-Paleozoic biostratigraphy and biogeography.

The main aims of this study are to: (1) introduce briefly geological settings of the mid-Paleozoic in China, (2) summarize the mid-Paleozoic vertebrates as currently known in China, establish

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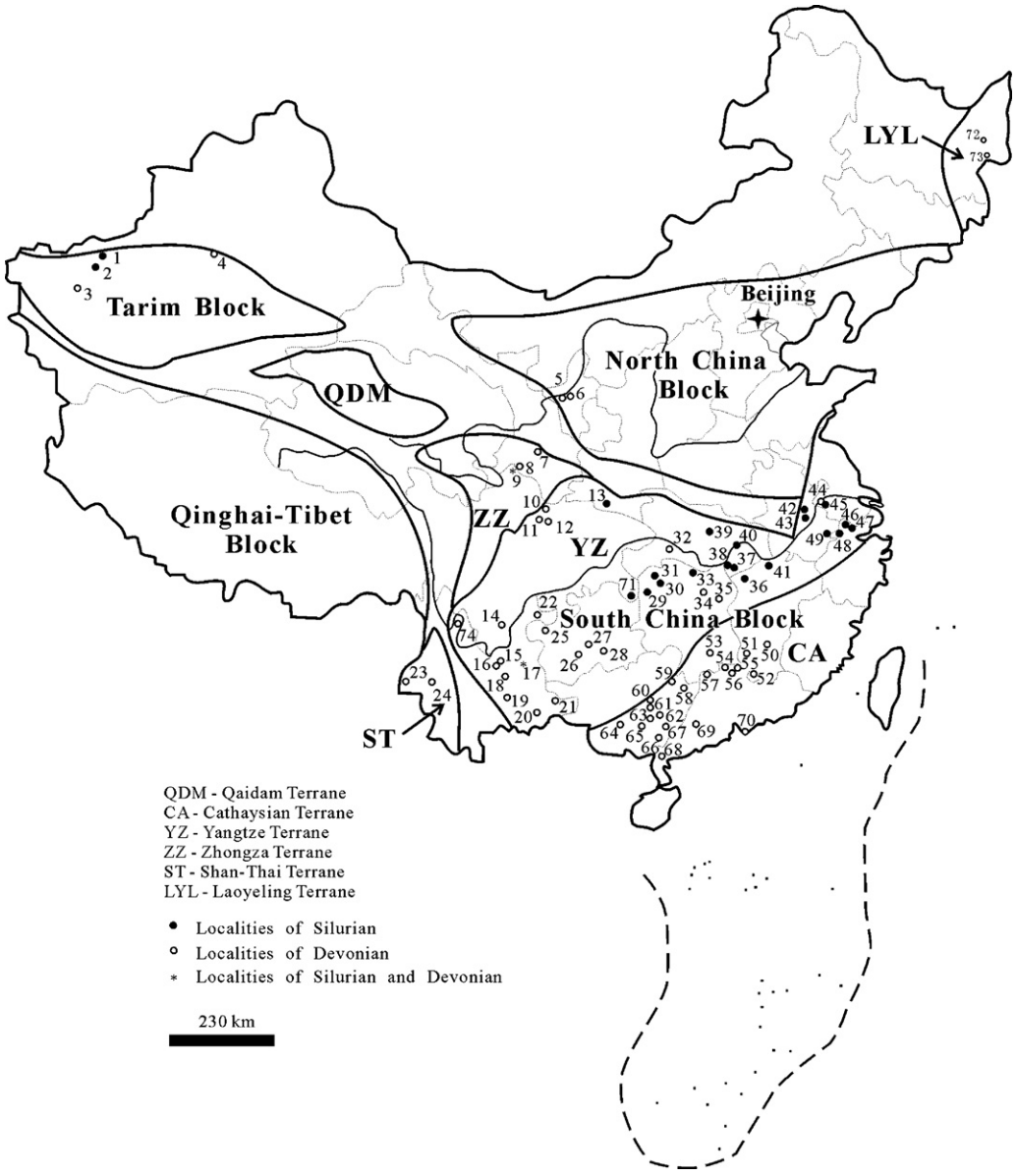

Fig. 1. Map showing the tectonic units and the distribution of mid-Paleozoic vertebrate localities in China. 1, Kalpin; 2, Bachu; 3, Shache; 4, Caohu; 5, Zhongwei; 6, Zhongning; 7, Zhangxian; 8, Tewo; 9, Zoige; 10, Pingwu; 11, Beichuan; 12, Jiangyou; 13, Ziyang; 14, Ningnan; 15, Luquan; 16, Wuding; 17, Qujing; 18, Kunming; 19, Huaning; 20, Wenshan; 21, Guangnan; 22, Zhaotong; 23, Yingjiang; 24, Shidian; 25, Hezhang; 26, Changshun; 27, Guiyang; 28, Duyun; 29, Baojing; 30, Zhangjiajie; 31, Sangzhi; 32, Changyang; 33, Lixian; 34, Yiyang; 35, Changsha; 36, Xiushui; 37, Chongyang; 38, Chibi; 39, Jingshan; 40, Wuhan; 41, Ruichang; 42, Chaoxian; 43, Wuwei; 44, Nanjing; 45, Jiangning; 46, Changxing; 47, Huzhou; 48, Anji; 49, Ningguo; 50, Yudu; 51, Chongyi; 52, Quannan; 53, Guiyang; 54, Lechang; 55, Renhua; 56, Shaoguan; 57, Lianxian; 58, Hexian; 59, Pingle; 60, Xiangzhou; 61, Wuxuan; 62, Guiping; 63, Guixian; 64, Nanning; 65, Hengxian; 66, Bobai; 67, Yulin; 68, Lianjiang; 69, Yunfu; 70, Hong Kong; 71, Xiushan; 72, Baoqing; 73, Mishan; 74, Lijiang.

the new vertebrate faunas and assemblages, and use this updated database to elucidate the mid-Paleozoic vertebrate biostratigraphy throughout China, and (3) outline the distribution pattern of the mid-Paleozoic vertebrates in China, and then discuss its biogeographic significance.

2. Geological settings

The west-east laying Tethys tectonic belt separated the globe into two large landmass groups: the Laurasia Landmass Group in the north and the Gondwana Landmass Group in the south (Xu et al., 1996; Pan et al., 1997). The main body of the Chinese paleo-continent belongs to neither the Laurasia Landmass Group nor the Gondwana Landmass Group, and has been termed the Pan-Cathaysian Landmass Group (Fig. 2A; Xu et al., 1996; Pan et al., 1997).

Based on paleomagnetic data and the analysis of geodynamics, sedimentary facies and various biota, it is suggested that China in the mid-Paleozoic succeeded the general paleogeographic characteristics of the Late Ordovician, and was composed mainly of the North China, South China (including the Yangtze, Cathaysian and Zhongza terranes), and Tarim blocks, as well as some terranes such as Qaidam, Shan-Thai, and Laoyeling terranes (Fig. 2A; Chen and Wang, 1999). The

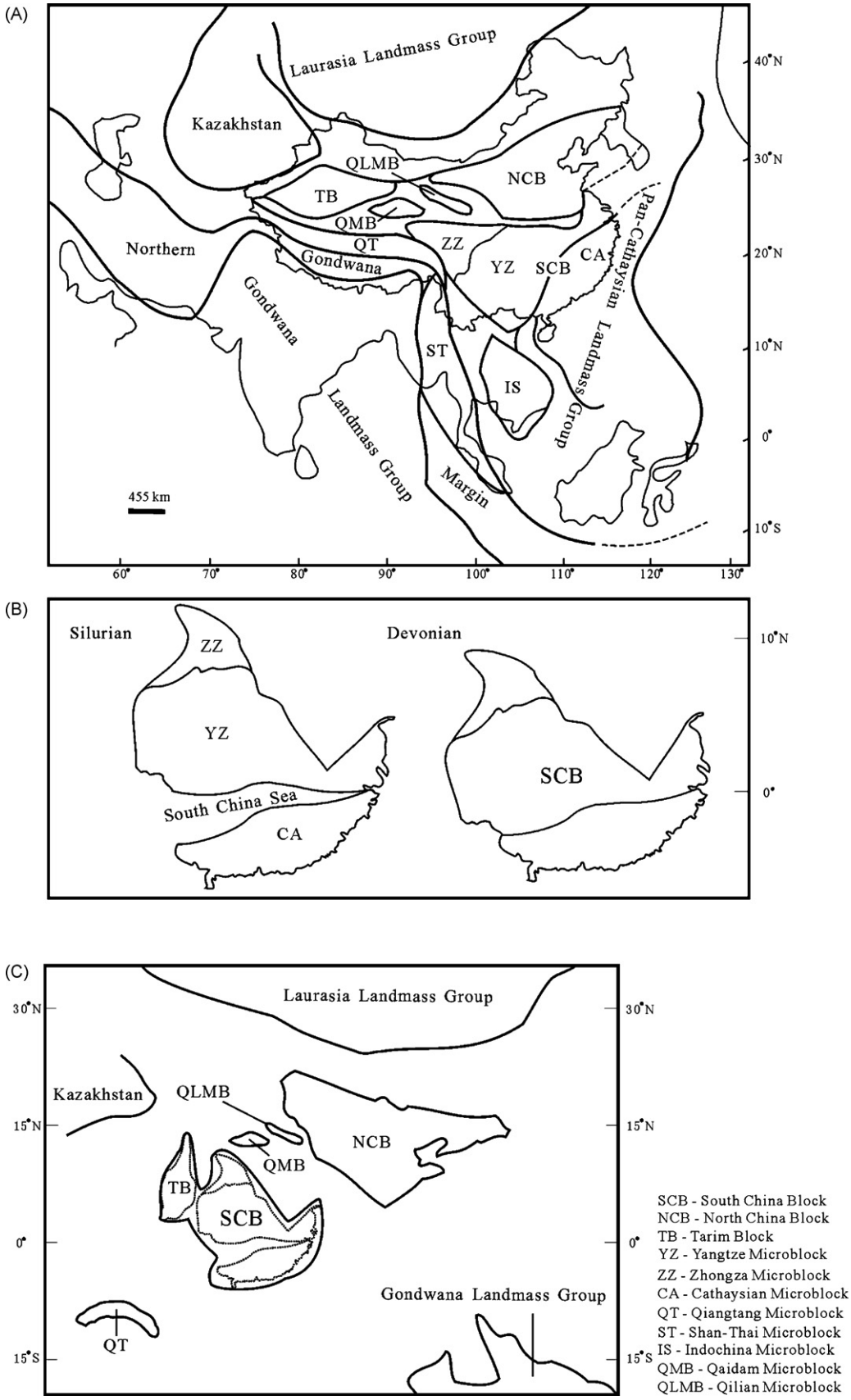

Fig. 2. (A) Outline map showing the Gondwanan, Laurasian, and Pan-Cathaysian landmass groups (revised from Xu et al., 1996); (B) The location of the South China Block in Silurian and Devonian respectively; (C) Sketch map showing the location of the Tarim-Yangtze Block in Silurian (revised from Zhao et al., 2009).

paleogeographic position and tectonic movement of the former three blocks play a pivotal role in the tectonic evolution of the mid-Paleozoic of China.

Geological and paleontological evidence indicates that the South China Block was not a uniform unit in the Silurian when the South China Sea was sandwiched between the Yangtze and Cathaysian terranes (Fig. 2B). Recent findings of Silurian galeaspids and chondrichthyans from the Tarim Basin also suggest that Tarim and the Yangtze Terrane were linked to each other, and formed a united Tarim-Yangtze Block during the Llandovery and Wenlock (Fig. 2C). The united block was separated into two blocks in the Ludlow or later, and the Tarim Block began to drift away to the northwest (Zhao et al., 2009). Therefore, the North China, Tarim-Yangtze, Qinghai-Tibet, Qilian, and Qaidam blocks or terranes constitute the main tectonic units of China in the Silurian. During the Silurian interval, all Chinese tectonic units were in the process of drifting to the north; the Tarim-Yangtze Block was located at a lower paleolatitude in the northern hemisphere (Opdyke et al., 1987; Chen et al., 2001), and the North China Block reached a middle-lower paleolatitude in the northern hemisphere (Huang et al., 1999).

The Caledonian Movement had strong effects on the Chinese paleoplates in the Silurian. The Yangtze and Cathaysian terranes converged into the South China Block by the end of the Silurian (Fig. 2B). Meanwhile, the Qaidam and Qilian terranes accreted to the southwest margin of the North China Block. In the Devonian, the main tectonic units of China were totally distributed at a middle-lower paleolatitude in the northern hemisphere (Fang et al., 1996; Huang et al., 1999, 2000). Geological and paleomagnetic data indicate that the North China Block gradually converged with the South China Block from east to west during the Devonian interval, but a remnant sea still existed in the west until the end of the Devonian. These two main blocks in China converged into a uniform tectonic unit in the Middle Triassic or later (Zhang, 1987; Yin et al., 1999). At the beginning of the Devonian, the Tarim Block was an independent block and drifted northwest. It collided with the Kazakhstan Block at the end of the Carboniferous (Li et al., 1989; Fang et al., 1996), and converged with the North China Block in the Late Permian or later (Wang et al., 1993).

3. Biostratigraphy of early vertebrates in China

Devonian fishes had been known from China (Ting and Wang, 1937; Chi, 1940; Young, 1945; Liu, T.S., 1948; Liu, H.T., 1955; Liu and P'an, 1958) since Mansuy (1907) reported the 'ichthyodorulite' from Panxi (Po-Si), Huaning County, Yunnan. However, the large-scale collection and research did not begin until the 1960s. The vertebrate-bearing Devonian rocks are now known to be distributed in the South China, North China, and Tarim blocks, as well as the Shan-Thai and Laoyeling terranes. Devonian vertebrates in China include all major groups of early vertebrates, and show the early diversification of some important vertebrate lineages, such as antiarchs and sarcopterygians. The research of Silurian fishes in China began with P'an (1959), although Ting and Wang (1937) reported the agnathan "*Cephalaspis*" from the Silurian of Qujing, Yunnan, presumably a galeaspid from the Lower Devonian of that area (Liu, 1965, 1975). Recently, new fossil fish materials, including agnathans, placoderms, acanthodians, chondrichthyans, and osteichthyans, were collected from the Maoshan Formation of Changxing, Zhejiang, the Huixingshao Formation of northwestern Hunan, and the Kuanti Formation of Qujing, Yunnan, enriching the diversity of Silurian vertebrates and shedding new light on the correlation between marine and non-marine strata in China. The fish-bearing Silurian rocks are distributed mainly in South China and Northwest China, and belong to the united Tarim-Yangtze Block (Zhao et al., 2009).

Up to now, Wang, J.Q. (1984), Pan (1986a), Pan and Dineley (1988), Wang, S.T. (1993), Zhu and Wang (2000), and Zhu et al. (2000) have reviewed Siluro-Devonian vertebrates in China. With the large number of new findings of early vertebrates in China since 2000, it is necessary to give an updated review of Siluro-Devonian vertebrates and related biostratigraphy. Based on the previous vertebrate data and new findings, the following six vertebrate faunas and 41 vertebrate assemblages are established for the Siluro-Devonian of China (Table 1), and some issues concerning the Siluro-Devonian stratigraphic correlation in China are discussed.

3.1. Xiaoxiyu Fauna

This fish fauna is characterized by the flourishing of galeaspids and sinacanths, and the occurrence of placoderms. The following eight fish assemblages are recognized.

3.1.1. Wentang Assemblage (early Telychian, Locality 30)

This assemblage, mainly distributed in Wentang of Zhangjiajie (formerly Dayong) area of Hunan, is represented by the fish remains from the Rongxi Formation. The vertebrates include two galeaspid genera, *Dayongaspis* (Fig. 3A, Pan and Zeng, 1985) and *Konoceraspis*, as well as chondrichthyan and acanthodian fin-spines (Zhu, 1998). Zhu (1998) erected the Family Sinacanthidae and assigned it to the Class Chondrichthyes based on the histological examination of these Chinese fin-spines. This new assignment was partially corroborated by Sansom et al. (2005), who placed the sinacanths crownwards of the placoderms, and possibly within the total-group Chondrichthyes.

The Rongxi Formation, or the 'Lower Marine Red Beds' (Chen and Rong, 1996), also yields invertebrate remains, such as brachiopods, trilobites, chitinozoans, and graptolites (Chen and Rong, 1996; Holland and Bassett, 2002). The chitinozoan *Eisenackitina daozhenensis* from the lower part of the formation (Geng, 1990) indicates an early Telychian age (*turriculatus* Biozone).

3.1.2. Tataaiertage Assemblage (early Telychian, Localities 1 and 2)

This assemblage is distributed in the Kalpin-Bachu area of Xinjiang, and has rich galeaspids and chondrichthyans similar to the Wentang Assemblage. The fish-bearing stratum is the Tataaiertage Formation in the northwestern margin of the Tarim Basin. The fossil fishes are as follows: *Platycaraspis tianshanensis*, *Nanjiangaspis kalpinensis*, *N. zhangi*,

Table 1
The mid-Paleozoic vertebrate assemblages of China.

System	Timescale			Vertebrate assemblages			
	Series	Stages	Age (Ma)		Previous numbering system	New name system	
Devonian	Upper	Famennian	359.2–374.5	XI	*Sinolepis*	Zhongning Fauna	Bachu, Daihau, Doushishan, Leigutai and Sanmentan
				X	*Remigolepis*		Niushoushan
		Frasnian	374.5–385.3	IX	*Changyangophyton-Chirodipterus*		Huangjiadeng, Tuqiaozi and Shetianqiao
	Middle	Givetian	385.3–391.8	VIII	*Panxiosteus-Eastmanosteus*	Haikou Fauna	Yidade and Jinbaoshi
				VII	*Bothriolepis kwangtungensis-B. lochangensis*		Xiawuna
		Eifelian	391.8–397.5	VI	*Bothriolepis sinensis-Hunanolepis*		Qujing and Bluff Head
							Dangduo, Shixiagou, Taiomajian and Shangshuanhe
	Lower	Emsian	397.5–407.0	V	*Wudingolepis-Yinosteus*	Jiucheng Fauna	Wuding and Chuandong
				IV	*Kueichowlepis-Sinopetalichthys*		Duyun, Banmandaodi, Yijiang and Wenshan
		Pragian	407.0–411.2	III	*Sanchaspis-Asiaspis*	Xitunn Fauna	Xujiachong
		Lochkovian	411.2–416.0	II	*Diabolepis-Nanpanaspis*		Cuifengshan, Shanjiang, Xiaputonggou and Xishancun
				I	*P. liaojiaoshanensis-Laxaspis*		
Silurian	Pridoli		416.0–418.7	7	*Nostolepis sinica*		
	Ludlow	Ludfordian	418.7–421.3	6	*Ligulalepis yunnanensis*	Xiaoxiang Fauna	Hongmiao
		Gorstian	421.3–422.9	5	*Silurolepis*		Kuanti
	Wenlock	Homerian	422.9–426.2	4	*Thelodus sinensis*	Xiaoxiyu Fauna	Miaogou
		Sheinwoodian	426.2–428.2	3	*Xiushuiaspis-Sinogaleaspis*		Keziretage and Yangtze
	Llandovery	Telychian	428.2–436.0	2	*Hanyangaspis guodingshanensis*		Maoshan
				1	*Dayongaspis-Kalpinolepis*		Fentou and Yimugantawu
		Aeronian	436.0–439.0				Wentang and Tataaiertage
		Rhuddanian	439.0–443.7				

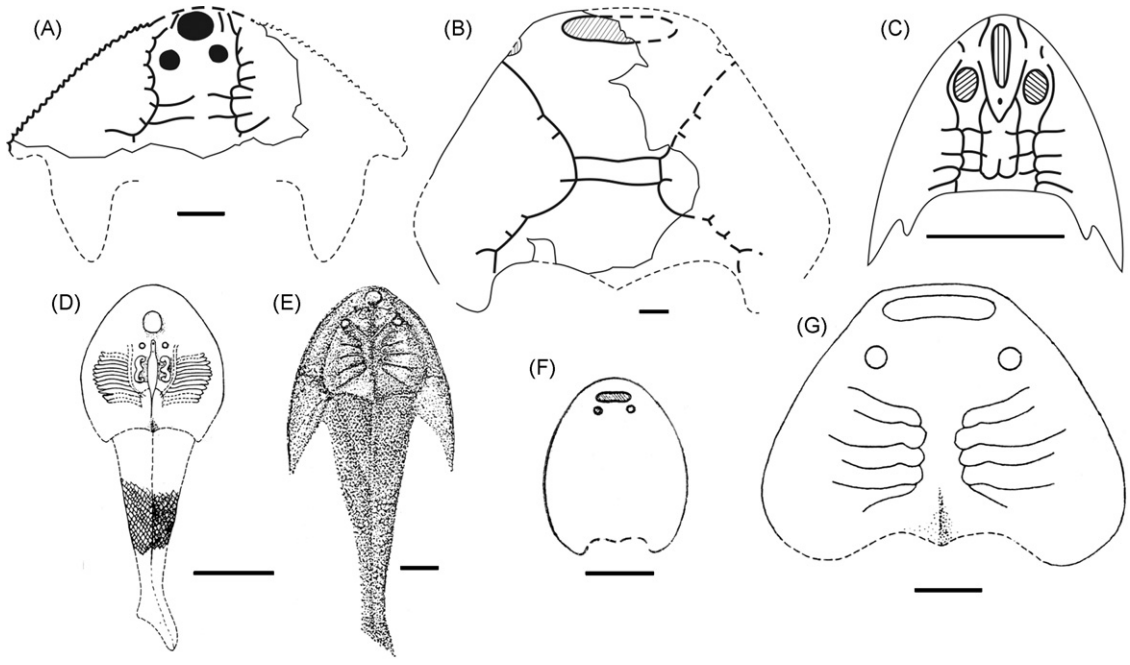

Fig. 3. Silurian fishes from China. (A) *Dayongaspis hunanensis* Pan et Zeng (1985); (B) *Hanyangaspis guodingshanensis* P'an et al. (1975); (C) *Sinogaleaspis shankouensis* P'an et Wang (1980); (D) *Pseudoduyunaspis bachuensis* Wang et al. (1996); (E) *Geraspis rara* Pan et Chen (1993); (F) *Xiushuiaspis ganbeiensis* Pan et Wang (1983); (G) *Kalpinolepis tarimensis* Wang et al. (1996). Scale bar = 1 cm.

Kalpinolepis tarimensis (Fig. 3G), *Hanyangaspis* sp., *Microphymaspis pani* and *Neosinacanthus planispinatus*, *N.* sp., *Sinacanthus wuchangensis* and *S.* sp. (Wang, P., et al., 1988; Wang, J.Q., et al., 1996, 2002; Zhu, 1998; Lu et al., 2007).

3.1.3. Fentou Assemblage (middle Telychian, Localities 13, 33, 39, 40, 42, and 71)

This assemblage is represented by the Hanyangaspididae and the Sinacanthidae and is distributed in the northern margin of the South China Block. The fish-bearing strata include the Fentou Formation (Hubei, Anhui and Jiangsu), the Wujiahe Formation (Shaanxi), and the Xiushan Formation (Chongqing, Hunan and Guizhou). The assemblage includes the galeaspids *Hanyangaspis guodingshanensis* (Fig. 3B, P'an et al., 1975), *H. chaohuensis* (Pan, 1986b), *Geraspis rara* (Fig. 3E, Pan and Chen, 1993), the chondrichthyans *Sinacanthus wuchangensis* (P'an, 1959), *S. triangulates*, *S.* sp., *Neosinacanthus planispinatus* (P'an et al., 1975), some remains of Mongolepididae and Shiqianolepidae (Sansom et al., 2000), and the yunnanolepiform antiarch *Shimenolepis graniferus* (Wang, 1991a). *Shimenolepis* represents the oldest occurrence of placoderms in the world.

The same assemblage indicates that the Fentou, Wujiahe, and Xiushan formations are coeval (Table 2). The Xiushan Formation was assigned to the *P. celloni* Biozone or *griestoniensis* Biozone of the middle Telychian based on the study of the conodont *Ozarkodina guizhouensis* (Sansom et al., 2000).

3.1.4. Yimugantawu Assemblage (middle Telychian, Localities 1 and 2)

This assemblage is distributed in the Kalpin-Bachu area of Xinjiang, and the fish-bearing stratum is mainly the Yimugantawu Formation. The assemblage includes the galeaspids *Hanyangaspis* sp., *Pseudoduyunaspis bachuensis* (Fig. 3D), and the chondrichthyans *Sinacanthus wuchangensis*, *S. triangulatus*, cf. *Mongolepis rozmanae*, cf. *Elegestolepis*, *Xinjiangichthys pluridentatus*, and *X. tarimensis* (Wang, J.Q., et al., 1996; Zhu, 1998; Wang, N.Z., et al., 1998a). *Xinjiangichthys* is assigned to the Mongolepididae, which was erected from the Late Llandovery of western Mongolia.

The similarity between the Yimugantawu and Fentou assemblages suggests that the age of the Yimugantawu Formation, like that of the Fentou and Xiushan formations in South China, is middle Telychian.

3.1.5. Maoshan Assemblage (late Telychian, Localities 46 and 48)

This assemblage, characterized by the occurrence of eugaleaspidiform galeaspids, is distributed in the lower part of 'Upper Marine Red Beds' (Chen and Rong, 1996) in South China. The galeaspids '*Sinogaleaspis*' *zhejiangensis*, *Meishanaspis lehmani*, *Changxingaspis gui*, *Hanyangaspis* sp. and *Anjiaspis reticularis* (Pan, 1986a; Gai et al., 2005) and some chondrichthyan remains (*Sinacanthus* sp.; Pan, 1986a) were reported from the lower part of the Maoshan Formation of Changxing, Zhejiang. In the Xikeng Formation of Xiushui, Jiangxi, '*Sinogaleaspis*' *xikengensis*, *Sinogaleaspis shankouensis* (Fig. 3C; P'an and Wang, 1980; Gai et al., 2005), *Xiushuiaspis jiangxiensis* and *X. ganbeiensis* (Fig. 3F, Pan and Wang, 1983) were described in the 1980s.

The Maoshan and Xikeng formations can be correlated to the Huixingshao Formation and the lower part of the Xiaoxiyu Formation (Table 2), but the age is poorly constrained because of the paucity of fossils. However, in light of the evidence from the underlying upper Xiushan Formation with its invertebrate fauna, the Huixingshao Formation might be latest Telychian to Wenlock (Chen and Rong, 1996; Holland and Bassett, 2002). On that evidence, we place the Maoshan Assemblage in the late Telychian.

3.1.6. Keziertage Assemblage (Late Llandvoery–Early Wenlock, Localities 1 and 2)

This assemblage is distributed in the Kalpin-Bachu area of Xinjiang, and the fish-bearing stratum is mainly the Keziertage Formation. Lu et al. (2007) described a fragment of placoderm trunk-shield from the upper part of the Keziertage Formation. Similar placoderm remains are found in the Yangtze Assemblage (see Section 3.1.7), which is dated as the Late Llandovery–Early Wenlock. Thus, the fish-bearing Keziertage Formation is dated from the late Telychian to the Early Wenlock, although its upper age limit remains unsettled. It can be correlated with the 'Upper Marine Red Beds' in South China (Table 2).

3.1.7. Yangtze Assemblage (Early Wenlock, Localities 17, 29-31 and 71)

This assemblage is widely distributed in the upper part of 'Upper Marine Red Beds' in South China, and is represented by the galeaspids *Eugaleaspis xiushanensis* and the placoderm '*Wangolepis*'. *Eugaleaspis xiushanensis* came from the Huixingshao Formation of Xiushan, Chongqing (Zhu and Wang, 2000). Although '*Wangolepis*' is not yet described, abundant fossil materials of that form have been found in the upper part of the Xiaoxiyu Formation in Zhangjiajie, northwestern Hunan, and the lower part of the Yuejiashan Formation in Qujing, Yunnan.

The assemblage can be dated to the Early Wenlock, although its upper age limit remains unsettled (Rong et al., 1990; Zhu and Wang, 2000; Zhao, 2005).

3.1.8. Miaogou Assemblage (Homerian, Wenlock, Localities 8, 9 and 17)

This assemblage is only distributed in the West Qinling Area. It is represented by acanthodians *Ischnacanthus* sp. and *Nostolepis tewonensis* from the Miaogou Formation (Wang et al., 1998b). Recent investigation on microvertebrate remains from the upper part of the Yuejiashan Formation indicates that the distribution of the assemblage extends to eastern Yunnan.

In association with cephalopods, trilobites, brachiopods, and ostracods (Wang et al., 1998b; Zhu and Wang, 2000), the Miaogou Assemblage can be referred to the Homerian stage of the Wenlock.

Table 2
Stratigraphic chart showing Silurian fish-bearing formations in China.

Localities / Strata	Xinjiang	Guizhou	Chongqing	Hunan	Hubei	Jiangxi	Anhui	Jiangsu	Zhejiang	Shanxi	Yunnan	West Qinling	Fish faunas	Vertebrate assemblages (Zhu and Wang, 2000)
	Kalpin-Bachu 1	Shiqian 2	Xiushan 3	Zhangjiajie 4	Hanyang 5	Xiushui 6	Chaoxian 7	Nanjing 8	Changxing 9	Ziyang 10	Qujing 11	12		
Overlying strata	Donghetang Formation (D_3)	Liangshan Formation (P_1)	Yuntaikuan Formation (D_2)			Wutung Formation (D_3)				?	Xishancun Formation	Xiaputonggou Formation	Xitun Fauna	
Silurian – Pridoli										Wafangdian Formation	Yulungssu Formation	Bailongjiang Group: Yanglugou Formation		7 *Nostolepis sinica*
Silurian – Ludlow											Miaokao Fm. / Kuanti Fm.		Xiaoxiang Fauna	6 *Ligulalepis yunnanensis*; 5 *Silurolepis*
Silurian – Wenlock				Xiaoxiyu Formation						Xianzhong-gou Formation	Yuejiashan Formation	Zhouqu Group: Miaogou Formation	Xiaoxiyu Fauna	4 *Thelodus sinensis*; 3 *Xiushuiaspis-Sinogaleaspis*
Silurian – Llandovery – Telychian	Keziertage Formation	Huxingshao Formation	Huxingshao Formation		Maoshan Formation	Xikeng Formation	Maoshan Formation	Maoshan Formation	Maoshan Formation			Jiannigou Formation		
Silurian – Llandovery – Telychian	Yimugantawu Formation	Xiushan Formation	Xiushan Formation	Xiushan Formation	Fentou Formation	Xiajiaqiao Formation	Fentou Formation	Fentou Formation	Kangshan Formation	Wujiahe Formation				2 *Hanyangaspis guodingshan-ensis*
Silurian – Llandovery – Telychian	Tataaiertage Formation	Rongxi Formation	Rongxi Formation	Rongxi Formation	Xintan Formation	Qingshui Formation	Gaojiabian Formation	Houjiatang Formation	Qingshui Formation	Doushangou Formation				1 *Dayongaspis-Kalpinolepis*
Silurian – Llandovery – Aeronian	Kepintage Formation	Majiaochong Fm. / Leijiatun Formation	Xiaoheba Formation	Xiaoheba Formation	Lungmachi Formation	Dianbei Formation		Gaojiabian Formation	Anji Formation	Banjiuguan Formation		Gezi Formation		
Silurian – Llandovery – Aeronian		Xiangshuyuan Formation	Lungmachi Formation	Lungmachi Formation		Lishuwo Formation				Maliu-shuwan Formation		Anzigou Formation		
Silurian – Llandovery – Rhuddanian		Lungmachi Formation												
Underlying strata	Yingan Fm. (O_3)	Guanyinqiao Formation (O_3)		Wufeng Formation (O_3)		Xinkailing Fm. (O_3)	Wufeng Formation (O_3)		Yankou Fm. (O_3)	Bajiaokou Fm. (O_3)	Shuanglong-tan Fm. (Є2)	Baiyigou Group (O?)		

3.2. Xiaoxiang Fauna

This fish fauna is characterized by the radiation of placoderms, and the first occurrence and divergence of osteichthyans. The following two assemblages are recognized based on their different facies and tectonic backgrounds.

3.2.1. Kuanti Assemblage (Gorstian–middle Ludfordian of Ludlow, Locality 17)

This fish assemblage is only distributed in eastern Yunnan of South China. Diverse osteichthyans, placoderms, and acanthodians have been collected from the middle-lower part of the Kuanti Formation. A new osteichthyan, *Guiyu oneiros* Zhu et al. (2009), has been recently described. As the oldest articulated yet not most basal osteichthyan, *Guiyu oneiros* provides unique insights into the sequence of character acquisition in the origin and early divergence of osteichthyans. The diverse placoderm and acanthodian material are waiting for detailed study. The assemblage represents an important radiation interval in the history of early vertebrates.

The assemblage is recovered from the muddy limestone of the middle-lower part of the Kuanti Formation immediately beneath the first appearance of *Ozarkodina crispa*. The assemblage can be assigned to the Ludlow (Gorstian–middle Ludfordian) based on the stratigraphic sequence.

3.2.2. Hongmiao Assemblage (late Ludfordian of Ludlow, Locality 17)

This assemblage in eastern Yunnan is erected on the basis of vertebrate micro-remains. It is composed mainly of acanthodians and osteichthyans. The acanthodians include *Poracanthodes qujingensis*, *Hanilepis wangi*, *Nostolepis* sp., and *Gomphonchus* sp. from the Miaokao Formation (Wang and Dong, 1989), and *Nostolepis striata*, *N. sinica*, *N.* sp., and *Hanilepis wangi* from the Yulungssu Formation (Gagnier et al., 1989; Wang and Dong, 1989). The osteichthyans include *Naxilepis gracilis* from the upper part of the Kuanti Formation, *Ligulalepis yunnanensis*, *Kawalepis comptus*, and *Naxilepis gracilis* from the Miaokao Formation, and Osteichthyes indet. from the lower part of the Yulungssu Formation (Gagnier et al., 1989; Wang and Dong, 1989). *Kawalepis comptus* was referred to the Thelodonti by Wang and Dong (1989). However, Märss et al. (2007) suggested it as an actinopterygian based on the rhombic flat scales. In addition, the assemblage includes *Thelodus*? *sinensis* from the upper part of the Kuanti Formation (Wang and Dong, 1989). This might represent an endemic genus reminiscent of *Lanarkia* scales, or broken placoderm tubercles or an acanthodian spine (Märss et al., 2007).

The conodont *Ozarkodina crispa* has been found from the upper part of the Kuanti Formation to the lower Yulungssu Formation (Walliser and Wang, 1989), placing the assemblage in the late Ludfordian stage of the Ludlow.

3.3. Xitun Fauna

This fish fauna is characterized by the radiation of Polybranchiaspidiformes, Huananaspidiformes, Yunnanolepidoidei, and crown sarcopterygians. The following seven assemblages are recognized based on the different tectonic backgrounds and facies.

3.3.1. Liaojiaoshan Assemblage (Pridoli, Locality 17)

This assemblage is exemplified by vertebrates from the Yulungssu Formation of Qujing, Yunnan. It is dominated by acanthodians (under study) and osteichthyans. The osteichthyans includes *Psarolepis* sp. from the upper part of the Yulungssu Formation (Zhu and Wang, 2000).

Based on stratigraphic study, the upper part of the Yulungssu Formation can be assigned to the conodont *Ozarkodina remscheidensis eosteinhornensis* zone of the Pridoli (Wang, 1980; Walliser and Wang, 1989).

3.3.2. Yanglugou Assemblage (Pridoli, Locality 9)

This assemblage is distributed in the West Qinling area, and is represented by some acanthodian micro-remains. Wang et al. (1998b) described the acanthodians *Gomphonchus sandelensis* and Ischnacanthidae indet. from the Yanglugou Formation of Zoige, Sichuan. The fishes are very silimar to those from the Liaojiaoshan Assemblage, suggesting that the fish-bearing stratum can be correlated to the upper part of the Yulungssu Formation (Table 2), and should be Pridoli.

3.3.3. Xishancun Assemblage (early Lochkovian, Localities 17 and 67)

This assemblage is characterized by the radiation of Polybrachiaspidiformes. In addition, there are many antiarchs, arthrodires, petalichthyids, sarcopterygians, and microvertebrate remains. The assemblage, from the Xishancun Formation (Qujing area, Yunnan), represents the first radiation of early vertebrates during the Devonian in China (Zhao and Zhu, 2007). The galeaspids include *Yunnanogaleaspis major*, *Polybranchiaspis liaojiaoshanensis* (Fig. 4A), *P. minor*, *P. yulongssus*, *P. zhanyiensis*, *Dongfangaspis yunnanensis*, *D. paradoxus*, *D. qujingensis*, *Laxaspis qujingensis*, *L. rostrata*, *Diandongaspis xishancunensis*, *Pentathyraspis pelta*, *Nochelaspis maeandrine*, *Damaspis vartus*, and *Stephaspis dipteriga* (Liu, 1965, 1975; P'an and Wang, 1978; Zhu, 2000; Zhu et al., 2000; Gai and Zhu, 2007). The antiarchs include *Yunnanolepis chii* (Fig. 4J), *Y. parvus*, *Y. porifera*, *Heteroyunnanolepis qujingensis*, *Chuchinolepis gracilis*, *Zhanjilepis aspratilis*, and *Minicrania lirouyii* (Liu, 1963; Zhu, 1996; Zhu et al., 2000). Arthrodires are only represented by *Szelepis* sp. (Zhu et al., 2000). The petalichthyids include *Diandongpetalichthys liaojiaoshanensis*, and the sarcopterygians include *Psarolepis* sp. and *Youngolepis* sp. (P'an and Wang, 1978; Zhu et al., 2000). In addition, microvertebrate remains include *Parathelodus scitulus*, *P. trilobatus*, and *P. cornuformis* (Zhu, 2000).

The correlated stratum, the Xishancun Formation, is characterised by sandstones intercalated with shales representing a foreshore-offshore environment. The *Emphanisporites micronatus–Strelispora newportensis* spore assemblage, associated with the fauna, is commensurate with the *uniformis* graptolite zone (Cai et al., 1994), which gives the assemblage an early Lochkovian age.

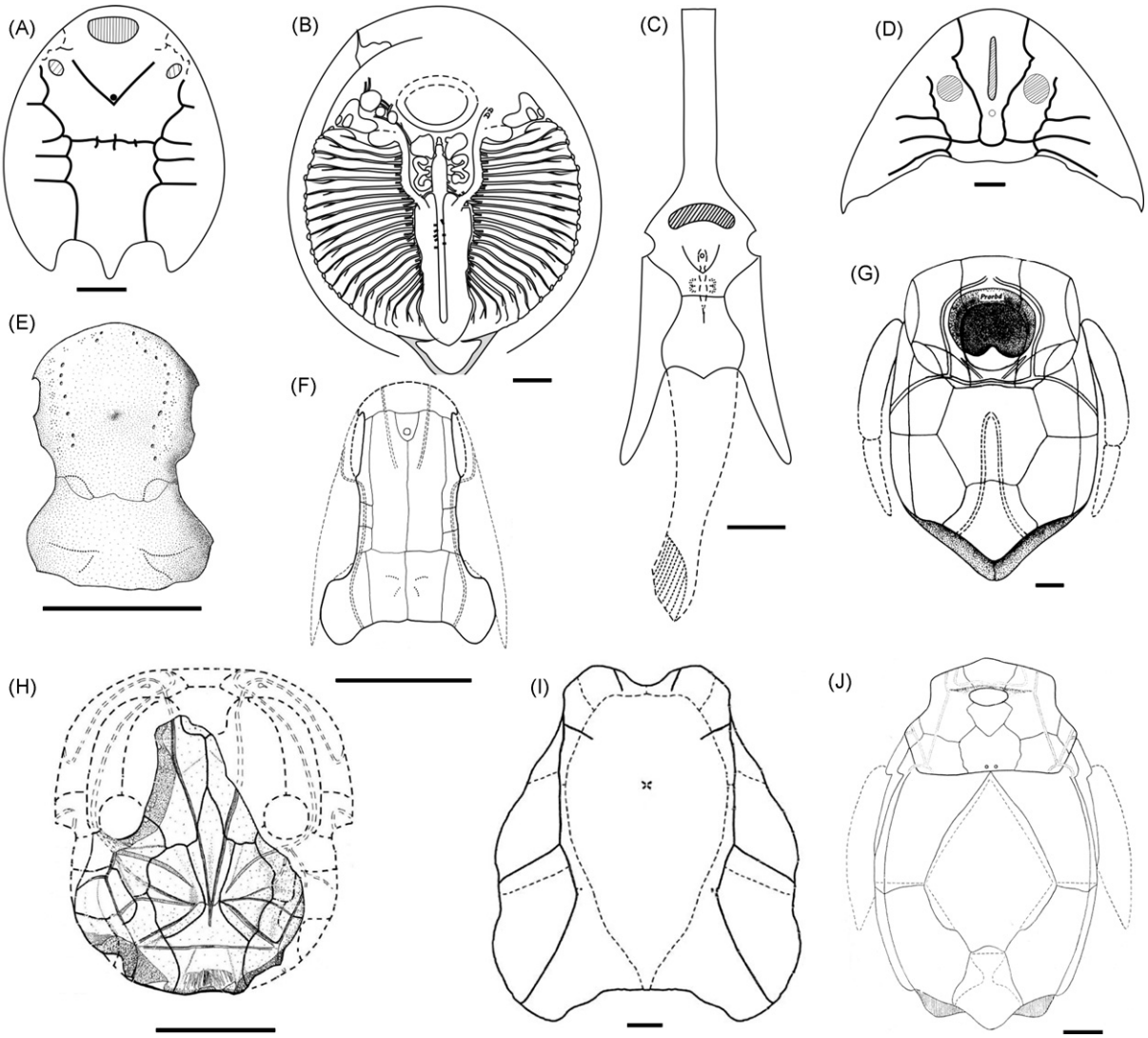

Fig. 4. Early Devonian fishes from China. (A) *Polybranchiaspis liaojiaoshanensis* Liu (1965); (B) *Duyunaspis paoyangensis* P'an et Wang (1978); (C) *Sanqiaspis rostrate* Liu (1975) (revised from Zhao et al., 2002); (D) *Eugaleaspis xujiachongensis* Liu (1975); (E) *Youngolepis praecursor* Chang et Yu (1981); (F) *Meemannia eos* Zhu et al. (2006); (G) *Microbrachius chuandongensis* Wang et Zhang (1999); (H) *Yiminaspis shenmo* Dupret (2008); (I) *Gavinaspis convergens* Dupret et Zhu (2008); (J) *Yunnanolepis chii* Liu (1963). Scale bar = 1 cm.

The assemblage can be extended to the Beijuntang Formation in Yulin, Guangxi, including the arthrodire *Buchanosteus* sp. and the antiarch? *Chuchinolepis* sp. (Zhu et al., 2000). Numerous brachiopods and graptolites (e.g., *Monograptus uniformis*, *M. praehercynicus*, *M. microdon*, *Neomonograptus hercynicus*) are present in the Beijuntang Formation (Mu et al., 1988; Wang and Yang, 1998). The fish-bearing lower part of the Beijuntang Formation is referred to the *Monograptus uniformis* graptolite zone of the early Lochkovian.

3.3.4. Xiaputonggou Assemblage (early–middle Lochkovian, Localities 8 and 9)

This assemblage is represented by vertebrate micro-remains from the lower and upper parts of the Xiaputonggou Formation in the Zoige and Tewo areas of the northwestern margin of the South China Block. The vertebrate micro-remains include thelodonts (*Parathelodus scitulus* and *Canonia* sp., Zhu et al., 2000), acanthodians (*Poracanthodes zoigenensis*, *Nostolepis striata*, *N. gracilis*, *N. tewonensis*, *Gansuichthys liui*, *Gomphochus sandelensis*, and *Poracanthodes* cf. *P. porosus*, Wang et al., 1998b), and a shark *Iberolepis* cf. *I. aragonensis* (Zhu, 2000).

Associated marine invertebrates (corals, trilobites, brachiopods, ostracods, and conodonts) suggest a shallow marine depositional environment (XIGMR and NIGPAS, 1987). The lower part of the formation yields the conodont *Icriodus woschmidti woschmidti*, and the upper part the conodont *Ozarkodina remscheidensis remscheidensis* (XIGMR and NIGPAS, 1987).

3.3.5. Shanjiang Assemblage (?Lochkovian, Locality 74)

This assemblage is represented by microvertebrate remains from the lower part of the Shanjiang Formation in Lijiang, Yunnan. The fossil fishes are dominated by acanthodians including

Nostolepis striata, *N. gracilia*, *Nostolepoides mingyinensis*, and *Cheiracanthoides* cf. *C. wangi* (Wang, 2003), associated with conodonts *Trichonodella trichonodelloides*, *Belodella devonica*, and *Panderodus unicostatus* (Wang, 1982). Wang (1982) placed the conodont-bearing bed in the *A. ploeckensis* and *P. siluricus* conodont zone of the Ludlow. However, the acanthodians from the lower part of the Shanjiang Formation show many similarities to the Early Devonian assemblage in central New South Wales, Australia, and West Qinling in South China (Wang, 2003). Here we provisionally place the assemblage in the Lochkovian, Early Devonian. Further work is needed for accurate age constraint.

3.3.6. Cuifengshan Assemblage (middle–late Lochkovian, Localities 17 and 63)

This assemblage is distributed mainly in eastern Yunnan, and is characterised by the diversification of primitive antiarchs and crown sarcopterygians. It also extends to the central part of Guangxi. Fishes include galeaspid agnathans: *Eugaleaspis changi*, *E. lianhuashanensis*, *Polybranchiaspis liaojiaoshanensis* (Fig. 4A), *Nanpanaspis microculus*, *Laxaspis qujingensis*, *L. rostrata*, *Microholonaspis microthyris*, *Hyperaspis acclivis*, *Cyclodiscaspis ctenus*, *Siyingia altuspinosa*, and *Diplohollcaspis daleensis* (Liu, 1965, 1975; Zhu, 2000; Wang et al., 2009); antiarchs: *Yunnanolepis chii* (Fig. 4J), *Y. parvus*, *Y. porifera*, *Y.* sp., *Phymolepis cuifengshanensis*, *P. guoruii*, *Chuchinolepis gracilis*, *C. qujingensis*, *C. sulcata*, *C. robusta*, *C.* sp., *Zhanjilepis aspratilis*, and *Z.* sp. (Liu, 1963; Zhu, 1996, 2000); arthrodires: *Szelepis yunnanensis*, *Gavinaspis convergens* (Fig. 4I), *Parawilliamsaspis yujiangensis*, *Asiacanthus kaoi*, and *A. suni* (Zhu, 2000; Dupret and Zhu, 2008); sarcopterygians: *Psarolepis romeri*, *Achoania jarviki*, *Styloichthys changae*, *Meemannia eos* (Fig. 4F), *Youngolepis praecursor* (Fig. 4E), *Youngolepis* sp., and *Diabolepis speratus* (Chang and Yu, 1981, 1984; Yu, 1998; Zhu et al., 1999, 2001, 2006; Zhu and Yu, 2002); microvertebrate remains: *Parathelodus scitulus*, *P. asiatica*, *P. catalatus*, *P. trilobatus*, *P. cornuformis*, *Nostolepis* sp., *Youngacanthus gracilis*, *Gualepis elegans*, *Changolepis tricuspidus*, *Peilepis solida*, *Ohiolepis*? *xitunensis*, and *Ohiolepis* sp. (Wang and Dong, 1989; Wang, 1997; Zhu, 2000).

The fossil-bearing strata are the Xitun and Guijiatun formations (mudstone and shale intercalated with marl) and the lower part of the Lianhuashan Formation (muddy siltstone and fine sandstone intercalated with mudstone). The correlated stratum is the lower part of the Pingyipu Formation in the Longmenshan area of Sichuan Province (Table 3). The associated spores (*Apiculiretusispora plicata*, *Streelispora newportensis*, *Stenozonotriletes pusillus*, *Breconisporites breconensis*, *Apiculatisporites microcanonus*, and *Emphanisporites neglectus*, etc.) indicate that the age of the Cuifengshan Assemblage is middle-late Lochkovian (Cai et al., 1994; Zhu et al., 2000). It represents a foreshore-shallow water marine environment.

3.3.7. Xujiachong Assemblage (Pragian, Localities 10-12, 17, 20, 22, 60, 63 and 65)

This assemblage is distributed mainly in the Qujing area of Yunnan, and is represented by the occurrence of Eugaleaspidiformes and Huananaspidiformes with a rostral process. The fish-bearing strata include the Xujiachong, Posongchong, Nakaoling, and Pingyipu formations in Qujing, Zhaotong and Wenshan of Yunnan, the central part of Guangxi, and northwest Sichuan, respectively.

The fishes from the Xujiachong and Posongchong formations include the agnathans: *Sanqiaspis zhaotongensis*, *S. rostrata* (Fig. 4C), *Lungmenshanaspis yunnanensis*, *Zhaotongaspis janvieri*, *Qingmenaspis microculus*, *Gantarostrataspis gengi*, *Gumuaspis rostrata*, *Macrothyraspis longicornis*, *Kwangnanaspis subtriangularis*, *Huananaspis wudinensis*, *Eugaleaspis xujiachongensis* (Fig. 4D), *Pterogonaspis yuhaii*, *Sanchaspis magalarostrata*, and *Wenshanaspis zhichangensis* (Liu, 1975; Zhu, 2000; Zhao et al., 2002); antiarchs: *Mizia longhuaensis* and *Yunnanolepis* sp. (Zhu, 1996); arthrodires: *Szelepis yunnanensis*, *S.* sp. (Zhu, 2000) and *Yiminaspis shenme* (Fig. 4H; Dupret, 2008); petalichthyids: *Brevipetalichthys gracilis* and *Pampetalichthys longhuaensis* (Ji and Pan, 1997, 1999; Zhu, 2000); and sarcopterygian: Onychodontidae indet., *Arquatichthys porous*, and *Qingmenodus yui* (Zhu and Janvier, 1994; Lu and Zhu, 2008, 2009). The fishes from the Nakaoling Formation are collected mainly in Hengxian and Xiangzhou areas of Guangxi, including galeaspids: *Asiaspis expansa* and *Antiquisagittaspis cornuta* (P'an et al., 1975; Zhu, 2000); antiarch: *Liujiangolepis suni* (Zhu, 2000); and arthrodires: *Yujiangolepis liujingensis*, *Asiacanthus multituberculatus*, *Szelepis* sp., *Buchanosteus guangxiensis*, Actinolepidae indet., ? Phlyctaeniidae indet., and Arctolepida indet. (Liu, 1948; Zhu, 2000; Wang, 2005). Some microvertebrate remains are also found in the formation, such as acanthodians *Gomphonchus liujingensis* and *Machaeracanthus*? *bohemicus*, and the sarcopterygian *Onychodus* sp. (Zhu, 2000). In the Guanshanpo Member of the Pingyipu Formation, the fishes include galeaspids: *Sinoszechuanaspis yanmenpaensis*, *Sanqiaspis rostrata* (Fig. 4C), *Lungmenshanaspis kiangyouensis*, *Dongfangaspis major*, and ? *Polybranchiaspis* sp. (Liu, 1973, 1975; P'an et al., 1975); antiarchs: *Grammaspis callima*, *Chuanbeiolepis jiangyouensis*, *Yunlongolepis liui*, and Yunnanolepidae gen. et sp. indet. (Hou et al., 1988; Zhu, 2000); arthrodire: Phlyctaeniidae gen. et sp. indet. (Hou et al., 1988); petalichthyids: *Xinanpetalichthys shendaowanensis*, *Neopetalichthys yenmenpaensis*, and *Parapetalichthys minor* (Liu, 1973, 1975; P'an and Wang, 1978; Hou et al., 1988); and sarcopterygian: Crossopterygii? gen. et sp. indet. (Hou et al., 1988).

The correlated strata (Xujiachong and Posongchong formations) are represented by mudstone, muddy siltstone and shale intercalated with sandstone and fine sandstone, the Nakaoling Formation is dominated by fine sandstone, siltstone and mudstone, and the Guanshanpo Member is composed of sandstone and siltstone. Besides rich fish remains, plants, spores and invertebrate fossils (bivalves, ostracodes, brachiopods, and conodonts) were reported from the above-mentioned four formations (Hao, 1988; Wang, 1994). Based on the fossil data and the stratigraphic sequence, the correlated strata are probably of Pragian age (Table 3; Hao, 1988; Wang, 1994; Zhu et al., 1994; Liu, 2002; Zhao et al., 2002).

Table 3
Stratigraphic chart showing Devonian fish-bearing formations in China.

Localities / Strata			Ningxia	Sichuan	Guizhou		Guangxi			Yunnan				Jiangsu	West Qinling	Fish faunas
			Zhongwei-Zhongning 1	Jiangyou 2	Duyun 3	Guiyang 4	Hengxian 5	Xiangzhou 6	Pingle 7	Qujing 8	Zhaotong 9	Wenshan 10	Baoshan 11	Nanjing 12	13	
Overlying strata			Yanghugou Fm. (C_2)	Changtanzi Formation	Gelaohe Formation	Tangpagou Formation	Eocene	Yingtang Formation	Unsubdivised	Wanshoushan Formation		Huanglung Formation	C1	Jinling Formation	Yiwa Formation	
D_3	Famennian		Zhongning Formation	Maoba Formation	Zhewang Formation	Gaopoyang Formation	Rongxian Formation	Rongxian Formation				Gedang Formation	Dujiacun Formation	Wutung Fm. Upper	Doushi-shan Formation	Zhongning Fauna
				Shawozi Formation	Yaosuo Formation									Lower		
	Frasnian		Dadaigou Formation	Xiaolingpo Formation	Wangchengpo Formation		Gubi Formation			Zaige Formation	Zaige Formation		Heyuan-zhai Formation		Cakuohe Formation	
				Tuqiaozi Formation				Baqi Fm.							Pulai Formation	
D_2	Givetian			Guanwushan Formation	Dushan Formation	Mazongshan Formation	Mintang Formation	Tungkang-ling Fm.	Tungkang-ling Fm.	Haikou Formation	Qujing Formation	Tungkang-ling Fm.	Malutang Formation		Xiawuna Formation	Haikou Fauna
	Eifelian		Shixiagou Formation	Jinbaoshi Formation	Bangzhai Fm.		Najiao Formation	Changcun Fm.	Xindu Formation	Shang-shuanhe Formation	Qingmen Formation	Gumu Formation			Lure Fm.	
					Longdongshui Fm.			Guche Fm.					Xibiantang Formation			
								Guba Fm.								
D_1	Emsian	Upper		Yangmaba Formation	Shujiaping Formation	Wudang Formation		Dale Formation	Hexian Formation	Chuandong Formation	Suotoushan Fm. Bianqinggou Formation	Zhichang Formation	Shabajiao Formation		Dangduo Formation	Jiucheng Fauna
				Ertaizi Formation												
		Lower		Xiejiawan Formation	Danlin Formation		Moding Formation	Guanqiao Fm.		Xujiachong Formation	Pojiao Formation	Pojiao Formation			Gala Formation	
				Ganxi Formation				Ertang Fm.								
								Shanglun Fm.								
				Bailiuping Formation			Yukiang Fm.	Yukiang Fm.								
	Pragian			Pingyipu Formation			Nakaoling Formation	Nakaoling Fm.	Shiqiao Formation		Posongchong Formation	Posongchong Formation	Wangjia-cun Formation		Shang-putonggou Formation	Xitun Fauna
								Lianhuashan Formation								
	Lochkovian						Lianhua-shan Formation			Guijiatun Formation						
										Xitun Formation			Xiang-yangsi Formation		Xia-putonggou Formation	
										Xishancun Formation						
Underlying strata			Xiangshan Group ($\in_2$)	Huixingshao Formation	Wengxiang Group (S)	Gaozhaitian Group (S_1)	Longshan Group ($\in_3$)			Yulungssu Formation	Bocaitian Formation ($\in_3$-O)		Niushiping Formation	Maoshan Formation	Yanglugou Formation	

3.4. Jiucheng Fauna

This fish fauna is characterized by the occurrence of tetrapodomorphs, euantiarchs, and derived arthrodires. The following six assemblages are recognized based on their different fossil fishes, environments, and tectonic backgrounds.

3.4.1. Wenshan Assemblage (early Emsian, Localities 20 and 21)

Only the lungfish *Erikia jarviki* has been described from the assemblage (Zhu, 2000). Associated antiarch materials under study have been collected from the Pojiao Formation in Gumu of Wenshan, Yunnan. The invertebrate Pojiao Fauna (characterized by *Rostrospirifer tonkinensis* and *Calceola sandalina*) indicates that the Pojiao Formation is typical of early Emsian deposits (Hou et al., 2000).

3.4.2. Yujiang Assemblage (early Emsian, Localities 10-12, 60, 61, 63, 65 and 66)

This assemblage is only distributed in South China, including central Guangxi (Hengxian, Xiangzhou, Wuxuan, and Bobai areas) and northern Sichuan (Longmenshan). The fishes were mainly collected from the Yujiang, Ertang, Dale, and Moding formations (limestone, marl and silty mudstone), and Bailiuping, Ganxi, Xiejiawan, and Ertaizi formations (limestone, muddy siltstone, and sandstone). The assemblage is characterized by dipnorhynchid lungfish, galeaspid and microvertebrate remains, including galeaspid *Tridensaspis magnoculus*, lungfish *Sorbitorhynchus deleaskitus*, thelodont *Turinia* sp.; arthrodires: Phlyctaenaspinae indet. and Williamsaspidae indet.; acanthodians: *Cheiracanthoides comptus*, *Ch.* cf. *C. comptus*, *Ch. dolosus*, *Ch. wangi*, *Ch. coraptus*, *Nostolepis guangxiensis*, *N.* sp., *Rhadinacanthus*? sp., *Gomphonchus liujingensis*, *G.* sp., *G.*? *liujingensis*, cf. *Trundlelepis* sp., *Tareyacanthus* aff. *T. magnificus*, *Acanthodes* cf. *A. dublinensis*, and *Machaeracanthus*? sp.; chondrichthyians: *Hercynolepis* sp., *Gualepis* sp., cf. *Gualepis* sp., cf. *Gualepis elegans*, *Ohiolepis newberryi*, *Ohiolepis* aff. *O. newberryi*, *Ohiolepis* cf. *O. newberryi*, cf. *Kadunglelepis* sp., *Wuxuanichthys wangi*, and cf. *Wuxuanichthys* sp.; actinopterygians: *Dialipina* cf. *D. markae*, *Ligulalepis* cf. *L. toombsi*, and *Ligulalepis*? *sinensis*; and sarcopterygian: *Onychodus* sp. (Hou et al., 1988; Burrow et al., 2000; Zhu, 2000; Zhu et al., 2000). In addition, placoderm remains occur in the Xiejiawan Formation (Burrow et al., 2000).

Associated invertebrates include conodonts, brachiopods, corals, and bivalves, which indicate the neritic shelf facies for the Yukiang Formation and correlated strata (Table 3). Associated conodonts place the fish-bearing strata in the *Polygnathus dehiscens–Polygnathus serotinus* conodont zone (Hou et al., 1988) of the early Emsian.

3.4.3. Banmandaodi Assemblage (early Emsian, Locality 74)

This assemblage is distributed in the lower part of the Banmandaodi Formation in Lijiang, West Yunnan, and is represented by acanthodians including *Nostolepis gracilis*, *Nostolepoides mingyinensis*, *Lijiangichthys lembodes*, *Cheiracanthoides* cf. *C. wangi*, and *C.* sp. (Wang, 2003). Associated invertebrates include corals (*Pseudoblothrophyllum*? *elegans* and *Fasciphyllum minor*), ammonoids (*Anetoceras*, *Erbenoceras*, and *Teicherticeras*), tentaculites (*Nowakia zlichovensis* and *N. barrandei*) and conodonts (*Ozarkodina denckmanni*, *Polygnathus dehiscens*, *Spathognathodus primus*, and *S.* sp.), indicating an early Emsian assemblage (Yu and Liao, 1978; Wang, 1982). The fish-bearing beds are dominated by limestones intercalating with shale and siltstone, representing a shallow-water shelf environment.

3.4.4. Duyun Assemblage (early Emsian, Localities 25, 27-28, 58 and 59)

This assemblage is distributed in the Duyun, Guiyang, and Hezhang areas of Guizhou, and the Hexian and Pingle areas of Guangxi. The fishes in the assemblage include galeaspids *Duyunolepis paoyangensis* (Fig. 4B), *Paraduyunaspis hezhangensis*, *Neoduyunaspis minuta*, and *Lopadaspis pinglensis* (P'an and Wang, 1978; Zhu, 2000; Wang et al., 2001), the arthrodire *Kueichowlepis sinensis* (P'an and Wang, 1978), the petalichthyid *Sinopetalichthys kueiyangensis* (P'an et al., 1975), and the antiarch *Dayaoshania youngi* (Ritchie et al., 1992).

The fish-bearing strata include the Wudang, Shujiaping, and Hexian formations, characterized by sandstone, fine sandstone, and siltstone intercalated with hematite beds. Associated marine invertebrates include brachiopods, ostracodes, and bivalves, indicating a foreshore-offshore depositional environment. The abundant brachiopods are represented by *Euryspirifer shujiapingensis–Otosprifer daleensis* assemblage (Hou et al., 2000) of the early Emsian.

3.4.5. Wuding Assemblage (late Emsian, Localities 15 and 16)

This assemblage is only distributed in the Wuding and Luquan areas of Yunnan, and is mainly characterised by the occurrence of higher arthrodires. Arthrodires include *Exutaspis megista*, *Jiuchengia longoccipita*, *Yinostius major*, *Livosteus sinensis*, *Holonema* sp., and *Xiangshuiosteus wui* (Zhu, 2000). Antiarchs include *Wudinolepis weni* and *Luquanolepis pileos* (Zhang, 1965; Zhang and Young, 1992). The fossil-bearing stratum is the Jiucheng Formation, represented by black shale intercalated with mudstone. The age of the assemblage is late Emsian (Wang and Zhu, 1995). Depositional environment was a restricted neritic shelf facies (lagoon).

3.4.6. Chuandong Assemblage (late Emsian, Localities 17, 22 and 59)

This assemblage comes mainly from the Chuandong Formation in Qujing, and represents the early occurrence of the Tetrapodomorpha. It includes sarcopterygians: *Kenichthys campbelli*, *Tarachomylax multicostatus*, and *Heimenia* sp. (Zhu and Wang, 1996b; Zhu, 2000; Qiao and Zhu, 2008); antiarchs: *Microbrachius chuandongensis* (Fig. 4G), *Xichonolepis qujingensis*, *Bothriolepis chuandongensis*, *B.* sp., *B.* cf. *tungseni*, and *Wudinolepis* cf. *weni* (Shen, 1991; Zhu and Wang, 1996b; Wang and Zhang, 1999). The distribution can be extended to Pingle (Guangxi) and Yiliang (Yunnan). The antiarch

Hohsienolepis hsintuensis (P'an and Wang, 1978) and the galeaspid *Wumengshanaspis cuntianensis* were collected from the Xindu Formation of Pingle and the Suotoushan Formation of Yiliang respectively (Zhu, 2000). The antiarch *Hohsienolepis* is very similar to *Wudinolepis* in the Chuandong and Jiucheng formations of Yunnan.

The fish-bearing Chuandong Formation is characterized by sandstone and siltstone intercalated with mudstone. Its depositional environment was a typical shelf facies (backshore-offshore-shallow sea). Associated ostracodes (*Briatina* sp., *Hermmannina* sp.) and spores (*Calyptosporites vetatus–Rhabdosporites langii* assemblage) indicate a range from Emsian to Eifelian or even Givetian (Xu and Gao, 1991; Cai et al., 1994; Zhu and Wang, 1996b; Cai, 2000; Liu, 2002). Based on the stratigraphical sequence in the Qujing area, and correlation with the Xindu Formation of the Pingle area in Guangxi and the Suotoushan Formation of the Yiliang area in northeast Yunnan (Table 3), we place the correlated fish-bearing strata in the late Emsian.

3.5. Haikou Fauna

This fish fauna is characterized by the radiation of antiarchs and arthrodires. The following nine assemblages are recognized.

3.5.1. Shangshuanhe Assemblage (early Eifelian, Localities 16 and 17)

This assemblage, represented by *Bothriolepis shuanghenensis*, *B. tungseni*, and *B.* sp. (Zhang, 1965; Shen, 1991), is known from the Haikou Formation (lower part) of Wuding, and the Shangshuanghe Formation of Qujing. Associated plants include *Taeniocrada* sp., *Protolepidodendron* sp., *Lepidodendropsis* sp., and cf. *Barrandeina dusliana*. In China, the strata yielding *Lepidodendropsis* are usually below the *Stringocephalus* bed, giving an early Eifelian age. Both the Shangshuanhe Formation and lower part of the Haikou Formation are characterized by sandstone and shale intercalated with some thin-bedded carbonates (e.g., muddy dolomite), indicating a foreshore-offshore depositional environment.

3.5.2. Tiaomajian Assemblage (middle Eifelian, Localities 16-18, 35, 54-57, 62, 66, 68 and 69)

This assemblage is widely distributed in central Hunan, northeastern Guangdong, the Kunming, Wuding and Qujing areas of Yunnan, and the Bobai area of Guangxi. The fish-bearing strata are the Haikou (lower-middle part), Tiaomajian (lower-middle part), Laohutou (equal to Dahepo), and Xindu (middle part) formations, mainly characterized by sandstone intercalated with muddy siltstone and limestone. The dominant fishes are antiarchs, including *Bothriolepis yunnanensis*, *B. tungseni*, *B. sinensis*, *B. lochangensis*, *B. kwangtungensis*, *B. shaokuanensis*, and *Hunanolepis tieni* (Fig. 5C) (Chi, 1940; Pan and Dineley, 1988; Wang, 1991b). Galeaspids, arthrodires and petalichthyids are also known from the assemblage, such as *Clarorbis apponomedianus*, *Yangaspis jinningensis*, *Kunmingolepis lucaowanensis*, *Quasipetalichthys haikouensis* (Fig. 5D), *Guangxipetalichthys tiaomajianensis*, *G. bobaiensis*, and *Eurycaraspis incilis* (Liu, 1973; Ji and Pan, 1997, 1999; Zhu, 2000).

Associated diverse invertebrates include brachiopods and bivalves. The brachiopod *Stringocephalus burtini* can be found in the lower part of the overlying strata (Qiziqiao Formation in Hunan), indicating the Tiaomajian Formation and related strata can be referred to the middle Eifelian (Table 3).

3.5.3. Shixiagou Assemblage (middle Eifelian, Localities 5 and 6)

This assemblage is represented by antiarchs, petalichthyids, and sarcopterygians from the Shixiagou Formation in the Zhongning and Zhongwei areas of Ningxia. The fishes include *Bothriolepis niushoushanensis* (Fig. 5B) and *Quasipetalichthys* cf. *Q. haikouensis* (Pan et al., 1987).

Tectonically, the Zhongning and Zhongwei areas belong to the North China Block during the Devonian. The fish-bearing stratum is characterized by fine sandstone and siltstone with plant fragments, indicating a continental sedimentary environment. We suggest this assemblage was coeval with the Tiaomajian Assemblage of South China, based on shared taxa such as *Quasipetalichthys* and *Bothriolepis*.

3.5.4. Qujing Assemblage (late Eifelian, Localities 16, 17 and 22)

This assemblage is known from the lower part of the Qujing Formation in Zhaotong and Qujing, and the middle part of the Haikou Formation in Wuding. In Wuding, antiarchs and sarcopterygians are diverse and abundant, represented by *Xichonolepis qujingensis* (Fig. 5A), *Dianolepis liui*, and *Thursius wudingensis* (Zhang, 1965; P'an and Wang, 1978; Fan, 1992; Ritchie et al., 1992). The sarcopterygian *Dongshanodus qujingensis* and antiarch *Microbrachius sinensis* come from the lower part of the Qujing Formation in Qujing (Zhu, 2000). Rich fish remains are known from Zhaotong, and include the lungfish *Sinodipterus beibei* (Qiao and Zhu, 2009), onychodonts, tetrapodomorphs, and placoderms (Zhu and Zhao, 2005). The fish-bearing horizon is muddy limestone, about 90 meters below the *Stringocephalus* bed. Associated invertebrates include the tentaculite *Nowakia otomeri* and the ostracode *Rishona* sp. (Liao et al., 1979). The assemblage, therefore, represents late Eifelian fishes living in a shallow sea.

3.5.5. Bluff Head Assemblage (?late Eifelian, Locality 70)

This assemblage in the New Territories of Hong Kong is represented by placoderms and microvertebrate remains (Wang and Li, 1997). The placoderm fragments are suggestive of bothriolepid antiarchs (Li, 1991). The fish-bearing Bluff Head Formation is characterized by interbedded quartzites and argillaceous siltstones. Here we provisionally place it in the late Eifelian based on the occurrence of placoderms.

3.5.6. Dangduo Assemblage (early-middle Eifelian, Localities 8 and 9)

This assemblage in Zoige (Sichuan) and Tewo (Gansu), is mainly represented by microvertebrate remains, including acanthodians: *Acanthodes* cf. *A. dublinensis*, *A. dublinensis*, cf.

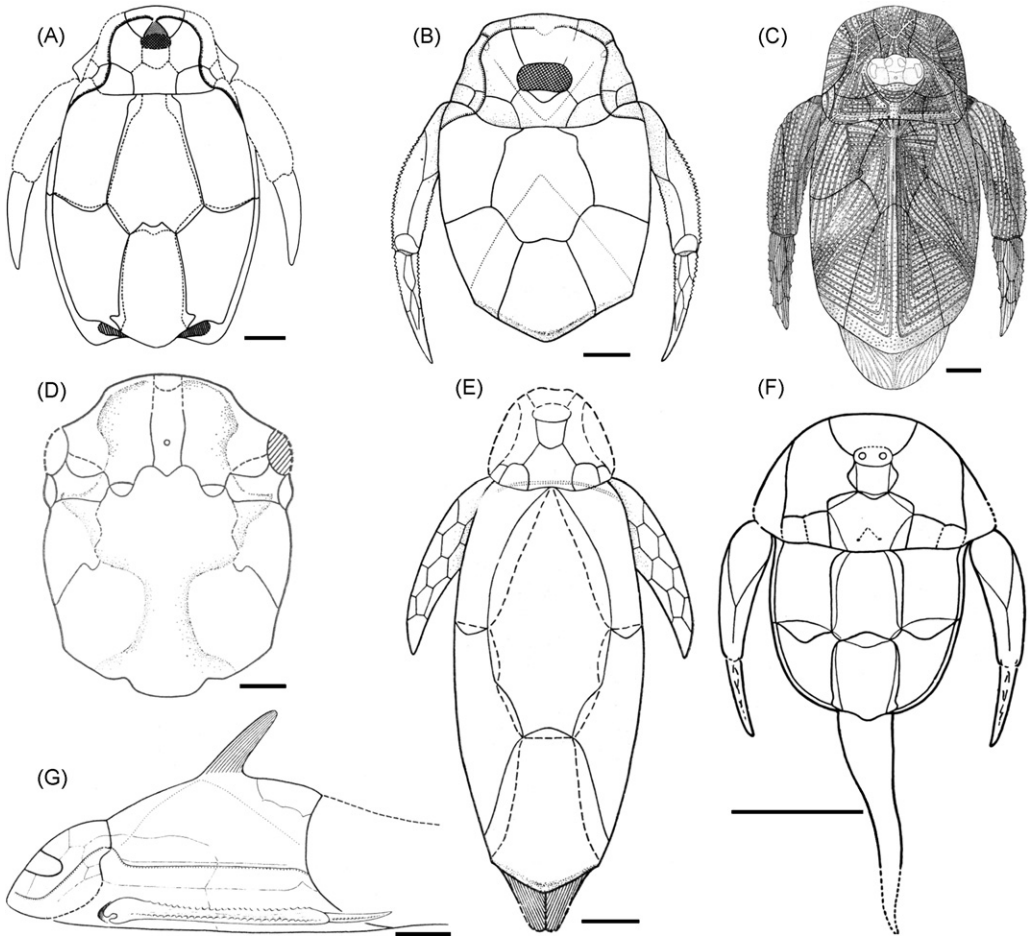

Fig. 5. Middle-Late Devonian fishes from China. (A) *Xichonolepis qujingensis* P'an et Wang (1978) (revised from Ritchie et al., 1992); (B) *Bothriolepis niushoushanensis* Pan et al. (1987); (C) *Hunanolepis tieni* Wang (1991b); (D) *Quasipetalichthys haikouensis* Liu (1973); (E) *Remigolepis zhongweiensis* Pan et al. (1987); (F) *Sinolepis macrocephala* Liu et P'an (1958); (G) *Jiangxilepis longibrachius* Zhang et Liu (1991). Scale bar = 2 cm.

Diplacanthus carinatus, cf. *Rhadinacanthus balticus*, *Cheiracanthoides* cf. *C. comptus*, *Dangdoouichthys liui*, and *Nostolepis* sp.; chondrichthyians: *Gualepis* sp., *Ohiolepis* sp.; actinopterygians: *Qinlingichthys lii*, *Q.* sp., *Ligulalepis* sp., *L.*? *sinensis*, and *Moythomasia* cf. *M. striata*; sarcopterygian: *Onychodus* sp. (Wang et al., 1998b). The correlated strata are the upper part of the Dangduo Formation and the lower part of the Lure Formation (limestone intercalated with shale). The fishes in the Dangduo and Lure formations are respectively associated with conodonts *Eognathodus bipennatus montensis* (mainly in the *P. costatus costatus* conodont zone) and *Icriodus regularicrescens* (mainly in the *T. k. kockelianus* conodont zone of Europe; XIGMR and NIGPAS, 1987). This early-middle Eifelian assemblage represents a shallow sea environment.

3.5.7. Xiawuna Assemblage (middle Givetian, locality 8)

This assemblage in West Qinling is mainly represented by microvertebrate remains from the middle part of the Xiawuna Formation, Tewo, Gansu, including the acanthodian *Acanthodes* sp., chondrichthyan *Ohiolepis* and an indeterminate actinopterygian (Zhu et al., 2000). The fish-bearing stratum is provisionally placed in the mid-Givetian by XIGMR and NIGPAS (1987) based on the occurrence of the conodont *Icriodus arkonensis*. The fishes of the assemblage lived in the shallow sea-gulf depositional environment.

3.5.8. Yidade Assemblage (late Givetian, Locality 19)

This assemblage is distributed in the Huaning area of Yunnan. The fishes from the Yidade Formation (marl intercalated with shale) are referred to the Arthrodira, including *Panxiosteus oculus*, *Huaningichthys omalodes*, *Eastmanosteus yunnanensis*, and *Clarkeosteus yidadeinsis* (Zhu et al., 2000). Associated invertebrates, such as *Stringocephalus obesus* var. *grandis* and *Grypohyllum tenue*, together with the plant *Pseudosporochus* (Liao et al., 1978), are typical of the late Givetian of western Europe. This shelf assemblage is referred to the late Givetian.

3.5.9. Jinbaoshi Assemblage (late Givetian, Localities 10, 11 and 12)

This assemblage is distributed in the Longmenshan area of Sichuan. The microvertebrate remains include the acanthodian *Acanthodes* cf. *A. dublinensis* and the sarcopterygian *Onychodus* sp. (Burrow et al., 2000). The fossil-bearing strata are the upper part of the Jinbaoshi Formation and the lower Guanwushan Formation (limestone). The bed yielding the arthrodire *Kiangyousteus yohii* (Liu, 1955) is located in the uppermost part of the

Stringocephalus burtini zone. Associated invertebrates include brachiopods, corals, and conodonts (Hou et al., 1988). The depositional environment was a shallow sea.

3.6. Zhongning Fauna

This fauna is characterized by the radiation of placoderms (mainly antiarchs) and osteichthyans, and the occurrence of early tetrapods. The following nine assemblages are recognized.

3.6.1. Shetianqiao Assemblage (Frasnian, Localities 60 and 65)

This assemblage is represented by the lungfish *Chirodipterus liangchengi* and chondrichthyans *Phoebodus* aff. *fastigatus* and *Ph. bifurcates* (Wang and Turner, 1995; Zhu et al., 2000). The fish-bearing strata are the upper part of the Shetianqiao Formation in the Guiyang area of Hunan, and the upper part of the Gubi Formation (Hengxian area) and the lower part of the Rongxian Formation (Xiangzhou area) in Guangxi, dominated by carbonate rocks. Associated brachiopods, corals, and conodonts indicate a shallow-water shelf to marginal platform environment. Based on the conodonts *Polygnathus asymmetricus* and *Palmatolepis linguiformis* respectively from the lower and upper parts of Gubi Formation (Hou et al., 2000), the assemblage is referred to the Frasnian.

3.6.2. Huangjiadeng Assemblage (Frasnian, Locality 32)

The only fish from this assemblage is the placoderm *Changyanophyton hupeiense* from the Huangjiadeng Formation in Changyang, Hubei (Zhu et al., 2000). The Huangjiadeng Formation is characterized by quartzitic sandstone and siltstone. Associated plants include *Leptophloeum rhombicum* and *Cyclostigma kiltorkense* (Cai and Li, 1982; Li, 2000), which are typical elements in the lower Upper Devonian of Europe, Australia and the Upper Reach of the Yangtze River. Thus the assemblage can be assigned to the Frasnian and represents a nearshore environment.

3.6.3. Tuqiaozi Assemblage (Frasnian, Localities 10, 11 and 12)

This assemblage is represented by microvertebrate remains from the Tuqiaozi Formation in the Longmenshan area, Sichuan. Fishes include acanthodians (*Acanthodes* cf. *A. dublinensis*) and some placoderms (Burrow et al., 2000), most of which have not been studied in detail. The fish-bearing beds of the Tuqiaozi Formation are carbonate rocks yielding abundant invertebrates, such as brachiopods (*Leiorhynchus* sp., *Striatopugnax triplicata*, *Gypidula beichuanensis*), corals, ostracods, and conodonts (*Polygnathus asymmetricus asymmetricus* and *P. alatus*) (Hou et al., 1988), indicating a shallow-water shelf facies of Frasnian age (Hou et al., 2000).

3.6.4. Niushoushan Assemblage (late Frasnian–Famennian, Localities 5 and 6)

This assemblage is represented mainly by galeaspids and antiarchs from the Dadaigou and Zhongning formations in the Niushoushan area of the Zhongning-Zhongwei Basin of Ningxia. The galeaspids include many indeterminate specimens from the lower part of the Zhongning Formation (Pan et al., 1987; Jia et al., 2010). The other early vertebrates are abundant, in particular the antiarchs including *Remigolepis major*, *R. microcephala*, *R. xiangshanensis*, *R. xixiaensis*, *R. zhongningensis*, *R. zhongweiensis* (Fig. 5E), *R.* sp., *Sinolepis szei*, and *Ningxialepis spinosa* (Pan et al., 1987; Jia et al., 2010). Tetrapods are represented by *Sinostega pani* (Zhu et al., 2002).

The Dadaigou and Zhongning formations represent a shallow lacustrine facies of the Late Devonian. The fish-bearing beds are characterized by purplish red siltstone intercalated with fine-grained feldspathic quartzose sandstone, and marl. Abundant plant remains, such as *Leptophloeum rhombicum* and *Sublepidodendron mirabile*, also occur (Pan et al., 1987), indicating that the upper part of vertebrate-bearing strata can be correlated with the Famennian Leigutai Member of the Wutong Formation in the South China Block (Table 3). The Dadaigou Formation and the lower part of the Zhongning Formation are probably Frasnian deposits (Jia et al., 2010).

3.6.5. Sanmentan Assemblage (Famennian, Localities 50, 51 and 52)

This assemblage is distributed in the Yudu, Chongyi and Quannan areas of Jiangxi, and the Liling and Liuyang areas of Hunan. It is characterized by antiarchs *Jiangxilepis longibrachius* (Fig. 5G; Zhang and Liu, 1991), *Remigolepis* sp. (Pan et al., 1999) and *Bothriolepis* sp. (undescribed), and the arthrodire *Gannanichthys chongyiensis* Wang et Wang (2000). The fossil-bearing strata are the Sanmentan Formation (sandstone, fine sandstone and siltstone) and the Xikuangshan Formation (shale intercalated with marl). Associated brachiopods including *Yunnanella hunanensis*, *Y.* cf. *Y. synplicata*, *Y.* cf. *Y. supersynplicata*, *Cyrtospirifer* cf. *C. sinensis*, *Productella* cf. *P. linglingensis*, and *Atrypa* sp., belong to the *Yunnanella–Yunnanellina* assemblage of the Famennian (BGMRJP, 1997).

3.6.6. Leigutai Assemblage (Famennian, Locality 44)

This assemblage is distributed in the Nanjing area of Jiangsu and the Shimen area of Hunan. It includes antiarchs *Sinolepis macrocephala* (Fig. 5F), *S. wutungensis* and *Jiangxilepis sinensis*, the arthrodire *Phymosteus liui*, and some sarcopterygian fragments (Liu and P'an, 1958; Ritchie et al., 1992; Zhu et al., 2000; Wang and Zhu, 2004). The fossil-bearing strata are the Leigutai Member of the Wutong Formation and the Xiejingsi Formation (sandstone, shale intercalated with limestone). Associated brachiopods and plants (Yang and Mu, 1953; Li, 2000) indicate a Famennian age.

3.6.7. Doushishan Assemblage (Famennian, Localities 8 and 9)

This assemblage in Zoige (Sichuan) and Tewo (Gansu) consists of shark and acanthodian microvertebrate remains. The acanthodians are *Acanthodes* sp. and *Acanthodes* cf. *A. dublinensis*, and the sharks are *Ctenacanthus* sp., *Phoebodus* sp. and *Gansuichthys acerrus* (Zhu et al., 2000). The fossil-bearing strata are the upper part of the Chakuohe Formation and the lower part of the Doushishan Formation (limestone intercalated

with shale). Brachiopods in the upper part of the Chakuohe Formation are dominated by *Cyrtospirifer*, associated with conodonts *Palmatolepis klapperi*, *P. glabra prima* and *P. poolei* (XIGMR and NIGPAS, 1987). In the lower part of the Doushishan Formation, the brachiopod fauna can be subdivided into two assemblages: *Yunnanella–Yunnanellina* assemblage and *Tenticospirifer hsikuangshanensis–Cyrtospirifer* cf. *pamiricus* assemblage, and conodonts are represented by the flourish of *Polygnathus perplexus*, *Apatognathus cuspidata*, and *Polygnathus semicostatus* (XIGMR and NIGPAS, 1987). All are common elements in the Famennian, indicating that the fish assemblage represents a Famennian shallow-shelf sea facies.

3.6.8. Daihua Assemblage (Famennian, Localities 26 and 54)

This assemblage, distributed in Changshun (Guizhou) and Lechang (Guangdong), is represented by microvertebrate remains, including sarcopterygian *Onychodus*, acanthodian cf. *A. guizhouensis*, chondrichthyians *Phoebodus* aff. *Ph. fastigatus*, *Ph.* sp., *Ph. australiensis*, *Ph.* cf. *Ph. australiensis*, *Ph.* cf. *Ph. limpidus*, *Protacrodus* cf. *P. dechodus*, *P.* sp., *Petalodus*? *daihuaensis*, cf. *Dittodus grabaui*, *Diplodus* cf. *D. priscus*, *D.* sp., *Ctenacanthus* sp., *Conchodontus ziegleri*, *C.* sp., *Stethacanthus* sp., *Symmorium* sp. and *Harpagodens ferox*; and some placoderm and actinopterygian scales (Wang and Turner, 1985, 1995).

The fish-bearing strata are the Daihua and Changlai formations (marl, shale, and limestone). Associated brachiopods (e.g., *Cyrtospirifer* sp.), corals (*Truncicarinulum* sp. and *Temnophyllum* sp.) and conodonts (*Polygnathus communis*, *Icriodus raymondi* and *Drepanodus circularis*) suggest a Famennian age (Zhao et al., 1988). The environment is interpreted as an open-shelf platform facies.

3.6.9. Bachu Assemblage (Famennian, Localities 3 and 4)

This assemblage in the Caohu and Shache areas of Xinjiang is represented by placoderms. A bothriolepid antiarch from the lower part of the Bachu Formation was described, and an arthrodire specimen from the Qizilafu Formation in the Shache area is under study (Wang et al., 1997). Associated brachiopods (*Cyrtospirifer* and *Ptychomaletoechia*), spores (*Retispora lepidophyta*, *Retusotriletes asthenolabratus*, and *Apiculiretusispora rarissima*) and plants (*Leptophloeum rhombicum*, *Sublepidodendron mirabile*, *Platyphyllum* sp., and *Archaeocalamites*? sp.) suggest a Famennian age (Chen, 1995; Liao et al., 2001). The environment is interpreted as a nearshore facies.

4. Biogeography of early vertebrates in China

The early vertebrates of China exhibit a high endemism, which documents the biogeographical connections among the South China, North China, and Tarim blocks in the middle Paleozoic (Liu, 1991; Pan et al., 1996; Zhao, 2005), and provides important evidence for global reconstructions (Halstead et al., 1979; Young, 1981, 1993, 2003; Pan and Dineley, 1988; Zhu and Zhao, 2006).

Based on the restricted distribution of galeaspids, Halstead et al. (1979) believed that South China was part of an isolated faunal province in which agnathans experienced an independent radiation from the rest of the world during the Early Devonian. Young (1981, 1993) later named this province as the 'galeaspid-yunnanolepid province', one of five distinct vertebrate faunal provinces in the Early Devonian. With the findings of galeaspids from North China and Tarim, and the sinacanths from Tarim, Liu (1991), Pan et al. (1996), and Zhao (2005) proposed that the Tarim, North China, and South China blocks formed a biogeographic province during the mid-Paleozoic, the Chinese province or the Pan-Cathaysian galeaspid province. Recent study confirms that the three main Chinese paleo-blocks (South China, North China, and Tarim blocks) comprised one highly endemic vertebrate faunal province. Janvier (1996) suggested the unique Chinese vertebrate fauna could be attributed to the isolation of the Chinese blocks from all other continents in the middle Paleozoic, with the high endemism interpreted as the effect of a closed sea (perhaps a closed depositional basin with special environmental conditions). Young and Janvier (1999) proposed isolation by wide marine barriers out in the 'paleo-Pacific' ocean (Pan Thalassia) to explain the high endemism in the middle Paleozoic.

Endemic taxa mainly include the galeaspid agnathans, at least three groups of placoderms (yunnanolepidoid and sinolepid antiarchs, and quasipetalichthyid petalichthyids), and some basal sarcopterygians. Appearance of some cosmopolitan taxa suggests later faunal exchange with the neighbouring vertebrate provinces, such as the East Gondwana wuttagoonaspid–phyllolepid province (Young, 1981, 1993). Connections between China and East Gondwana and between China and Kazakhstan can be determined by the evidence of some endemic and cosmopolitan vertebrate taxa.

The early vertebrates from China are characterized by their distinctive anatomical features, their diversity, and their relatively early appearance in the stratigraphic record (Pan and Dineley, 1988), suggesting that the Chinese blocks could be the place of origin of some major early vertebrate groups. (1) Abundant endemic galeaspids have been collected from the South China, North China, and Tarim blocks since 1960s. They first appeared in the Silurian (Llandovery), flourished in the Early Devonian, and survived until the Late Devonian. Hence, the Chinese blocks are probably the place of origin and diversification of galeaspids. (2) Placoderms are the dominant vertebrate group in the mid-Paleozoic, in China represented by antiarchs, petalichthyids and arthrodires. The yunnanolepidoid *Shimenolepis* from the Telychian of northwest Hunan (Wang, 1991a) is the oldest record of antiarchs so far, and the South China Block may be the place of origin of antiarchs (Pan and Dineley, 1988; Wang, 1993). Petalichthyid and arthrodire groups have a similar evolutionary pattern. Zhu and Wang (1996a) studied the Macropetalichthyidae from China, and first proposed that Petalichthyida originated in South China. Recently, Dupret (2008) described a wuttagoonaspid arthrodire, *Yiminaspis shenme* (Fig. 4H), from the Pragian Posongchong Formation in Zhaotong, Yunnan. *Yiminaspis* was regarded as a very basal member of Wuttagoonaspididae, the most basal

Arthodira (Dupret, 2008). The Wuttagoonaspididae previously were only found from the late Pragian-Eifelian of Australia (Young, 2005a,b; Dupret, 2008). The discovery of *Yiminaspis* in the Early Pragian of China suggests a Chinese origin of the Arthodira. (3) Recent fossil discoveries of stem sarcopterygians in the Silurian and Devonian of China renewed the interest in the origin of sarcopterygians and osteichthyans. The earlier occurrence of some most basal sarcopterygians in China, including *Psarolepis*, *Achoania*, *Meemania* (Fig. 4F), and *Guiyu* (Zhu et al., 1999, 2001, 2006, 2009; Zhu and Zhao, 2006), suggests a South China origin for sarcopterygians.

Although a Chinese origin for some mid-Paleozoic vertebrate groups outlines the high endemism of the Pan-Cathaysian Landmass Group, the more widespread of cosmopolitan taxa in the Pan-Cathaysian galeaspid province documents faunal exchange with neighbouring vertebrate provinces (Fig. 6A). We suggest three dispersal routes of vertebrates among the adjacent continents or blocks during the mid-Paleozoic (Fig. 6B, C).

(1) Northern Route (Fig. 6B): This route runs from the Pan-Cathaysian Landmass Group to Kazakhstan, Baltica and Laurentian or Siberia blocks, similar to the 'stepping stone' migration route proposed by Li et al. (1993).

Up to now, the mid-Paleozoic fishes documented from the Kazakhstan Block have been limited to the Devonian, including some Givetian-Famennian genera such as the widespread *Bothriolepis* and the endemic antiarchs *Turanolepis*, *Tenizolepis*, and *Stegolepis* (Malinovskaya, 1973, 1989; Blieck and Janvier, 1993). The latter two are possibly related to taxa in South China and Ningxia (Zhang and Liu, 1991; Wang, 1991b; Jia et al., 2010). *Tenizolepis rara* is the only one in which the postpineal plate is developed as in *Dianolepis* from South China (Zhang and Liu, 1991). The antiarch *Hunanolepis* from South China is a possible close relative of *Stegolepis* from Kazakhstan. A close connection with Kazakhstan may have been attained in the Middle-Late Devonian.

Some early vertebrate taxa from the Baltic, Laurentian and Siberian blocks also show some affinities with fishes from the Pan-Cathaysian Landmass Group and Kazakhstan Block (e.g., the agnathan *Ilemoraspis*, and the antiarchs *Microbrachius*, *Byssacanthus*, *Bothriolepis*, *Remigolepis*, and *Taeniolepis*, phyllolepids, and quasipetalichthyids) (Denison, 1978; Young, 1981; Wang, 1993; Zhu, 2000), which suggests the 'stepping stone' migration route during the Devonian. The antiarchs *Microbrachius*, *Bothriolepis*, and *Remigolepis* are the only taxa occurring both in China and the Baltic, Laurentian, Siberian and Kazakhstan blocks.

(2) Southern Route (Fig. 6B): This route goes from the Pan-Cathaysian Landmass Group to East Gondwana including some terranes along the northern margin of the continent (e.g., IndoChina, Shan-Thai, Cimmeria), and West Gondwana containing Arabia, Armorica (now the Iberic Peninsula and France up to Normandy), Bohemia (down to the alpine area), Africa and South America blocks along the continental coast of the Gondwana Landmass Group. The relative discussion on East Gondwana will be given in the next part.

The Indochina Terrane yields some vertebrates with South China affinities from Late Ludlow to Emsian, including a "*Wangolepis*"-like placoderm, *Psarolepis*-like and *Guiyu*-like osteichthyans mainly from Central Vietnam (Thanh et al., 1996, 1997; Janvier and Thanh, 1998; Wang et al., 2010). The similar placoderms and osteichthyans imply that the vertebrates from Indochina Terrane belong to the Xiaoxiang fauna, strongly supporting a close connection between the Indochina Terrane and South China Block as early as the Ludlow in the Silurian.

Vertebrate remains from the Shan-Thai Terrane include the acanthodian *Nostolepis* and thelodont scales from the Early Devonian of Thailand reported by Blieck and Goujet (1978) and Blieck et al. (1984), a Devonian fauna including turiniid scales (e.g., *Turinia pagoda* from Shidian of western Yunnan) and a macropetalichthyid bone from West Yunnan (Wang et al., 2010), and a Late Devonian chondrichthyan microfauna (late Famennian) from nearby Mae Sam Lap on the Burmese border (Long, 1990). A contemporaneous record of *Turinia* cf. *T. pagoda* from South Australia suggests a close relationship between the Shan-Thai Terrane and East Gondwana (Wang et al., 2010). Ginter (1990) examined one tooth from northern Thailand interpreted as a partial tooth of *Phoebodus* cf. *P. gothicus*, which has since been found in China (Wang and Turner, 1985; Wang and Dong, 1989). The turiniid scales from the Shan-Thai Terrane also occurred in the Early?–Late Devonian of Iran (Turner and Janvier, 1979). Hence, the close paleogeographical relationship among the Shan-Thai Terrane, South China Block, and Cimmeria Terrane are supported by mid-Paleozoic fossil fishes.

In addition, many findings of early vertebrate micro-remains and macro-remains in Iran, Afghanistan, Azerbaidjan, Saudi Arabia, Turkey, Bohemia, France, Spain, Portugal, Bolivia, Venezuela, Colombia, Morocco, Libya, Algeria, and South Africa, showed specific resemblances to Chinese species. This suggested a shallow marine dispersal along the northern Gondwana margin during the mid-Paleozoic (Lelièvre et al., 1993; Young, 2003; Mark-Kurik, 2004; Janvier et al., 2007; Dupret, 2008; Dupret and Zhu, 2008; Hairapetian et al., 2008; Young et al., 2010).

(3) Circum-Panthalassic Ocean Route (Fig. 6C): This route runs from the Pan-Cathaysian Landmass Group to Australia, Antarctica, South American and North American continents, and the Siberia Block. It was proposed by Zhu and Zhao (2006) to explain the distribution of early sarcopterygians. Other mid-Paleozoic fish groups also provide convincing evidence of fish dispersal around the Panthalassic Ocean.

Young (1981) first proposed the similarity of Givetian bothriolepiform antiarchs between South China and East Gondwana. Since that analysis, many discoveries of mid-Paleozoic fishes from both China and Australia were reported and further confirmed the biogeographical affinity (Young, 1993, 2003; Ritchie et al., 1992; Wang, 1993; Pan et al., 1996; Zhu and Zhao, 2006; Dupret, 2008; Dupret and Zhu, 2008; Young et al., 2010). Among the major vertebrate lineages (Agnatha, Placodermi, Acanthodii, Chondrichthyes, and Osteichthyes), similar fossil fishes can be found from these two areas, such as thelodonts and galeaspids (agnathans), bothriolepids, groenlandaspids, sinolepids, buchanosteids, remigolepids, wuttagoonaspids and phyllolepids (placoderms), and dipnoans,

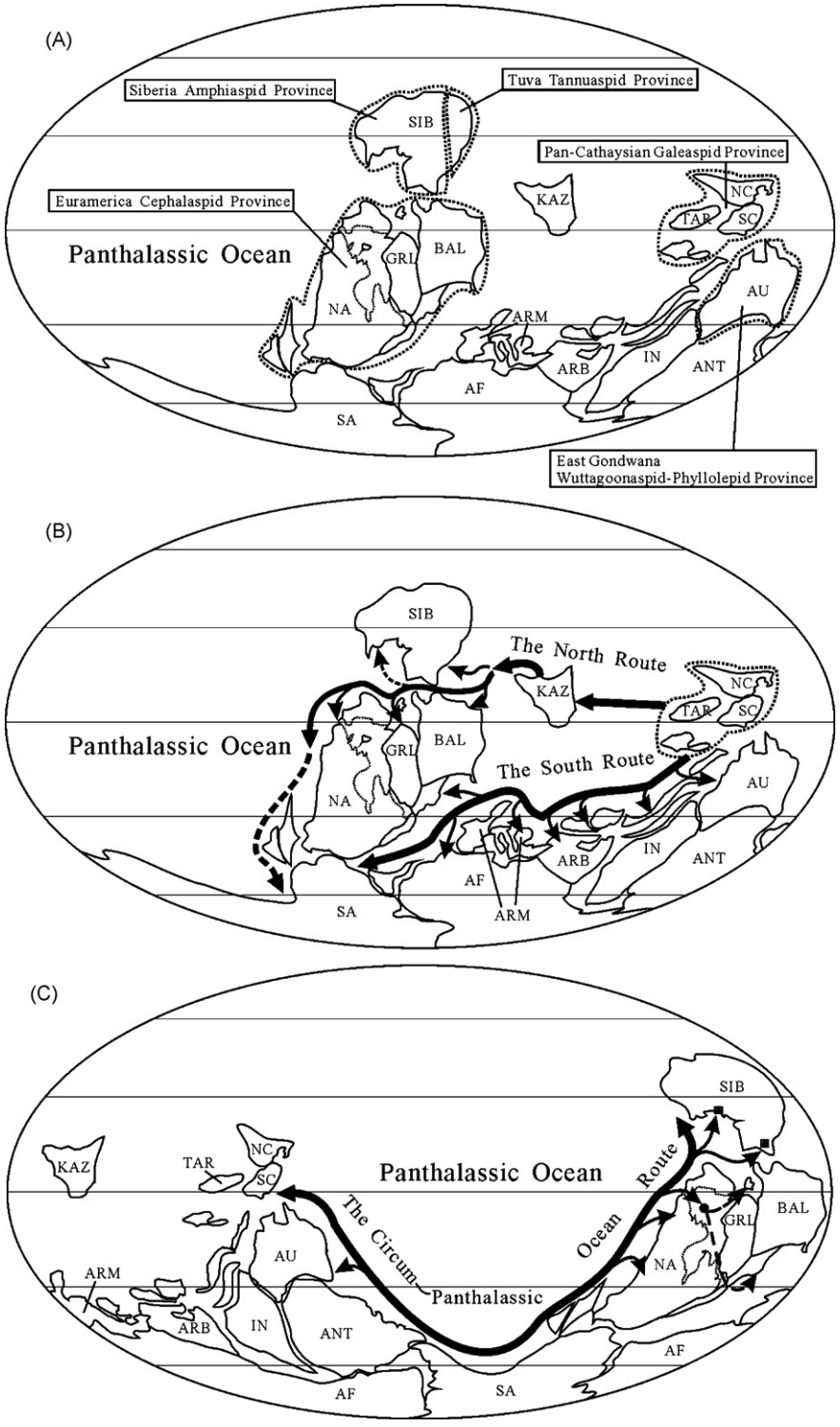

Fig. 6. (A) Five major vertebrate faunal provinces for the Early Devonian; (B) The two dispersal routes (Northern Route and Southern Route). Paleogeographic reconstruction for A–B revised from Scotese (1997); (C) The circum-Panthalassic Ocean Route on the Early Devonian paleogeographic reconstruction revised from Zhu and Zhao (2006). AF-Africa; ANT-Antarctica; ARB-Arabia; ARM-Armorica; AU-Australia; BAL-Baltica; GRL-Greeland; IN-India; KAZ-Kazakhstan; NA-North America; NC-North China; SA-South America; SC-South China; SIB-Siberia; TAR-Tarim.

coelacanths, tetrapodomorphs (osteichthyans). It is noteworthy that the study of the vertebrate faunas from two areas indicates the faunal exchange between China and Australia first occurred at the Pragian-Emsian boundary, during the E'Em bioevent (Zhu, 2000).

It is generally acknowledged that Australia and East Antarctica were united during the mid-Paleozoic as part of Gondwana, and the strong similarities in the key taxa of antiarchs, phyllolepids, acanthodians, sharks, dipnoans, and actinopterygians have already been well documented (Young, 1982, 1989, 2007;

Long, 1983; Long and Young, 1995; Young and Long, 2005; Long et al., 2008). This supports the concept of an endemic fish faunal province of East Gondwana (*Wuttagoonaspis* Province), and reinforces the strong biogeographical connections between Australia and Antarctica.

New findings of early vertebrates from Bolivia, Brazil, Venezuela, and Colombia (Goujet et al., 1984, 1985; Gagnier et al., 1989; Janvier and Villarroel, 2000; Young et al., 2000; Young and Moody, 2002) shed light on the possible 'eastward' dispersal routes–from the Pan-Cathaysian Landmass Group to Australia, Antarctica, South American and North American continents, and the Siberia Block. Increasing faunal affinity between South America and East Gondwana/Asia during the mid-Paleozoic has been discussed by Young (1993), Young et al. (2000), and Dupret and Zhu (2008), and some exchanges with East Gondwanan fish faunas are evidenced by studies of both microvertebrates (e.g., the scales of turiniid thelodonts, the acanthodian spines and the dipnoan scales) and macrovertebrates (e.g., the shark *Antarctilamna*, phyllolepid, bothriolepid, and asterolepid placoderms, and the *Koharalepis*-like osteolepiform sarcopterygians). The eastward invasion of mid-Paleozoic fish faunas (to South America) mainly occurred during the Late Devonian.

Many findings of early vertebrates from westernmost North America showed affinities with Gondwana, South America, and possibly South China. Among the placoderms, phyllolepids were also found from the Famennian of Euramerica (North America, Greenland, West Europe, and Russia) (Denison, 1978; Dupret and Zhu, 2008), indicating the Late Devonian exchange of the group. Some placoderm forms from Colombia in South America resemble those from Euramerica (e.g., *Asterolepis* and *Holoptychius*). In addition, some new arthrodire genera (e.g., *Lurapullaspis* and *Toombalepis*) erected by Young and Goujet (2003) from western New South Wales (Australia) have similar taxa in the Early Devonian of western USA, Spitsbergen and Severnaya Zemlya (Young et al., 2010). The sarcopterygian *Powichthys* from Arctic Canada has close affinities to *Youngolepis* from South China (Chang and Yu, 1981; Zhu and Zhao, 2006), suggesting an earlier dispersal of the group between the two areas.

Although some other dispersal routes for early vertebrates (e.g., the possible route along the north margin of Gondwana, into South Europe and then to North Europe or the Baltic block) are likely, the above-mentioned three dispersal routes are considered to have played key roles in the dispersion and radiation of Siluro-Devonian vertebrates.

5. Conclusions

Based on the above analysis and discussions, the following conclusions related to Siluro-Devonian vertebrates in China can be reached:

(1) The three East Asian blocks (South China, North China, and Tarim blocks) yielding abundant early vertebrates belong to neither the Laurasia Landmass Group nor the Gondwana Landmass Group, and constitute a distinct independent geological region termed the Pan-Cathaysian Landmass Group during the mid-Paleozoic. This is characterized by a highly endemic vertebrate faunal province, namely "the Pan-Cathaysian galeaspid province".

(2) Six Siluro-Devonian vertebrate faunas can be recognized based on the revised database for early vertebrates in China. Detailed analysis of these faunas has shed new light on some problems concerning the Siluro-Devonian stratigraphic correlation in China, specifically the ages of some non-marine beds, and the correlations between non-marine and marine deposits.

(3) Some major vertebrate groups such as galeaspids, placoderms, and sarcopterygians occur earlier in the Chinese blocks than in the rest of the world. They might have originated and diversified in the mid-Paleozoic of China and Vietnam, and then invaded other areas. Three dispersal routes for early vertebrates (Northern Route, Southern Route, and Circum-Panthalassic Ocean Route) probably bridged the Chinese blocks with the adjacent continents during the mid-Paleozoic. The close connection between the Pan-Cathaysian galeaspid province and adjacent vertebrate provinces (e.g., the wuttagoonaspid–phyllolepid province in East Gondwana) is corroborated.

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