

中国三叠纪鱼类综述¹⁾

金 帆

(中国科学院古脊椎动物与古人类研究所 北京 100044)

摘要:三叠纪鱼类在中国分布广泛。与当时“南海北陆”的古地理格局一致,淡水鱼类主要分布于北方大陆的河湖相盆地,但也见于扬子板块与北方大陆碰撞后的四川盆地;海生鱼类则主要分布于华南和喜马拉雅地区。值得注意的是,鄂尔多斯盆地已知的三叠纪鱼类中,多数为海生类型或与海生鱼类密切相关。中国的淡水三叠纪鱼群主要由原始辐鳍鱼类组成,它们与西伯利亚和中亚的鱼群最为相近,但也有与劳亚大陆其他地区及冈瓦纳大陆鱼类相似的属种。海生鱼群则以“亚全骨鱼类”为主,并包含鲱亚部的进步类群和真骨鱼类的基干类型。华南扬子区拉丁至卡尼早期的鱼群远较早三叠世的鱼群丰富,且这一时期的鱼群与西特提斯同期的鱼群关系已极为密切,约有1/3的种类可归入相同的属。华南中下扬子区很可能是部分后来繁盛于特提斯区的三叠纪鱼类的发源地,如龙鱼类。中国的三叠纪鱼类虽然十分丰富,但大多已知鱼类仅限于零星发现和初步报道,因而仍有待全面深入的调查研究。

关键词:中国,三叠纪,鱼类

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AN OVERVIEW OF TRIASSIC FISHES FROM CHINA

JIN Fan

(*Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences Beijing 100044*)

Abstract The Triassic fishes are widely distributed in China. The freshwater ichthyofaunas mainly from northern China are characterized by primitive actinopterygians, and they are closest to those from Siberia and Middle Asia, and also contain some forms similar to the fishes from other regions of Laurasia and the Gondwanan continents. Most of the known fishes from the Ordos Basin are possibly of marine. The marine ichthyofaunas from southern China are characterized by “subholosteans”, and include the modern groups of halecomorphs and the basal forms of teleosts. The Middle-Late Triassic marine fish fauna is much more diversified than the Early Triassic one, and is closely related with the ichthyofaunas in western Tethys. The Lower Yangtze region of South China is probably the cradle of some Triassic fish groups, e. g. Saurichthyidae. The Triassic fishes in China still await comprehensive investigations.

Key words China, Triassic, fishes

1 Introduction

The Triassic is a crucial period in the fish evolving history. This period is usually known as the age of “subholosteans”, for it was during this time that there flourished the varied groups

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phylogenetically intermediate between primitive actinopterygians and neopterygians. Further, there developed the modern groups of halecomorphs and the basal forms of teleosts, as well as a few sarcopterygians and chondrichthyans.

In China, Triassic fishes were widely spread over the territory. In consistent with the tectonic and palaeogeographic outline, “sea in the south and land in the north” (Fig. 1), the fishes from the landmasses of northern China are mainly of freshwater, and those from southern China are mostly marine fishes. Up to now, quite a lot Triassic fishes have been discovered from both the fluviolacustrine basins and the marine regions. The known fishes from China, in addition to those not yet formally described, include the representatives of almost all the major Triassic fish groups (see the Appendix). They are of great importance to understand the transition of primitive actinopterygians to neopterygians, and the early evolving history of halecomorphs

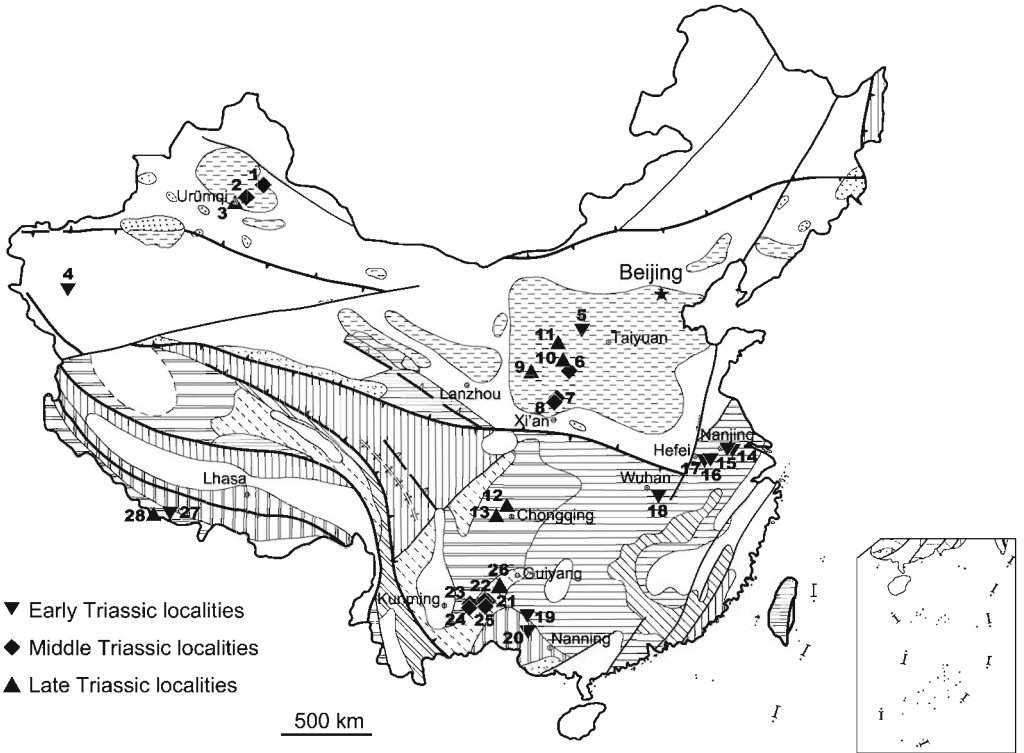


Fig. 1 Triassic fish localities in China, the base paleotectonic map in the Indosinian stage is simplified from Liu (2002)

1. Zhangpenggou, Qitai, Xinjiang; 2. Quanshuigou, Fukang, Xinjiang; 3. Urümqi, Xinjiang; 4. Duwa, Pishan, Xinjiang; 5. Watang, Xingxian, Shanxi; 6. Zhangjiatan, Yanchang, Shaanxi; 7. Jinsuoguan, Tongchuan, Shaanxi; 8. Zoumawan, Yaoxian, Shaanxi; 9. Oil well Hua-184, Huachi, Gansu; 10. Tuorxiang, Zichang, Shaanxi; 11. Qilingou, Hengshan, Shaanxi; 12. Dongchuan Coalfield, Hechuan, Chongqing; 13. Xinxing Coalfield, Yongchuan and Rongchang area, Chongqing; 14. Dongchang, Jurong, Jiangsu; 15. Longtan, Nanjing, Jiangsu; 16. Simashan, Hexian, Anhui; 17. Majiashan and Pingdingshan, Chaohu, Anhui; 18. Tieshan, Huangshi, Hubei; 19. Kangdong, Fengshan, Guangxi; 20. Zuodeng, Tiandong, Guangxi; 21. Qingshan, Pu'an, Guizhou; 22. Xinmin, Panxian, Guizhou; 23. Yuwang, Fuyuan, Yunnan; 24. Changdi, Luoping, Yunnan; 25. Dingxiao and Wusha, Xingyi, Guizhou; 26. Xinpu and Gangwu, Guanling, Guizhou; 27. Qubu, Tingri, Xizang; 28. Tulong, Nyalam, Xizang

For legends of the paleotectonic map, refer to Liu (2002: p. 55)

and teleosts, and at the same time, they also play a unique role in paleogeography and historical biogeography.

This overview of the Triassic fishes from China intends to provide an introduction to all known fishes according to the present data, including the information of their localities, horizons and possible relationships. The fishes are presented after their stratigraphic provinces in the Triassic, which result from the integration of tectonic and paleogeographic outline, depositional models and complexes, bioprovinces and biofacies (Yang et al., 2000), and could be as a framework to enclose the fishes. Moreover, the present work also deals with the fish faunas and their implications in paleogeography and historical biogeography. At the end of this paper, there adds a systematic list of all known Triassic fishes in China, including those not yet reported.

In order to alleviate confusion, the names of localities and stratigraphic units in this paper are spelt in the Pinyin romanization system, and followed by names in the Wade-Giles romanization system in brackets if they were thus spelt in the original papers. For the Xinjiang and Xizang Autonomous Regions, place names are derived from "Atlas of the People's Republic of China" (1989), China Cartographic Publishing House.

2 Freshwater fishes

2.1 Middle and Late Triassic fishes from Junggar Basin

The Junggar Basin was the largest one of a series of intermontane grabens and fluvio-lacustrine basins in the Northern Xinjiang-Beishan stratigraphic province during the Triassic. In this basin, Triassic fishes were first discovered as early as in 1931, but only three monotypic forms, viz. *Sinosemionotus urumchii* Yuan et Koh, 1936, *Sinkiangichthys longipectoralis* Liu, 1958, and *Fukangichthys longidorsalis* Su, 1978, have been described since then (Table 1). *Sinosemionotus*, a semionotid fish in general close to *Semionotus*, was found in the south of Ürümqi (Urumchi) by the southern margin of the basin. Its horizon was initially considered to be the Middle Triassic (Yuan and Koh, 1936), later was verified in the field to be the lowest part of the Huangshanjie Formation (Cheng, 1986). *Sinkiangichthys*, a redfieldiid fish similar

Table 1 Triassic fishes from Junggar and Ordos Basins

Series	Stage	CCTS*	Junggar Basin		Ordos Basin	
			Formation	Fish	Formation	Fish
Upper	Rhaetian	Wayaopuan	Haojiagou		Wayaopu	<i>Saurichthys huanshenensis</i> <i>Perleidus</i> cf. <i>P. woodwardi</i> <i>Palaeoniscus</i> sp. <i>Cyrolepis</i> sp. <i>Boreosomus</i> sp. <i>Wayaobulepis zichangensis</i>
	Norian	Yongpingian	Huangshanjie	<i>Sinosemionotus urumchii</i>	Yongping	
	Carnian	Hujiacunan			Hujiacun	Laugiidae indet.
Middle	Ladinian	Tongchuanian	Kelayayi	<i>Sinkiangichthys longipectoralis</i> <i>Fukangichthys longidorsalis</i>	Tongchuan	<i>Hybodus youngi</i> Coelacanthidae indet. <i>Triassodus yanchangensis</i>
	Anisian	Ermayingian			Ermaying	
Lower	Olenekian	Heshanggouan	Shaofanggou		Heshanggou	<i>Ceratodus heshanggouensis</i>
	Induan	Dalongkouan	Jiuciyuan		Liujagou	

* Chinese continental Triassic stage.

to *Helichthys* and *Ischnolepis* from southern Africa, was discovered from the Zhangpenggou (Chang-p'eng-kou) anticline in Qitai (Chitai) near the eastern margin of the Junggar Basin (Liu, 1958), and its horizon was recognized to be the upper part of the Kelamayi Formation or the lower part of the Huangshanjie Formation (Zhao, 1980, pers. comm.). *Fukangichthys*, a palaeoniscoid fish discovered from the upper part of the Kelamayi Formation (Cheng, 1986) at Quanshuigou of Fukang, was compared with *Tanaocrossus* from North America, *Evenkia* from Siberia, and *Scanilepis* from South Sweden, and provisionally assigned to the family Scanilepidae by Su (1978).

2.2 Early Triassic fishes from Tarim Basin

The Tarim Basin was the principal body of the Tarim stratigraphic province. In this region, the only possible Triassic fish record is *Duwaichthys mirabilis* Liu et al., 1990, which was discovered from Duwa, Pishan near the southwestern margin of the basin. The fish-bearing strata were previously assigned to the Jurassic, and subsequently considered to be probably corresponding with the upper part of the Guodikeng Formation (earliest Triassic in age) in northern Xinjiang after their conchostracan assemblage. *Duwaichthys* is a palaeoniscoid fish, but it is rarely known for limited material, and its assignment has not been determined yet.

2.3 Early to Late Triassic fishes from Ordos Basin

The Ordos Basin was a vast and extensively investigated basin in the North China stratigraphic province. Except for the lowest Dalongkouan Stage, all other Chinese continental standard sections of the Triassic stages are located in this basin (NCS, 2002). According to the investigations of local geologists from Shaanxi, Gansu and Ningxia (SRSTCG, 1983; GRSTCG, 1980; NRSTCG, 1980), Triassic fishes are widely distributed in quite a few horizons of the basin. However, only a few fishes have been identified and reported since 1957 (Table 1), and most fossils remain to be studied.

The lungfish, *Ceratodus heshanggouensis* Cheng, 1980, was discovered from the upper part of the Heshanggou Formation at Watang, Xingxian, Shanxi Province. In China, *C. heshanggouensis* is the earliest fossil record of ceratodontids, and *Ceratodus* are usually found from the Jurassic continental deposits in large-scale basins such as Junggar, Ordos, Sichuan. The two other sarcopterygians known from the Ordos Basin are actinistians—*Coelacanthidae* gen. et sp. indet. and *Laugiidae* gen. et sp. indet., which were discovered respectively from the upper part of the Tongchuan Formation at Jinsuoguan of Tongchuan, Shaanxi Province and the Hujiacun Formation (third member of the Yanchang Group) at Oil well Hua-184, Huachi, Gansu Province (Su, 1984; Liu et al., 1999).

Of the Triassic fishes from the Ordos Basin, palaeoniscoids of the Actinopterygii are most abundant in number of taxa and individuals. Currently known forms include *Triassodus yanchangensis* Su, 1984 from the upper part of the Tongchuan Formation at Zoumawan, Yaoxian, Shaanxi Province; *Wayabulepis zichangensis* Su, 1999 from the Wayaopu Formation (fifth member of the Yanchang Group) at Tuoxiang, Zichang, Shaanxi Province; and *Palaoniscus* sp., *Gyrolepis* sp. and *Boreosomus* sp. from the uppermost member of the Wayaopu Formation at Qilingou (Chi-lin-kou), Hengshan (Huanshan), Shaanxi (Shensi) Province (Chou and Liu, 1957).

Besides those mentioned above, in Ordos Basin there are other three known fishes: *Hybodus youngi* Liu, 1962, *Saurichthys huanshenensis* Chou et Liu, 1957 and *Perleidus* cf. *P. woodwardi* Stensiö, 1921. *H. youngi* was discovered from the upper part of the Tongchuan Formation (Changchiatan black shales of the former Yenchang Formation) at Zhangjiatan (Changchiatan), Yanchang (Yenchang), Shaanxi (Shensi) Province; and *S. huanshenensis* and *P. cf. P. woodwardi* were found together with the palaeoniscoids from Qilingou, Hengshan, Shaanxi

Province. The fish-bearing strata near Qilingou were recognized to be the uppermost fifth member of the Wayaopu Formation by SRSTCG (1983), even though Chou and Liu (1957) suggested their age should be no later than Middle Triassic based on the discovered fishes. This inconsistency is quite possibly due to the limited material and misidentification of the fish remains, especially those of palaeoniscoids.

2.4 Late Triassic fishes from Sichuan Basin

The Sichuan Basin was in the Upper Yangtze region of the South China stratigraphic province during the Triassic. Along with the early Indosinian Movement (Middle Triassic) and the Ladinian marine regression, the Yangtze Block was already connected with the northern landmasses to form a united continent, and its sediments were gradually dominated by continental deposits in Late Triassic. The fishes of the Sichuan Basin were discovered from the fifth member of the Xujiahe Formation, the uppermost horizon of the Triassic and composed of fluvio-alluvial and lacustrine deposits.

The currently known fishes from this basin include *Shuniscus longianalis* Su, 1983 and *Jialingichthys serratus* Su, 1983. *Shuniscus*, a palaeoniscoid fish discovered from the Dongchuan Coalfield of Hechuan (Huchuan), was considered to be similar to *Turseodus* from North America, and also close to *Triassodus* from the Ordos Basin in North China (Su, 1983, 1984). *Jialingichthys* was found together with *Shuniscus* from the Dongchuan Coalfield of Hechuan, and also known from the Xinxing Coalfield in Yongchuan and Rongchang area. This district of the eastern Sichuan Basin was included in Sichuan Province before 1997, but now belongs to Chongqing, the fourth municipality in China. *Jialingichthys* was compared with *Hengnania* from Hunan Province, and assigned to the family Pholidophoridae by Su (1983).

3 Marine fishes

3.1 Early to Late Triassic fishes from Yangtze region

The Yangtze region, also termed as the Yangtze Block or Yangtze Platform, was included in the South China stratigraphic province during the Triassic. In this region, Triassic fishes were first discovered from Guizhou Province in 1957. Afterwards in about forty years, only a few fossils were found from Anhui, Jiangsu and Hubei Provinces. Recently, many well-preserved Triassic marine fishes have been excavated in this region. Of these newly discovered materials, a small part have been preliminary reported since 1997, but most remain to be systematically studied (Table 2). Because of the evident facies differentiation and variation in this region, the Early Triassic fishes are mostly distributed in the Middle and Lower Yangtze region to the east of Wuhan, and the Middle and Late Triassic fishes are mainly concentrated in southwestern Guizhou and eastern Yunnan of the Upper Yangtze region.

In the Middle and Lower Yangtze region, there are 5 known localities along the Yangtze River (Fig. 1). Among them, the quarries around Dongchang of Jurong in Jiangsu Province have yielded most of the Early Triassic fish fossils from this region. These fossils were first identified as two new forms—*Perleidus jiangsuensis* and *Lepidotes jurongensis* by Qian et al. (1997). Later on, Liu et al. (2002) recognized and nominated other 6 genera and 8 species: *Perleidus piveteaui*, *Perleidus* aff. *P. madagascariensis*, "*Perleidus*" *eurylepidotrichia* sp. nov., *Zhangina cylindrica* gen. et sp. nov., *Stensiönotus dongchangensis* sp. nov., *Jurongia fusiformis* gen. et sp. nov., *Qingshania cercida* gen. et sp. nov., and *Suius brevis* gen. et sp. nov. In a most recent revision of the perleidid fishes from the Lower Yangtze region by Jin et al. (2003), *Perleidus jiangsuensis*, *P. piveteaui* and *Zhangina cylindrica* were revised as *Zhangina jiangsuensis* (Qian et al., 1997); "*Perleidus*" *eurylepidotrichia* was considered as a possible synonym of *Perleidus yangtzensis* Su, 1981; and *Perleidus* aff. *P. madagascariensis* was believed not to be a perleidid.

The left nominated fishes from Dongchang of Jurong are all parasemionotids, and they are also problematic, and need to be further investigated. The fish-bearing strata of this locality are recognized to be the lower part of the Qinglong Group, and probably corresponding to the upper part of the Yinkeng Formation.

Table 2 Triassic fishes from Yangtze region

Series	Stage	CMTS*	Formation	Fish	
Upper	Rhaetian	Tulongian	Huobachong		
	Norian				
Middle	Ladinian	Yazhiliangian	Banan		
			Falang	Wayao Member	Elasmobranch ichthyoliths <i>Birgeria</i> sp. <i>Colobodus</i> sp. nov.
	Zhuganpo Member	Hybodontidae gen. et sp. indet. ; Elasmobranch ichthyoliths <i>Guizhouniscus microlepidus</i> ; Acrolepidae gen. et sp. nov. <i>Birgeria liui</i> ; <i>Saurichthys</i> sp. nov. <i>Peltopleurus orientalis</i> , <i>Peripeltopleurus</i> sp. nov. ; <i>Guizhoubranchysomus minor</i> <i>Eosemionotus</i> sp. nov. ; <i>Asialepidotus shingyiensis</i> , <i>Archaeosemionotus</i> sp. nov. <i>Xingyia gracilis</i> ; Marosemiidae gen. et sp. nov. <i>Sinoeugnathus kweichowensis</i> , <i>Guizhoueugnathus analilepida</i> , Caturidae gen. et sp. nov. <i>Guizhouamia bellula</i> ; Pholidophoridae gen. et sp. nov.			
		Yangliujing			
Lower	Anisian	Qingyanian	Guanling	Member II	<i>Saurichthys</i> sp. nov. ; Perleididae gen. et sp. nov. Eosemionotidae gen. et sp. nov. ; Semionotidae gen. et sp. nov. Parasemionotidae gen. et sp. nov.
				Member I	
Lower	Olenekian	Chaohuan	Qinglong, or Daye Group	Nanlinghu	
				Helongshan	Coelacanthidae gen. et sp. indet. <i>Saurichthys</i> sp. <i>Zhangina jiangsuensis</i> , <i>Zh. Yangtzensis</i> , <i>Plesioperleides dayeensis</i> , Perleididae gen. et sp. indet. " <i>Lepidotes</i> " <i>jurongensis</i> , Parasemionotidae gen. et sp. indet.
	Induan	Yinkengian		Yinkeng	

* Chinese marine Triassic stage.

Another important locality in the Middle and Lower Yangtze region is Chaohu, Anhui Province. The Chinese marine standard section of the Chaohuan stage and the candidate Global Standard Section and Point (GSSP) of the Induan-Olenekian boundary is situated at this locality (NCS, 2002; Tong et al., 2004). From Majiashan and Pingdingshan of Chaohu, perleidid fossils were known long ago (Su, 1981). Recently, a field group from the China University of Geosciences has found and collected lots of fish specimens, of which most are perleidids

and parasemionotids, and a few are coelacanthids etc. (Tong et al., 2004; Zhou X G, pers. comm.). The fish-bearing strata of this locality include the Helongshan and Nanlinghu Formations.

The other three localities in the Middle and Lower Yangtze region are little concerned with in recent years. The known fishes from them include *Perleidus yangtzensis* Su, 1981, *Plesioperleidus dayeensis* Su et Li, 1983 and *Saurichthys* sp., which are all represented by few specimens. *Perleidus yangtzensis* was discovered from the Qinglong Group at Simashan, Hexian, Anhui Province. Since *P. yangtzensis* is more closely related to *Zhangina jiangsuensis* than to the species of *Perleidus*, it has been reassigned to the Chinese genus *Zhangina* (Jin et al., 2003). *Plesioperleidus dayeensis*, also a perleidid fish and similar to *Zhangina yangtzensis*, was found from the fourth member of the Daye Group at Tieshan, Huangshi, Hubei Province. *Saurichthys* sp. was known from the upper part of the Qinglong Group at Longtan, Nanjing, Jiangsu Province, but it had not been formally reported (Su and Li, 1983).

In the Upper Yangtze region, Triassic marine fishes were first found from the Zhuganpo Member of the Falang Formation at Lüyin, Dingxiao, Xingyi, Guizhou Province. Recently, numerous fish fossils have been discovered from more horizons at many localities in the area of southwestern Guizhou and eastern Yunnan (Fig. 1). These fishes can be attributed to three assemblages after their horizon and composition. The first assemblage is distributed in the upper Anisian Member II of the Guanling Formation, and its known specimens have been mainly collected from Xinmin of Panxian and Qingshan of Pu'an. The second assemblage is widely distributed in the upper Ladinian Zhuganpo Member of the Falang Formation, its macrofossils are mostly discovered from Dingxiao and Wusha of Xingyi, Changdi of Luoping and Yuwang of Fuyuan; and some microfossils are also found from Xinpu of Guanling. The third assemblage is distributed in the lower Carnian Wayao Member of the Falang Formation, and its fossils are only known from Xinpu and Gangwu of Guanling at present (Li and Jin, 2003).

Of the three assemblages, little is known about the earliest one for lack of extensive investigation. The collected specimens of this assemblage include fishes of five families; Saurichthyidae, Perleididae, Eosemionotidae, Semionotidae, and Parasemionotidae. These fishes show some resemblances to the known Ladinian forms from the Upper Yangtze and western Tethyan regions, but evidently differ from them.

The second fish assemblage is comparatively well known. In addition to the first found three fishes—*Peltopleurus orientalis*, *Asialepidotus shingyiensis* and *Sinoeugnathus kueichowensis* (Su, 1959), Jin (2001) described a new birgeriid fish, *Birgeria liui*, from Changdi of Luoping; Liu et al. (2002, 2003) reported a few important new forms from Dingxiao and Wusha of Xingyi: *Guizhouniscus microlepidus*, *Guizhoubrachysomus* (preoccupied generic name, *Brachysomus*) *minor*, *Xingyia gracilis*, *Guizhoueugnathus* (preoccupied generic name, *Guizhouella*) *analilepida*, and *Guizhouamia bellula*; Chen (2002), Chen and Cuny (2003) described a possible hydodontid tooth and some elasmobranch ichthyoliths from Xinpu of Guanling (for the list, see the Appendix). Besides these nominated fishes, there remain respectable new forms to be studied in this assemblage, of which we already have materials include Acrolepidae gen. et sp. nov., *Saurichthys* sp. nov., *Peripeltopleurus* sp. nov., *Eosemionotus* sp. nov., *Archaeosemionotus* sp. nov., Marosemiidae gen. et sp. nov., Caturidae gen. et sp. nov., and Pholidophoridae gen. et sp. nov. Among the known fishes of this late Ladinian assemblage, most are closely related to the contemporaneous fishes from Monte San Giorgio of Switzerland and Lombardy of Italy in western Tethys, and some can be referred to the same genera.

The third fish assemblage from the lower Carnian, as the earliest one, currently is also little known. The only nominated fishes of this assemblage are those of elasmobranch ichthyoliths presented by Chen (2002), Chen and Cuny (2003). For the time being, we have some fragments collected from Xinpu and Gangwu of Guanling, which no doubt belong to the genera

Birgeria and *Colobodus*.

3.2 Early Triassic fishes from Youjiang region

The Youjiang region was a pull-apart chasmic trough behind the Yangtze Block in the South China stratigraphic province during the Triassic. In this region, the known Triassic fishes have been discovered from the area near the northeastern margin, and include *Sinocoelacanthus fengshanensis* Liu, 1964, *Hybodus zuodengensis* (Yang et al.), 1984, *H. yohi* (Yang et al.), 1984, *Polyacrodus tiandongensis* Wang et al., 2001, and an incomplete osteichthyan tooth plate. *Sinocoelacanthus*, the first described coelacanthid in China, was found from the Luolou Formation at Kangdong (K'angtung), Fengshan, Guangxi (Kwangsi) Zhuang Autonomous Region. The three chondrichthyans and the osteichthyan tooth plate were also discovered from the Luolou Formation, but at a different locality—Zuodeng of Tiandong, Guangxi. These chondrichthyans are the earliest fossil records of hybodontids and polyacrodontids in China, and their assemblage is the first Chinese Triassic fish zone with precise range and age (early Spathian of Olenekian) after the concurrent conodont zone (Wang et al., 2001).

3.3 Early and Late Triassic fishes from Himalaya region

The Himalaya region was a portion of the Gondwanan supercontinent in the Triassic. The known Triassic fishes were collected from the Qomolangma vicinity at an altitude of over 4800 meters by geological explorers in 1970s. The discovered fossils include a hybodontid tooth and two fragments of an edestid shark (Dong, 1972; Zhang, 1976). The edestid shark, i. e. *Sinohelicoprion qomolangma* Zhang, 1976, was found from the lower part of the Tulong Group at Qubu, Tingri (Dingri), Xizang (Tibet) Autonomous Region. *Sinohelicoprion* was initially believed to be close to *Helicoprion*, and assigned to the family Helicoprionidae. Later, it was considered as closer to *Helicampodus* than *Helicoprion* and should be placed in the family Edestidae (Chang and Jin, 1996). The hybodontid was found from the middle member of the Qulonggongba Formation at Tulong, Nyalam, Xizang.

4 Discussions

In about seventy years, quite a lot Triassic fishes have been discovered from the vast territory of China. Even though we still know little about most of these fishes for lack of comprehensive investigation, especially in terms of their comparative anatomy and phylogeny, they may still throw some light on paleogeography and historical biogeography.

First of all, the Triassic fishes from China can be divided into two groups in general; the freshwater fish faunas mainly from the northern landmasses and the marine ones from the southern regions. This partition of fish faunas was consistent with the tectonic and palaeogeographic outline of China, which was once "sea in the south and land in the north" in the Early and Middle Triassic. At the time, the northern landmasses of China were mostly in central Laurasia, and separated with South China by the Paleo-Tethys Ocean (Wang et al., 1985; Yin and Lin, 1994). By the end of the Middle Triassic, this configuration was changed due to the Indosinian Movement, and North China had merged with the northwards-moving Yangtze Block. This alteration also influenced the distribution of fishes. *Shunisiscus*, a palaeoniscoid fish from the Sichuan Basin of the Upper Yangtze region, is close to *Triassodus* from the Middle Triassic of the Ordos Basin and *Turseodus* from the Upper Triassic of North America, respectively (Su, 1983, 1984). The resemblance of freshwater fishes from the Yangtze Block and the northern landmasses of Laurasia indicates that there already existed faunal exchanges between these two realms in Late Triassic, and that the Paleo-Qinling and Dabie Mountains, the welding belt of the North and South China Blocks, had not yet completely acted as a geographic barrier to the northern

and southern biotas as in later times.

The Triassic freshwater fish faunas of China, as a whole, are closest to those from Siberia and Middle Asia both in faunal composition and relationships. The fish faunas of these regions are all mainly composed of lower actinopterygians such as palaeoniscids, scanilepids, saurichthyids and perleidids, with the addition of semionotids, ceratodontids, actinistians and hybodontids. Su (1978) first noted the resemblance between fishes from the Junggar Basin and Siberia, and later, Sytchevskaya (1999) further confirmed the close relationships among the related fishes from Siberia, Middle Asia and China. Most recently, Chang and Miao (2004) even believed that the fishes from these regions most likely belonged to the same ichthyofauna.

To a wider extent, the Triassic freshwater fish faunas of China also include fishes that are closely related with those from other regions of Laurasia. For example, *Fukangichthys* is similar to *Tanaocrossus* from the Upper Triassic of North America and *Scanilepis* from the Rhaetian of South Sweden, and *Wayaobulepis* resembles *Gyrolepis* from the Middle and Upper Triassic of Germany and France. Furthermore, some forms of the Triassic freshwater fish faunas from China, e. g. *Sinkiangichthys*, are similar to the fishes from the Gondwanan continent (Liu, 1958). This implicates that large contiguous landmasses of both Laurasia and Gondwana were interconnected in Triassic.

For the Triassic freshwater fish fauna from the Ordos Basin in China, it is also noteworthy that most of the known fossils belong to marine fishes or show close relationships with marine forms in respect that the environment of the basin has been thought to be continental during the Triassic period. It is possible the same for some fishes from Siberia and Middle Asia. Among the Triassic fishes from the Ordos Basin, *Saurichthys*, *Perleidus*, *Gyrolepis*, *Boreosomus* and *Hybodus* are all mostly from marine deposits worldwide; the Chinese genus *Wayaobulepis*, in fact, resembles *Gyrolepis*; and the indeterminate laugiid is similar to *Laugia*, a marine fish as well. These facts seem to suggest that the Triassic sediments of the Ordos Basin, at least some fish-bearing strata (e. g. the upper part of the Tongchuan Formation, the uppermost member of the Wayaopu Formation) were under the influence of seawater more or less at the time.

With the exception of the fishes from the Himalaya region, all other known Triassic marine fishes in the southern part of China can be attributed to a few interrelated assemblages or faunas because they are from the same stratigraphic and paleobiogeographic province, of which, the fish faunas from the Yangtze region are relatively well understood thanks to the recent discovery of numerous fish fossils.

The Early Triassic fish fauna from the Middle and Lower Yangtze region is mainly composed of perleidids and parasemionotids, accompanied by saurichthyids and coelacanthids. In comparison with those intensively studied contemporaneous ichthyofaunas from Madagascar, Spitzbergen, East Greenland, etc., the diversification of this fish fauna is significantly lower if not for inadequate explorations. As for its nature, the predominant perleidid and parasemionotid fishes were formerly compared with or even referred to the related genera from Madagascar, and the fish faunas from these two regions were believed to be closely allied (Liu et al., 2002). In fact, the perleidids of this Early Triassic fish fauna are distinct from all other known forms of the family (Jin et al., 2003). The same should be true for the parasemionotids from the Middle and Lower Yangtze region. Moreover, in this region there are successive fossil records such as saurichthyids and coelacanthids near the Permian-Triassic boundary (Wang and Liu, 1981; Liu and Wei, 1988). Of those fishes from the uppermost Permian, *Eosaurichthys chaoi* is the earliest record of saurichthyids in the world. It seems that this region is probably the cradle of some Triassic fish groups subsequently flourishing in the Tethyan realm, which is worthy of further investigation to prove in the future.

In contrast with the Early Triassic fish fauna from the Middle-Lower Yangtze region, the Middle-Late Triassic fish fauna from the Upper Yangtze region is much more diversified. It

contains almost all of important Triassic fish forms, such as acrolepids, saurichthyids, birgeriids, perleidids, peltopleurids, luganoiids, eosemionotids, semionotids, marosemiids, parasemionotids, caturids, pholidophorids and elasmobranch ichthyoliths. This ichthyofauna is characterized by “subholosteans”, and also includes the modern groups of halecomorphs and the predecessors of teleosts. On the other hand, most fishes of this fauna are closely related to those from Italy, Switzerland, Austria, and about one third can find their almost identical fishes in western Tethys (cf. : Griffith, 1977; Bürgin, 1999; Tintori and Lombardo, 1999). The close relationship between the fish faunas from South China and western Tethys indicates that these two regions must be closely related biogeographically during the Middle and early Late Triassic time.

5 Conclusions

The Triassic fishes are widely distributed in China. The freshwater fishes from the northern landmasses and the Upper Yangtze region include palaeoniscids, scanilepids, ptycholepids, saurichthyids, redfieldiids, perleidids, semionotids, pholidophorids, ceratodontids, coelacanthids, laugiids, and hybodontids. The marine fishes from South China and the Himalaya region contain acrolepids, saurichthyids, birgeriids, perleidids, peltopleurids, luganoiids, eosemionotids, semionotids, marosemiids, parasemionotids, caturids, pholidophorids, coelacanthids, hybodontids, polyacrodontids, edestids, elasmobranch ichthyoliths, etc. However, it is noteworthy that most of the known fishes from the Ordos Basin are possibly of marine.

The freshwater fish faunas are characterized by primitive actinopterygians, and they are closest to those from Siberia and Middle Asia, and also contain some forms similar to the fishes from other regions of Laurasia and the Gondwanan continent. The marine fish faunas, most diversified in Ladinian and early Carnian, are characterized by “subholosteans”, and also include the modern groups of halecomorphs and the basal forms of teleosts. The Ladinian and early Carnian marine fish fauna is already closely related with the contemporaneous ichthyofaunas in western Tethys. The Lower Yangtze region of South China is probably the cradle of some Triassic fish groups (e. g. Saurichthyidae) subsequently flourishing in the Tethyan realm.

Although the Triassic fishes are abundant in China, most of the known fishes are only preliminarily reported based on sporadic finds, and remain to be comprehensively investigated in terms of their exploration, excavation, preparation, comparative anatomy and phylogeny.

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Appendix Systematic list of Triassic fishes in China

Class Chondrichthyes Huxley, 1880

Subclass Elasmobranchii Bonaparte, 1838

Order Euselachii Hay, 1902

Family Hybodontidae Owen, 1846

Hybodus youngi Liu, 1962 (Loc. 6; late Ladinian; freshwater)

Hybodus zuodengensis (Yang et al.), 1984 (Loc. 20; late Olenekian; marine)

Hybodus yohi (Yang et al.), 1984 (Loc. 20; late Olenekian; marine)

Hybodontidae gen. et sp. indet. 1 (Loc. 26; late Ladinian; marine)

Hybodontidae gen. et sp. indet. 2 (Loc. 28; Norian; marine)

Family Polyacrodontidae Glückman, 1964

Polyacrodus tiandongensis Wang et al., 2001 (Loc. 20; late Olenekian; marine)

Order Eugeneodontida Zangerl, 1981

Family Edestidae Jaekel, 1899

Sinohelicoprion qomolangma Zhang, 1976 (Loc. 27; Early Triassic; marine)

Elasmobranch ichthyoliths (Classification after Johns et al., 1997)

Supergroup I

LOBATICORONA cf. *L. floriditurris* (Loc. 26; early Carnian; marine)

New paragenus A (Loc. 26; early Carnian; marine)

PARVICORONA DACRYSULCA Chen et Cuny, 2003 (Loc. 26; late Ladinian-early Carnian; marine)

Supergroup II

FRAGILICORONA PARALABRITRICUSPIS Chen, 2002 (Loc. 26; late Ladinian-early Carnian; marine)

SERRATOCORONA HALBERDIFORME Chen, 2002 (Loc. 26; early Carnian; marine)

LABRILANCEA GLABRISUBCUSPIS Johns et al., 1997 (Loc. 26; late Ladinian; marine)

ORNATHILABRILANCEA sp. (Loc. 26; late Ladinian; marine)

CARINASUBCORONA BAMAOLINENSE Chen, 2002 (Loc. 26; early Carnian; marine)

Indet. gen. et sp. A (Loc. 26; late Ladinian; marine)

Indet. gen. et sp. B (Loc. 26; early Carnian; marine)

ANNULICORONA PYRAMIDALIS Chen et Cuny, 2003 (Loc. 26; early Carnian; marine)

SACRISUCORONA cf. *S. circabasis* (Loc. 26; early Carnian; marine)

GLABRISUBCORONA sp. (Loc. 26; late Ladinian; marine)

GLABRISUBCORONA cf. *G. arduidevexa* (Loc. 26; early Carnian; marine)

New paragenus B (Loc. 26; late Ladinian-early Carnian; marine)

Class Osteichthyes Huxley, 1880

Osteichthyes incertae sedis

gen. et sp. indet. (Loc. 20; late Olenekian; marine)

Subclass Sarcopterygii Romer, 1955

Infraclass Actinistia Cope, 1871

Family Coelacanthidae Agassiz, 1843

Coelacanthidae gen. et sp. indet. 1 (Loc. 7; late Ladinian; freshwater)

Coelacanthidae gen. et sp. indet. 2 (Loc. 17; Olenekian; marine)

SINOCOELACANTHUS FENGSHANENSIS Liu, 1964 (Loc. 19; Olenekian; marine)

Family Laugiidae Berg, 1940

Laugiidae gen. et sp. indet. (Loc. 9; Carnian; freshwater)

Infraclass Dipnoi Müller, 1845

Family Ceratodontidae Gill, 1872

Ceratodus heshangouensis Cheng, 1980 (Loc. 5; late Olenekian; freshwater)

Subclass Actinopterygii Cope, 1887

Infraclass Actinopteri Cope, 1871

Family ? Scanilepidae Romer, 1945

Fukangichthys longidorsalis Su, 1978 (Loc. 2; Ladinian; freshwater)

Family Palaeoniscidae Vogt, 1852

Triassodus yanchangensis Su, 1984 (Loc. 8; late Ladinian; freshwater)

Wayaobulepis zichangensis Su, 1999 (Loc. 10; late Rhaetian; freshwater)

Palaeoniscus sp. (Loc. 11; late Rhaetian; freshwater)

Gyrolepis sp. (Loc. 11; late Rhaetian; freshwater)

Shuniscus longianalis Su, 1983 (Loc. 12; late Rhaetian; freshwater)

Family Ptycholepididae Brough, 1939

Boreosomus sp. (Loc. 11; late Rhaetian; freshwater)

Family Acrolepidae Aldinger, 1937

Acrolepidae gen. et sp. nov. (Locs. 23, 25; late Ladinian; marine)

Family Saurichthyidae Goodrich, 1909

Saurichthys huanshenensis Chou et Liu, 1957 (Loc. 11; late Rhaetian; freshwater)

Saurichthys sp. (Loc. 15; Olenekian; marine)

Saurichthys sp. nov. 1 (Loc. 22; late Anisian; marine)

Saurichthys sp. nov. 2 (Locs. 24, 25; late Ladinian; marine)

Family Birgeriidae Aldinger, 1937

Birgeria liui Jin, 2001 (Locs. 24, 25; late Ladinian; marine)

Birgeria sp. (Loc. 26; early Carnian; marine)

Family Redfieldiidae Berg, 1940

Sinkiangichthys longipectoralis Liu, 1958 (Loc. 1; Ladinian; freshwater)

Family Perleididae Brough, 1931

Perleides cf. *P. woodwardi* (Loc. 11; late Rhaetian; freshwater)

Zhangina jiangsuensis (Qian et al.), 1997 (synonym: *Zhangina cylindrica* Liu et al. , 2002) (Loc. 14; Induan; marine)

Zhangina yangtzensis (Su) , 1981 (possible synonym: “Perleides” eurylepidotrichia Liu et al. , 2002) (Locs. 14, 16; Early Triassic; marine)

Perleididae gen. et sp. indet. (Loc. 17; Olenekian; marine)

Plesioperleides dayeensis Su et Li, 1983 (Loc. 18; Olenekian; marine)

Perleididae gen. et sp. nov. (Locs. 21, 22; late Anisian; marine)

Colobodus sp. nov. (Loc. 26; early Carnian; marine)

Family Peltopleuridae Brough, 1939

Peltopleurus orientalis Su, 1959 (Locs. 24, 25; late Ladinian; marine)

Peripeltopleurus sp. nov. (Loc. 24; late Ladinian; marine)

Family Luganoiidae Brough, 1939

Guizhoubranchysomus minor Liu et al. , 2003 (Loc. 25; late Ladinian; marine)

Actinopteri incertae sedis

Duwaichthys mirabilis Liu et al. , 1990 (Loc. 4; ? early Induan; freshwater)

Guizhouniscus microlepidus Liu et al. , 2003 (Loc. 25; late Ladinian; marine)

Series Neopterygii Regan, 1923

Family Eosemionotidae Brgin et al. , 1991

Eosemionotus sp. nov. (Loc. 24; late Ladinian; marine)

Eosemionotidae gen. et sp. nov. (Loc. 22; late Anisian; marine)

Family Semionotidae Woodward, 1890

Sinosemionotus urumchi Yuan et Koh, 1936 (Loc. 3; early Carnian; freshwater)

Asialepidotus shingyiensis Su, 1959 (Locs. 23, 24, 25; late Ladinian; marine)

Archaeosemionotus sp. nov. (Loc. 25; late Ladinian; marine)

Semionotidae gen. et sp. nov. (Loc. 22; late Anisian; marine)

Family Marosemiidae Thiollire, 1858

Marosemiidae gen. et sp. nov. (Loc. 25; late Ladinian; marine)

Neopterygii incertae sedis

Xingyia gracilis Liu et al. , 2003 (Loc. 25; late Ladinian; marine)

Subdivision Halecomorphi Cope, 1872

Family Parasemionotidae Stensi, 1932

"*Lepidotes*" *jurongensis* Qian et al. , 1997 (probable synonyms: *Stensinotus dongchangensis* Liu et al. , 2002; *Jurongia fusiformis* Liu et al. , 2002; *Qingshania cercida* Liu et al. , 2002; *Suius brevis* Liu et al. , 2002) (Loc. 14; Induan; marine)

Parasemionotidae gen. et sp. indet. (Loc. 17; Olenekian; marine)

Parasemionotidae gen. et sp. nov. (Loc. 22; late Anisian; marine)

Family Caturidae Owen, 1860

Sinoeugnathus kueichowensis Su, 1959 (Locs. 23, 24, 25; late Ladinian; marine)

Guizhoueugnathus analilepida Liu et al. , 2003 (Loc. 25; late Ladinian; marine)

Caturidae gen. et sp. nov. (Loc. 25; late Ladinian; marine)

Halecomorphi incertae sedis

Guizhouamia bellula Liu et al. , 2002 (Loc. 25; late Ladinian; marine)

Subdivision Teleostei Mller, 1845

Family Pholidophoridae Woodward, 1890

Jialingichthys serratus Su, 1983 (Locs. 12, 13; late Rhaetian; freshwater)

Pholidophoridae gen. et sp. nov. (Loc. 25; late Ladinian; marine)