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中国中生代晚期及第三纪鱼类区系中的若干分布格局问题[1)]

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摘要 日本列岛和中国大陆东部的现生淡水鱼类区系存在显著的差异，但这两地上新世和中新世的鱼类区系已发现的组成成分却似乎比现代鱼类区系要接近得多。而在中国东部渤海沿岸发现的早第三纪或始新世的鱼类区系成分则显示出与北美西岸同时代鱼类区系的惊人相似，展现出一个"跨太平洋格局"。中国中生代晚期或早白垩世的鱼类区系从组成和分布上可以划分为两个组合。分布于北部的一个组合中土著类型较多，分布于东南部的组合表现出一些与南美东北部及非洲西部鱼类区系的相似性，这种分布格局涉及到南、北两半球的大陆。

本文对上述分布格局作一简单介绍，并作初步解释：

1) 早白垩世的副鲑鱼亚科鱼类在西非、南美洲东北部的分布曾被解释为 1)历史上曾存在过一个包括副鲑鱼亚科在内的广布单系类群；2)中国东南部早白垩世鱼类区系起源于冈瓦纳；3)中国东南部早白垩世鱼类区系中至少有某些种类是近岸鱼类。本文倾向于接受后两种建议。

2) 始新世渤海沿岸及北美绿河页岩鱼类区系的"跨太平洋"分布格局曾有人用"太平洋洲假说"来说明。本文作者不赞成这种解释，认为这一分布格局的形成有多种原因，如当时宽阔的白令陆桥及露出海面的北极地区可作为两地鱼类的通道；两地的近岸鱼类可沿当时连续的海岸来往，等等。

3) 晚第三纪中新世和上新世中国东部和日本列岛共有许多鲤科鱼类，表明两地当时相连并属于同一鱼类区系，在日本列岛和中国大陆分离后，这一鱼类区系也一分为二，由于东亚大陆受到特有的季风气候影响，该处的现代鱼类区系比日本列岛现代存在于古老湖泊中的鱼类区系发生了更大的变化。

关键词 中国，中生代，新生代，鱼类区系，分布格局

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LATE MESOZOIC AND TERTIARY ICHTHYOFAUNAS FROM CHINA AND SOME PUZZLING PATTERNS OF DISTRIBUTION

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Abstract The Recent freshwater ichthyofauna from the Japanese islands is, in many respects, different from that of eastern China. The Pliocene and Miocene ones from both areas, however, resemble each other in a greater extent in composition than the Recent ones. The Early Tertiary, i.e. Eocene fish fauna along the coast of the Bohai Gulf, east China shows striking similarity in composition to those of the same age along the west coast of North America demonstrating a "transpacific" distributional pattern. According to their composition and distribution the late Mesozoic, i.e. the Early Cretaceous freshwater ichthyofauna from China, can be subdivided into two distinct assemblages. The one from North China is endemic, while the one from southeastern China exhibits some affinities with the Early Cretaceous ichthyofaunas from northeastern South America and West Africa displaying a distributional pattern involving both northern and southern continents.

Discussions on and tentative interpretations about the distributional patterns mentioned above are given in the text.

Key words China, Mesozoic, Cenozoic, fish faunas, distributional patterns

1 Introduction

Late Mesozoic and Cenozoic lacustrine deposits are widely spread in eastern China. From these deposits abundant fossil fishes have been discovered. Based on differences in their distribution and composition, the Early Cretaceous and Eocene freshwater fishes were divided into two assemblages, respectively (figs. 1, 3; Chang and Chow, 1986). The Early Cretaceous fish fauna from northern China and its adjacent areas of Mongolia and Siberia was considered as endemic at its time. On the contrary, the one of more or less the same age from southeastern part of China was thought to be related to those from northeastern South America and West Africa (Chang and Chow, 1986). The Eocene fish fauna from the region around the Bohai Gulf shows striking similarity to the contemporaneous one from the Green River area, western North America on the other side of the Pacific (Chang and Chow, 1978; Grande, 1982a; Zhang *et al.* 1985; Chang and Zhou, 1993). A recent paper on xenocyprinine by

Chang, Chen and Tong (1996) mentioned the similarities between the Miocene and Pliocene ichthyofaunas from eastern China and Japan, and the differences between the Recent fish faunas of the two areas.

The following summarizes new information and discussion on the three puzzling distributional patterns: 1) that of the late Mesozoic ichthyofaunas from West Africa, northeastern South America and southeastern China; 2) the "transpacific" distribution of the Eocene ichthyofaunas from the Bohai Gulf region and Green River area; and 3) the distributional patterns of Neogene and Recent fish faunas from eastern China and Japan.

2 Discussion

2.1 Distributional pattern related to the Early Cretaceous fish fauna from southeastern China

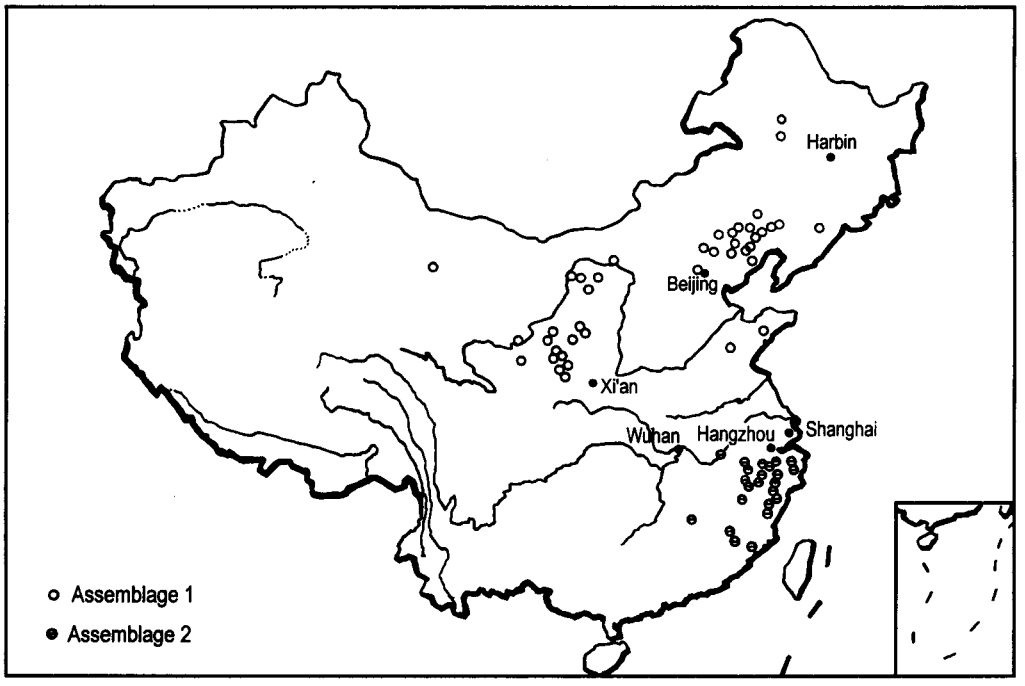

Fig.1 Map of distribution of Early Cretaceous fishes in China (After Chang and Chow, 1986 with modification)

As mentioned by Chang and Chow (1986) this fauna is similar at the family level to those from West Africa and northeastern South America, i.e. east and west coast of the southern Atlantic (fig.2, also see table 1, Chang and Chow, 1986). The existence of comparable Early Cretaceous non-marine fish faunas on both sides of the Atlantic was demonstrated long ago by Patterson (1975). It is not surprising that the two faunas contain closely related taxa, because the data are congruent with the

evidence provided by other vertebrates and invertebrates, and the successions of the deposits on the two sides are almost identical. All evidences point to the close connection between the two continents during the Early Cretaceous. Yet there is no information so far indicating a past close geographical relationship between the west coast of north hemisphere Pacific and Gondwana.

Fig.2 Map of distribution of Early Cretaceous ichthyofaunas in Brazil, West Africa and southeastern China (After Chang and Chow, 1986)

A detailed comparison of members of each group of the three faunas should be performed in order to test whether they are really closely related to each other. Paraclupeids from the Early Cretaceous deposits of the three continents were chosen as the first group to be worked out in this respect (Chang and Grande, 1997).

As the result of comparison *Paraclupea chetungensis* from China was proved to have close relationship with *Ellimmichthys longicostatus* from Brazil and *E. goodi* from Equatorial Guinea. They were suggested to be grouped together as a subfamily Paraclupeinae within the family Paraclupeidae (Chang and Grande, 1997) which, in addition to this subfamily also includes *Diplomystus* (Grande, 1982a, 1985), a genus which will be mentioned below.

To interpret this puzzling pattern the following tentative suggestions have been proposed.

1) Chang and Grande (1997) suggested a past existence of a widespread monophyletic group including the Early Cretaceous paraclupeine from the areas mentioned above and Kyushu, Japan (Yabumoto, 1994); Late Cretaceous species of *Diplomystus* from the east coast of Mediterranean (Mount Lebanon); and the Middle Eocene species of *Diplomystus* from eastern China and North America. This suggestion, however, does not solve the problem of the Early Cretaceous distribution of the Paraclupeinae because: a) the existence of *Diplomystus* was later than that of the Paraclupeinae and can not be counted as part of "a past widespread monophyletic group" for the Paraclupeinae. The known earliest paraclupeids, i.e. paraclupeine, do not seem widespread. To suggest the existence of a widespread monophyletic group of the Paraclupeinae we have to make an *ad hoc* assumption that either their remains in other areas of the world have not yet been found or have been obliterated by later geological events; b) the monophyletic status of Paraclupeinae+*Diplomystus* is,

according to the present status of study, not supported by any synapomorphies. Consequently, the suggestion of the existence of a past widespread monophyletic group prior to or contemporaneous with the Paraclupeinae does not seem well corroborated.

2) The second possibility is that there is a widely accepted view that the present southeastern Asia, including southern or southeastern China was formerly a part of Gondwana (Ridd, 1971, 1980; Tarling, 1972; Rage, 1988). It is worth to mention that the Early Cretaceous ichthyofauna from southeastern China, in addition to *Paraclupea,* included other fishes such as the early ichthyodectiform *Mesoclupea,* early osteoglossid *Paralycoptera* etc. (Chang and Chow, 1977). These latter forms probably also have their equivalents in the ichthyofauna of the same age from Gondwana (Chang and Chow, 1986) although further work is required to verify their identity. In this case, it is reasonable to regard southeastern Asia as the carrier of fauna from Gondwana. The suggested time of accretion of this part of the mainland Asia, late Triassic at the latest (Buffetaut, 1985; Buffetaut and Martin, 1985; Rage, 1988) is, however, a bit too early for the occurrence of the Early Cretaceous paraclupeine in southeastern China. Besides, the fossil evidence for the Gondwanan origin of the fauna of southeastern Asia is still too scanty.

3) The third possibility is that the forms we are dealing with might be of marine origin and thus their distribution might have certain connection with the sea. The localities of *Ellimmichthys* and *Paraclupea* are all situated along the present coastline. The deposits containing *Ellimmichthys* from Brazil are reported to be estuarine. *Paraclupea* occurs only in localities along the coast of the East China Sea. It has not been found from the contemporaneous deposits of more inland areas (Chang and Chou, 1977). The deposits containing *Paraclupea* have been suggested as transitional based on the lack of the rich fauna of typical freshwater bivalves and other invertebrates from the adjacent inland areas (Chang and Chow, 1978).

2.2 Distributional pattern related to the Eocene fish fauna from the Bohai Gulf area, North China

Since the discovery of the Eocene fish fauna from the oil fields around the coastal region of the Bohai Gulf (fig. 3) and recognition of its striking similarities to the fish fauna from the Green River Shales (Chang and Chow, 1978, 1986; Chang and Zhou 1993; Grande, 1982a, b, 1994; Zhang *et al.,* 1985) a "transoceanic" character of distribution of many groups of the two faunas seems quite obvious (fig. 4). Among nine families occurring in the areas around the Bohai Gulf seven are shared with the Green River Formation. They are Dasyatidae, Amiidae, Hiodontidae, Paraclupeidae, Clupeidae, Gonorhychidae and Catostomidae (Table 1). From these families four shared genera are identified: *Amia* sp. (Chow, person. comm.), *Eohiodon shuyangensis* (Shen, 1989), *Diplomystus shengliensis* and *Knightia bohaiensis* (Zhang

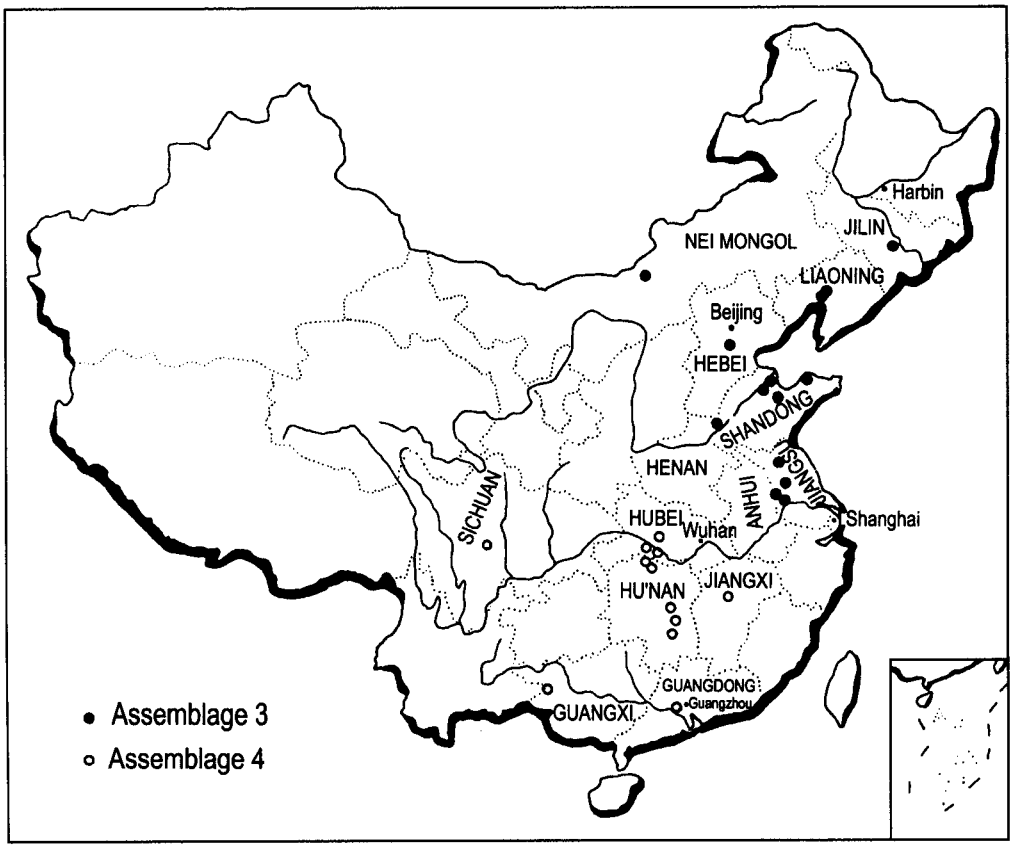

Fig.3 Map of distribution of Eocene fishes in China (After Chang and Zhou, 1993)

et al., 1985). Some members of the two faunas, namely *Diplomystus* and *Knightia,* are so similar to each other that it would be very difficult to distinguish them as separate

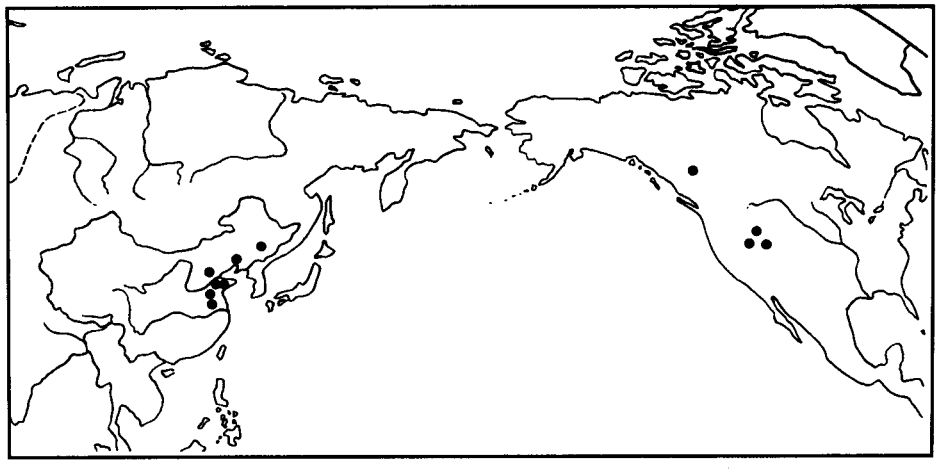

Fig.4 Map of distribution of Eocene fishes in Bohai Gulf Region, China and Green River Area, U.S.A.

species if they were not discovered from different basins on different sides of the Pacific.

Grande (1994) mentioned a repeating pattern of area relationship between the early Tertiary west North America and west Pacific region based on the transoceanic relationships of five families of the Green River Formation teleosts and those from the west Pacific region including China, Indonesia and Australia. He (1985, 1989, 1994) specifies this distribution as a transpacific pattern and uses the Pacifica hypothesis[1)] (Nur and Ben-Avraham, 1977; Nelson and Platnick, 1984) as a method of transporting organisms across the Pacific.

The many groups of fishes shared by the two sides, however, show different ranges of distribution (Table 1).

Table 1 Comparison between Eocene ichthyofaunas from South China, Bohai Gulf Region, Green River Area and East Khazakstan

South China	Bohai Gulf Region, China	Green River, USA	East Kazakhstan
	Dasyatidae	Dasyatidae	
		Heliobatis radians	
	Amiidae	Amiidae	Amiidae
	Amia sp.	*Amia scutata*	
		and other species	
Osteoglossidae		Osteoglossidae	
		Phareodus testis	
		and other species	
	Hiodontidae	Hiodontidae	Hiodontidae
	Eohiodon shuyangensis	*Eohiodon falcatus*	
	Paraclupeidae	Paraclupeidae	
	Diplomystus shengliensis	*Diplomystus dentatus*	
	Clupeidae	Clupeidae	
	Knightia bohaiensis	*Knightia eocaena*	
	Gonorhynchidae	Gonorhynchidae	
		Notogoneus osculus	
Catostomidae	Catostomidae	Catostomidae	Catostomidae
		Amyson gosiutensis	
Cyprinidae	Cyprinidae		Cyprinidae
several genera			
?Bagridae	?Bagridae	Ictaluridae	
		Astephus antiquus	
Perciformes	Perciformes	Perciformes and many	
		other groups, e. g.	
		Polyodontidae,	
		Lepisosteidae etc.	

1) There was an early continent situated in South Pacific, adjacent to Australia and Antarctica. It started to rift apart in Triassic or Jurassic. Its fragments drifted away and finally collided with the Pacific rim.

Three families are uniquely shared by the Bohai Gulf and Green River areas. They are Dasyatidae, Paraclupeidae and Clupeidae. Members of these families, at least those from the two latter families, i.e. *Diplomystus* and *Knightia,* both extinct genera, from the two sides of the Pacific show very close affinities. Phylogenetic study indicates that *D. shengliensis* from the Bohai gulf and *D. dentatus* from the Green River form each other's sister species. Members of the three families are not found in any other areas elsewhere, not even found north to the Green River area in North America, e. g. from the Middle Eocene deposits of Washington State, U. S. and British Columbia, Canada (Wilson, 1977, 1978 and person. comm.) where other forms of fossil fishes are shared with both or either of the Green River and Bohai Gulf regions. They are not found in the inland area of South China and East Kazakhstan where Eocene fishes are also abundant (Sytchevskaya, 1986; Chang and Zhou, 1993).

Three other groups had much wider distribution than the two areas just mentioned. On the western side of the Pacific, aside from Bohai Gulf Area, the Hiodontidae occur in East Kazakhstan, Central Asia. In addition to East Kazakhstan Catostomidae are widely spread in the vast plain area of East Asia, from Mongolia in the north to Guangdong province at the very south of China. Besides Australia and Indonesia (the latter might be Oligocene in age) Osteoglossidae are now found in Sichuan (*Sinoglossus*, Su, 1986) and Hubei (Song, in prep.) provinces, South China. Whether the same genus *Phareodus* as from the Green River Formation is present in China can not be decided prior to the study of the material from Hubei. On the eastern side of the Pacific, in addition to the Green River Formation, members of all three families are found in British Columbia, Canada (Wilson, 1977).

The bowfins (Amiidae) which are present in the two areas have still wider distribution to include North China, East Kazakhstan and Europe, e. g. Messel, Germany and many other localities (Grande and Bemis, 1998).

Besides, there are forms occurring only on one side of the Pacific. For instance, the gars (Lepisosteidae) which are frequently seen in the Green River area and western Canada, do not occur on the west side of the Pacific. Instead, the group shows a transatlantic relationship (Wiley, 1976). The Cyprinidae, on the contrary, were widespread in Asia including the Bohai Gulf area, South China and East Kazakhstan but had no traces yet in North America and were probably not present in Europe during the Eocene.

The different ranges of distribution of these groups of fishes cause the subdivision of the west Pacific region into several areas with fish faunas of different composition. They are: the Bohai Gulf area, inland North China (Nei Mongol), East Kazakhstan, South China, Indonesia and Australia. The repeating pattern of relationship mentioned by Grande (1994) is, strictly speaking, shared by the Green River area on the east coast of the Pacific and several areas jointly on the west side

of the Pacific. In fact, most of the repeating pattern of relationship is shown only between the Bohai Gulf and Green River: seven families with four genera already identified. Each of the other areas on the west side of the Pacific shares with Green River much less taxa: one family with Australia and Indonesia (Osteoglossidae), two with South China (Osteoglossidae and Catostomidae) and inland North China (Amiidae and Catostomidae), and three with East Kazakhstan (Amiidae, Hiodontidae and Catostomidae) so far recognized. All mainland Asian faunas share Catostomidae and Cyprinidae. Amiids and hiodontids only occur in the northern part of China and East Kazakhstan but not found south to these areas.

The similarities of the middle Eocene fish faunas from both sides of the Pacific in composition are, on the whole, in congruence with the data of the contemporaneous terrestrial vertebrates from the same sides (Russell and Zhai, 1987).

The holarctic distribution of *Amia* during the Eocene is in accordance with the distribution of quite a number of riparian and terrestrial vertebrates forming the pan-Arctic fauna in the Late Cretaceous and early Cenozoic (Estes and Hutchinson, 1980). Without detailed study of Amiidae, however, it is difficult to discuss about their biogeographical implication, though Arctic connections between the northern continents must have played a significant role in its dispersal as well as in the dispersal of certain groups of mammals (McKenna, 1975, 1980, 1983, 1984).

The distribution of Hiodontidae and Catostomidae from Central Asia through East China to west North America must have formed, like that of other middle Eocene terrestrial vertebrates, when the connection between Asia and North America in the area of Bering Strait was broad enough (Russell and Zhai, 1987) to house freshwater bodies for freshwater vertebrates to traverse.

Members of the three families uniquely shared by Bohai Gulf and Green River, e. g. Dasyatidae, Paraclupeidae and Clupeidae, do not seem strictly primary freshwater forms. The reasons are: a) these forms are absent in the inland areas of Asia; b) the living forms of Dasyatidae and Clupeidae are frequently found in the sea; c) some members of the third fossil family (Paraclupeidae), e. g. *Diplomystus birdi* and *D. dubertreti* occurred in the Late Cretaceous marine limestone in Lebanon; and d) foraminifera have been found (Wang *et al.*, 1975) associated with the fish remains, and a transitional environment between land and sea for the fauna from Bohai Gulf was proposed (Chang and Chow, 1978). If this were the case the fishes of the three groups could have marine origin and could have swum freely along the coast when the coast line of the two sides of the Pacific were continuous and situated at much lower latitude than it is at present. The absence of the members of the three families with possible connection with the sea in west Canada might be interpreted in the way that the passageway between Asia and North America was so broad that it excluded west Canada from the coastline. It is difficult to imagine how could the presence of

so closely related Eocene forms like *D. shengliensis* and *D. dentatus* be explained as originated from forms carried by the fragments drifted from the rifted Pacifica in the Triassic or Jurassic, finally collided with the continents of the Pacific rim in Late Jurassic or Cretaceous at the latest.

In conclusion, for interpretation of the Eocene transpacific pattern of distribution we would prefer the Arctic connection of the northern continents, the broad connection between Asia and North America in the Bering Strait area proposed by mammalogists and the marine origin of certain groups of fishes jointly rather than the Pacifica theory.

2.3 Distributional pattern related to the Neogene and Recent fish faunas from East China and Japan

As mentioned by Nakajima and Yamasaki (1992) and Chang *et al.* (1996) the Miocene and Pliocene fish faunas from localities of eastern China and along the northwestern coast of Japan share quite a few taxa at the generic level (fig. 5) yet the Recent faunas from the two areas are, in many ways, different.

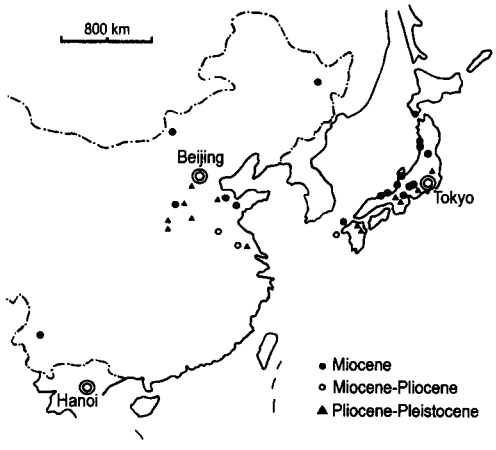

Fig. 5 Map of distribution of Neogene and Pleistocene cyprinids in East China and Japan (After Nakajima and Yamasaki, 1992, with additional information from Chang *et al.*, 1996)

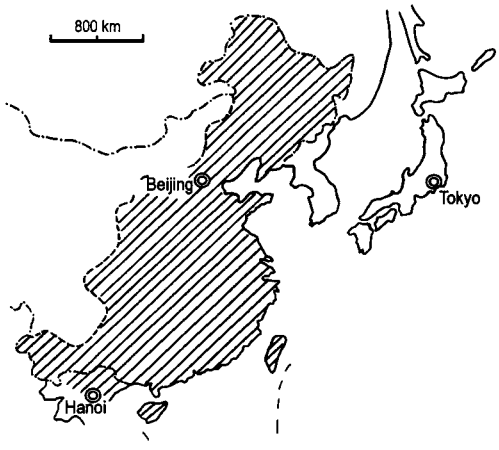

Fig. 6 Map of distribution of living xenocyprinine as an example showing differences in Recent ichthyofaunas of East China and Japan (After Chang *et al.*, 1996, with modification)

The freshwater fish fauna of China contains about 800 species while that of Japan, 300. It is difficult to give a strict definition to freshwater fish fauna, for, aside from primary freshwater forms, it also includes fishes which adapt to brackish water or are migratory between freshwater and the sea. So it would be very complicated to deal with biogeographical problems based on the freshwater fish faunas as a whole. Since the group of Cyprinidae is more or less strictly primary freshwater, and the comparison of forms of this group reveals some interesting phenomena in the evolution of the faunas from the two areas, our discussion is restricted only to the

members of this family.

There are altogether 538 species and subspecies of Cyprinidae in the Recent fish fauna of China (Chen, 1998), while there are only 57 species and subspecies of the same family present in Japan (Kawanabe and Mizuno, 1989). The dominant group of Cyprinidae in Japan is Gobioninae (*sensu* Wu, 1977, i. e. including Sarcochilichthinae and *Gnathopogon,* both were later removed from the subfamily by Hosoya [1986] and the latter was referred to Barbinae by Kawanabe and Mizuno [1989]) which contains 18 species and consists 31.4% of the cyprinids present in Japan. The next main group of Cyprinidae is Acheilognathinae, which has 15 species and covers 26.3% of the whole amount of the family in Japan. The third chief component, the Leuciscinae has 9 species and comprises 14% of the cyprinids in Japan. All the three subfamilies were considered to be derived from the primitive subfamily Danioninae (Chen *et al.,* 1984; Chen *et al.,* 1986; Chen, 1998). If the 6 species of Danioninae are incorporated, the entire group, i. e. Danioninae and its offsprings, consists 87.7% of the Recent cyprinids of Japan. This component part of the Recent Japanese fish fauna is rather similar in composition to the Neogene cyprinid fauna from East China (Liu and Su, 1962; Zhou, 1990; Chang *et al.* 1996) and Japan (Nakajima and Yamasaki, 1992). Later, when the Japanese islands separated from the Asian mainland, this part of the ichthyofauna continued to exist in the Recent Japanese fish fauna with a few endemic genera such as *Hemigrammocypris, Ischikauia, Biwia, Tanakia* etc. and many endemic species and subspecies derived from them added to it. Based on the cyprinid fossil records from Neogene of both eastern China and Japan Nakajima and Yamasaki (1992) came to the conclusion that "there were large lakes between Chinese continent and Japanese Islands in early Miocene" and "the new cyprinid fauna" "spread from Japanese area, the margin of Chinese continent, to the inside of the continent during middle Miocene to Pliocene". The different interpretations to the similarity of the Neogene and differences of the Recent ichthyofaunas of eastern China and Japan are, in fact, due to different approaches in study of biogeography. Nakajima and Yamasaki apply the traditional theory of dispersal while we think what occurred, in this case, was differentiation through separation from a previously widespread ichthyofauna (Nelson and Platnick, 1984).

No authentic Cultrinae and Hypophthalmichthyinae have been recorded from the Recent fish fauna of Japan. To meet their spawning requirements most fishes of these groups adapt to shallow lakes with rich water plants and linked with large rivers, an ecological environment brought about by the East Asian Monsoon climate in the vast plain area of the East Asian mainland.

The possible plesiomorphic sister-group of Cultrinae–Xenocyprinae, widely spread both in the Neogene and Recent fish faunas of eastern China, has plenty fossil records in Japan during Neogene and Quaternary but became extinct later (fig. 6).

One of the predominant component in the Recent cyprinid fauna of China, Barbinae and their derivatives Labeoinae and Schizothoracinae, have neither Recent representatives nor fossil record in Japan. From this fact we can infer that these groups of fishes, distributed at present mainly in Africa, Europe and Central Asia, probably had not yet reached East Asia in the early stage of Neogene. Although their remains were found from the late Neogene (Liu, 1954) and Quaternary deposits of North China there is only one related species (*Onychostoma macrolepis*) surviving in the Recent fish fauna north to the River Yangtze. Their disappearance from North China is possibly due to the climate change. Judging from the analysis of Recent faunas and fossil records, Cyprininae might not be derivatives of primitive Barbinae, contrary to the suggestion by many ichthyologists. Plenty of Cyprininae fossils have been found from Neogene deposits of East China and Japan (fig. 5). There are still seven species (or subspecies) of Cyprininae remaining in Japan. Among them quite a few are endemic species and subspecies derived from *Carassius*. All this indicates that Cyprininae is an independent, early branch of Cyprinidae.

To sum up, the comparatively primitive cyprinid fauna, consisting mainly of fishes related to Danioninae and Cyprininae were widely spread over the Japanese islands and the mainland East Asia during the Neogene. Many forms of these groups are at present still surviving in both areas. After the separation of the two areas the environment of the mainland East Asia has greatly influenced by the East Asian Monsoon climate. As a result, the cyprinid fauna of this area is enriched by both the new derived forms adapting to the new environment caused by the Monsoon climate, and the new comers entered the area from other parts of the world after the separation. The Recent cyprinid fauna of the Japanese Islands continues to be dominated by Danioninae (*Sensu lato*) and Cyprininae and their derivatives, probably, owing to the inconsiderably changed environment of the ancient water system, e. g. Biwa Lake, formed in early Neogene.

3 Conclusions

1) The distribution of the Early Cretaceous Paraclupeinae in West Africa, Northeast South America and Southeast China is suggested to be interpreted with a) the past existence of a widespread monophyletic group including Paraclupeinae; b) the Gondwana origin of the fish fauna from Southeast China; and c) the nearshore habitat of, at least, some forms of the fish fauna. The authors incline to the latter two suggestions.

2) The "transpacific" distribution of the Eocene fish faunas from the Bohai Gulf region, China and the Green River area, U. S. A. has been explained by the Pacifica theory and multiple origin of the members of the fish fauna. The authors prefer the latter explanation.

3) The many similar Neogene cyprinids shared by eastern China and Japan indicate that they formed a widespread ichthyofauna and the two areas were closely connected. After the separation of the two areas the fish fauna split and differentiated into two. The mainland East Asian one shows more changes than that of the Japanese Islands owing to greater environmental changes.

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