Journal of Biogeography, **29**, 1187–1199

On the distributional patterns of Southeast-East Asian freshwater fish and their history

S. Y. Yap *Institute of Biological Sciences, University of Malaya, Kuala Lumpur, Malaysia*

Abstract

Aim The extensively published data on Southeast-East Asian freshwater fish communities and distributions were compiled and expressed into phenograms.

Location River basins of Southeast China, the Indochinese Peninsula and Sundaland were studied and compared for possible lineages.

Methods The Hennig86 program was employed to cluster the basins of the various subregions on the basis of their similarity in fish assemblages. In this cluster analysis, the outgroup comparison method was used, in which a reference was based on which to make corrections for unequal rates of evolution among the lineages.

Results South-eastern China, the Indochinese Peninsula and Sundaland are groups of landmass that share a common ancestor and that evolved at distinct epochs and through different geological processes, as shown from the association between the distribution of freshwater fish of Southeast-East Asia and the twenty-one river basins they inhabit.

Main conclusions Southeast-East Asia comprises an estimated 3500 cyprinid species. The phenograms obtained, based on their compositional and distributional patterns, suggest that the riverine fish communities of the area studied fall into nineteen biogeographical zones defined by the main river systems and their underlying geology.

Keywords

Biogeography, dispersal, fish assemblage, fish distribution, geological events, phenograms.

INTRODUCTION

Based on their observations that inland aquatic ecosystems supported a diversity of primary and secondary fishes, some ichthyologists have demarcated the Southeast Asian/eastern China region as the 'centre of dispersal' of the freshwater fishes of the world (Darlington, 1957; Wang *et al.*, 1981; Banarescu & Nalbant, 1982; Menon, 1987). However, some biogeographers (Myers, 1951; Kottelat, 1989; Zakaria-Ismail, 1994) have been able to map out distinct subregions. The differing views relied solely on ecological observations of fish community and distribution patterns. Fish faunal diversity and compositional similarity are often correlated with the morphological features of river basins, which were formed through geological processes such as movement of tectonic plates, submerging of continental shelves and river capture. As diversity is engendered by speciation, fish phylogeny would explain how the fishes (Xiao *et al.*, 2001 on subfamily Xenocyprinae; Dodson *et al.*, 1995 on Bagridae) adapt to the changing riverine environments. As both distributional data on the freshwater fishes (Rainboth, 1996; Doi, 1997; Chen & He, 2001) and geological data (Molengraaff, 1921; Gregory, 1925) on Southeast Asia are available in the literature, this study has utilized the information to re-examine the relation between the geological processes and the origin of the main river systems (including the insular environments) as well as its influence on the freshwater fish.

Correspondence: Institute of Biological Sciences, University of Malaya, 50603 Kuala Lumpur, Malaysia. E-mail: yap@um.edu.my

MATERIALS AND METHODS

The river basins are those bordered by the Salween basin of the Indochinese Peninsula in the west, Java island of Sundaland in the south, Borneo in the east and Southeast China in the north (from the Minjiang-Jiulongjiang) (Fig. 1). The boundary demarcates nineteen river drainage basins (Annam, upper Mekong River, middle Mekong River, lower Mekong River, Chao Phraya, south-eastern Thailand and south-western Kampuchea, Salween and Mae Khlong in the west; the Malay Peninsula, Sumatra and Java in the south; Borneo island in the east; Minjiang-Jiulongjiang, upper

© 2002 Blackwell Science Ltd

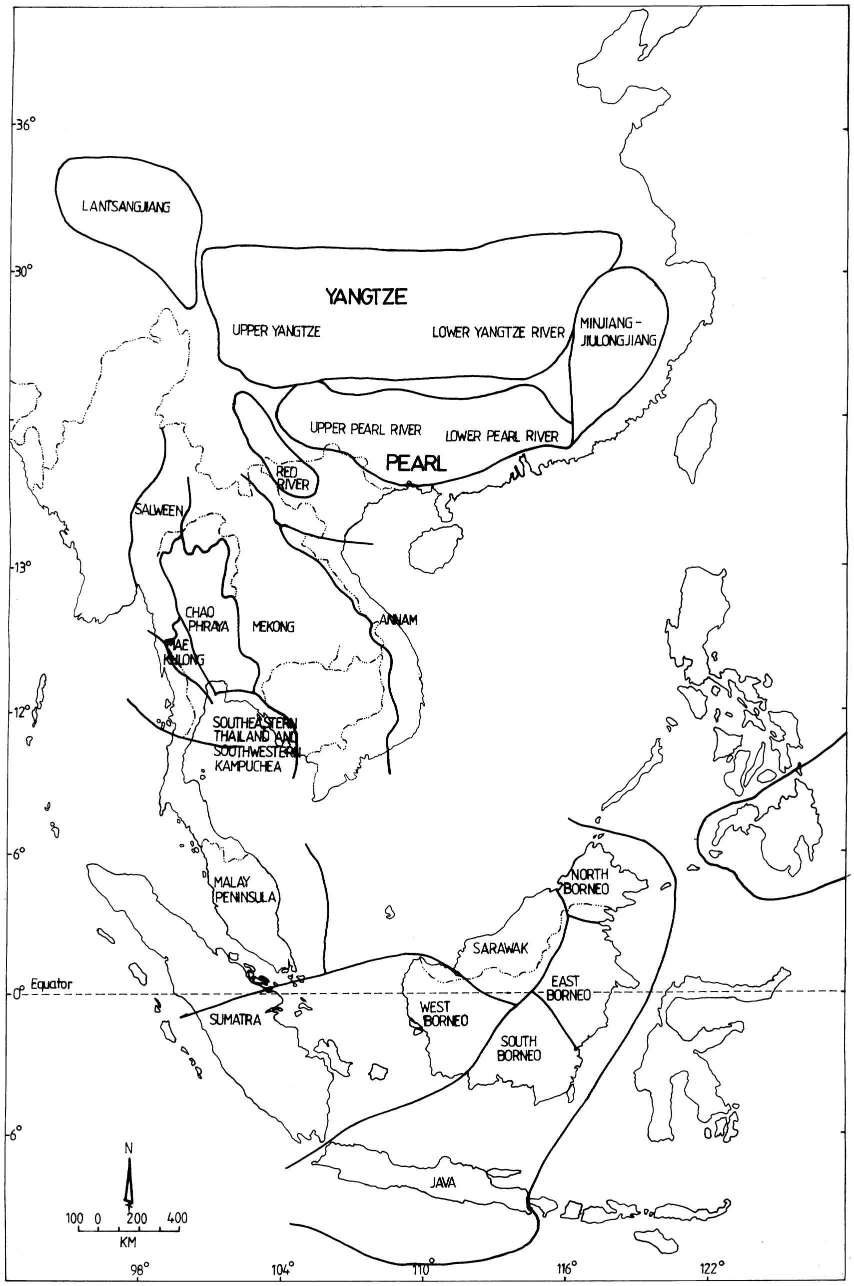

Figure 1 Major biogeographical regions of the freshwater fishes in South-east-East Asia.

Yangtze River, lower Yangtze River, upper Pearl River, lower Pearl River, Red River and Lantsangjiang/upper Mekong River in the north).

The biogeographical units and their fish distribution are extracted from published sources (Chu, 1984; Chu, 1985; Kottelat, 1989; Rainboth, 1996; Zhang *et al.*, 1996; Doi, 1997; Chen & He, 2001) as is the geological information (Molengraaff & Weber, 1919; Gregory & Gregory, 1923; Gregory, 1925; Workman, 1975; Audley-Charles, 1983; Rainboth, 1991). Outgroup comparison analysis (Watrous & Wheeler, 1981) on the nineteen river basins and fish distribution (cypriniformes, siluriformes, perciformes; Appendix 1) yielded the matrix (Table 1) for the computation of the phenogram (Li & Graur, 1991) (Fig. 2a) by the Hennig86 program (Farris, 1988). The nineteen river basins were then re-classified into twenty-one drainage systems; the matrix and tree diagram (Fig. 2b) were similarly computed on 163 cyprinids (Appendices 2 and 3). For this set of calculations, the middle and lower Mekong rivers were considered as the Mekong River; the Borneo island was split into west Borneo, south Borneo, east Borneo and north Borneo-Sarawak.

Table 1 A matrix of nineteen river basins and twenty-one common fish genera of Southeast-East Asia, used for phenogram construction

River basins	Distribution of freshwater fish																			
Outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Annam	0	0	0	1	0	1	1	0	1	0	0	0	1	0	0	0	0	1	1	1	0
Upper Mekong River	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Mid-Mekong River	0	1	1	1	1	1	1	1	1	1	0	1	1	1	1	0	1	1	1	1	1
Lower Mekong River	0	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1
Chao Phraya	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
SE Thailand and SW Kampuchea	1	0	0	1	1	1	1	1	1	0	0	1	1	0	1	1	1	1	1	1	1
Salween	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1
Mae Khlong	1	1	1	1	1	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1
Malay Peninsula	1	1	0	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1
Sumatra	1	0	0	0	1	1	1	1	1	1	0	1	1	1	1	0	1	1	1	1	1
Borneo	1	1	0	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1
Java	1	0	0	0	1	1	1	1	1	1	0	1	1	1	1	0	1	1	1	1	1
Lantsangjiang	0	0	1	1	0	0	0	0	1	1	1	0	1	0	0	1	1	0	0	0	0
Red River	0	1	1	1	0	1	1	1	0	1	1	0	1	0	1	1	1	1	1	1	0
Upper Yangtze River	0	0	1	1	0	0	0	0	1	1	1	0	1	1	1	1	1	1	0	1	1
Lower Yangtze River	0	0	1	1	0	1	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1
Upper Pearl River	1	0	1	1	0	0	0	1	1	1	1	0	0	1	1	1	1	1	0	1	0
Lower Pearl River	0	0	1	1	0	1	0	0	1	0	0	0	0	1	1	1	1	1	0	1	0
Minjiang and Jiulongjiang	1	0	1	1	1	1	1	0	1	1	1	1	0	1	0	1	1	1	0	1	0

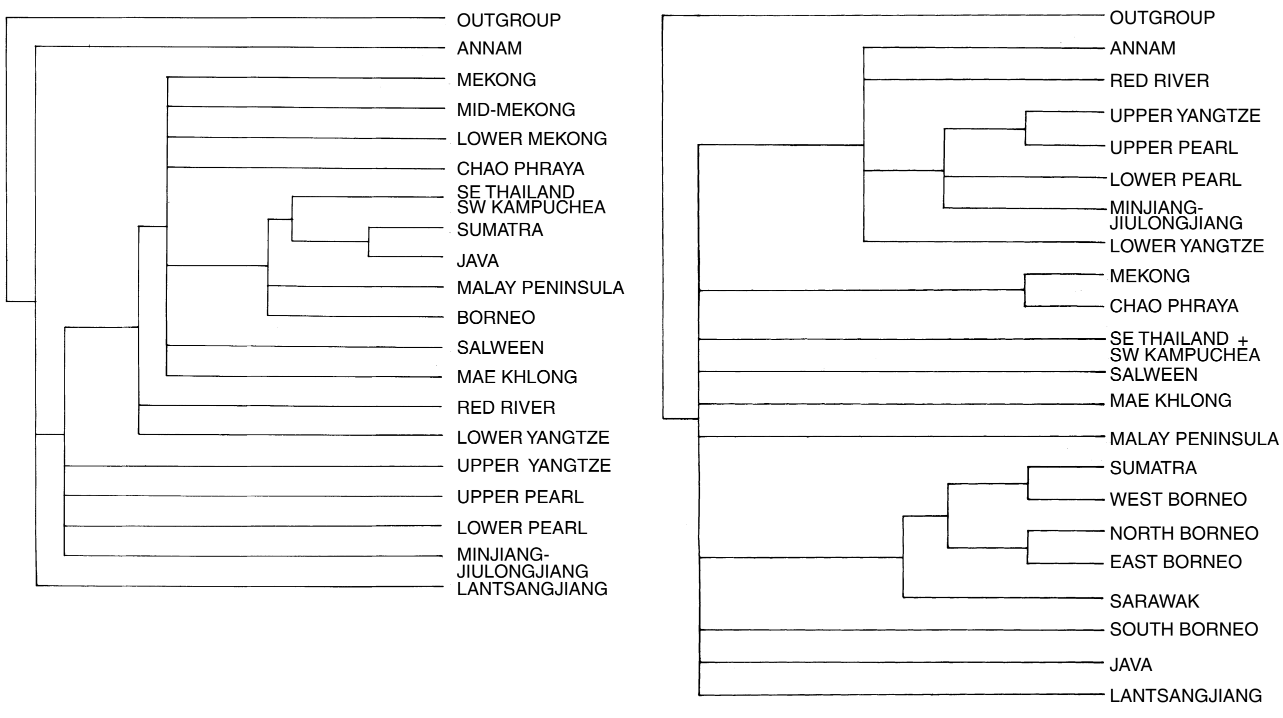

Figure 2 (a) Phenogram constructed based on common fish genera, showing groupings of related drainage river basins and divergence from a common origin (tree length = 51, CI = 0.41, RI = 0.66). (b) Phenogram reconstructed based on 163 cyprinid genera (tree length = 32, CI = 0.75, RI = 0.75).

RESULTS AND DISCUSSION

The fifty-one-length phenogram, which summarizes more than 100 trees (consistency index = 41%, retention index = 66%), shows three clades of river basins, of which the Sundaland grouping is the most recent (Fig. 2a). The out group provides the reference for comparison of the time of divergence on the basis of available palaeontological evidence. An outgroup is an extant taxonomic unit under comparison, an unit used as a reference to make corrections for unequal rates of evolution among the lineages under study. The unit is an operational taxonomic unit (OTU) (Li & Graur, 1991) for which we have external knowledge such as taxonomic or palaeontological information, clearly shows it had diverged from the common ancestor prior to all the other OTUs. The Chinese grouping is the oldest clade, but its Red River is as new as the Indochinese clade. The groupings into divisions and subdivisions are complementary to those reported (Kottelat, 1989), which largely used fish affinities in classifying the basins into four divisions (Annam, Salween, Mekong-Chao Phraya-Mae Khlong, Malay Peninsula-SE Thailand-SW Kampuchea). The phenogram implies that the Annam and Lantsangjiang basins are primitive and are closely linked to the four Chinese rivers. These basins constitute a sister-area starting from the upper Yangtze-Pearl Rivers to the Minjiang-Jiulongjiang. The Red and lower Yangtze Rivers are also closely related as they form a clade that is related to the Indochinese-Sundaland river basins. Similarly, coastal south-eastern Thailand and south-western Kampuchea (formerly Cambodia) form a group with the Sundic Islands that parallels the cluster formed by the Mekong-Chao Phraya-Salween-Mae Khlong basins. The second phenogram, which is thirty-two-length, summarizes six trees (consistency index = 75%, retention index = 75%) (Fig. 2b) and is similar to the previous phenogram except that the Annam and Chinese rivers are of the same age, forming the oldest clade.

The Annam and Lantsangjiang basins probably diverged from a common continent before the other drainage basins were formed. A different grouping of the Chinese drainage basins has been presented for the geological events to account for the distribution pattern of the fishes of south-eastern China (Chen & He, 2001). This explanation invokes the elevation of the Qinghai-Tibet plateau (Xu, 1981) and the model requires homogenous ecological conditions to prevail starting from the Himalayas to south-eastern China. Following the collision of the European and Indian tectonic plates in the early Tertiary, this plateau gradually rose up to divide the Mekong River, Yuanjiang and Hainan island from Yangtze and Pearl Rivers, as well as from the adjacent basins (Annam). Later, the Yangtze River separated from the Pearl River, and the Pearl River, in turn, split from these Chinese mainland rivers. Such geological events led to the configuration of the present river systems and distribution patterns of freshwater fishes. Accordingly, the Red River, Nanpangjiang and the Yangtze River, as well as the Annam district, should be grouped together (Banarescu, 1972). On the other hand, the relationship between the river systems and the common shared fish genera in six drainage basins in the Yunnan Province implicates two main groups (Chu, 1986): the upper Nanpangjiang-Yuanjiang rivers (which are more related to the upper Yangtze River) and upper Salween-Irrawaddy drainage basin (which pairs with the Lantsangjiang). This study's results suggest that the Chinese rivers and the Annam must be grouped together; however, the Salween basin shows little resemblance to the Lantsangjiang. The Lantsangjiang basin is a discrete entity having its own distinct fauna; the fauna is, however, allied with the Chinese and lower Mekong rivers, the links being supported by the high similarity of modern-day fish fauna (Appendices 1–3). The Lantsangjiang has a less diverse fauna that inhabit the waterways flowing through the mountainous Himalayan ecosystem, as exemplified by the presence of *Cyprinus*, *Garra* and *Onychostoma* spp. (Cyprinidae), besides the montane species of Balitoridae, Siluridae and Sisoridae. The Himalayan orogenic movement, the ancient plate separated and subsided as well as the special habitat requirements led to the speciation of the sparse montane population; depending on the ecological opportunities, environmental conditions and the appearance of new genetically engendered features, speciation should occur at a variable rate (Cox & Moore, 1993).

The Indochinese Peninsula is of Gondwanan origin as it was formed through the collision of tectonic plates during the lower Mesozoic period (Workman, 1975). Continental East Asia (which includes the Indochinese Peninsula) in the post-Oligocene age (Gregory & Gregory, 1923; Gregory, 1925) had the Salween and upper Mekong Rivers connected to separate tributaries of the Chao Phraya, but unfortunately, the three rivers now retain little of their original individual fauna (Kottelat, 1989; Rainboth, 1996; Doi, 1997). This study's findings suggest that the Salween basin is closely allied to the Mae Khlong and that the Mekong River is also closely related to the Chao Phraya. These sister-area connections most likely resulted from the capture of lower-order streams than from the capture of the principal rivers, as reflected by the composition of the fish assemblages; it is noted that only a small portion (36%) of the fauna of Salween and Mae Khlong rivers are shared, one pair being the *Poropuntius hampaloides* Vinciguerra and *P. vernayi* Norman. The south-eastern Thailand-south-western Kampuchea grouping appears to be the most recent; it is a coastal area bordered by the Gulf of Thailand, whose fauna had been affected by changes in the sea level of the Sunda Shelf (Biswas, 1973).

The Sundaland river basins evolved during and after the Pleistocene as their ecological preferences and modes of dispersal of lifeforms are almost identical to those of modern-day system. The Southeast Asian freshwater fishes have provided insights into the relationships between the Pleistocene sea-level changes on the Sunda Shelf and the ichthyological responses to the historical changes (Dodson *et al.*, 1995). The drop in the sea level that halted the dispersal (Molengraaff, 1921; Beaufort, 1951) and formation of the river basins have been hypothesized as the principal factor governing the distribution motif in the Sundaland (Rainboth, 1996). There after the Sunda seas themselves would have prevented any exchange.

The Malay Peninsula, which is approximately midway between the Sundaland and continental Indochina, has high diversity whose community is a mix of Indochinese and Sundaic fauna that is predominantly Cyprinidae (approximately 116 genera; Appendix 3). More than 75% is of Sundaic origin that shares some traits with those of Borneo, Sumatra and Java; the *Oxygaster* species is the indicator species found in the Malay Peninsula but not in Indochina. The eastern portion of this region has a fish community that is affiliated with those of south-eastern Thailand and south-western Kampuchea; for example, they share *Paralaubuca*, *Probarbus* and *Sikukia* spp. Such parallels can be explained by other freshwater fish families (Kottelat, 1989; Yap, 1999) including Siluridae (*Silurichthys* sp.), Belontidae (*Belontia*, *Parosphromenus* and *Sphaerichthys* spp.), Clariidae (*Encheloclarias* sp.) and Balitoridae (*Vaillantella* sp.), attributing to the interconnected drainage of the Sunda Shelf during the Pleistocene glaciations (Molengraaff & Weber, 1919; Emmel & Curray, 1982). This study's results reveal that Sumatra-Java is closely allied to south-eastern Thailand-south-western Kampuchea, the Malay Peninsula and Borneo. On the basis of these subdivisions, the Sundaic islands are re-grouped into four pairs: the Malay Peninsula-north Sumatra, central Sumatra-west Borneo, north Borneo-east Borneo-Sarawak and south Borneo-Java island. The geographical pairing of basins is also corroborated by their ichthyofaunal communities. For example, for the Malay Peninsula-north Sumatra pair, the fauna of Perak River (Yap *et al.*, 1988) and that of the Sumatran rivers are similar, whereas for the central Sumatra-west Borneo pair, the fauna of rivers in Sumatra parallels that of the Kapuas River of west Borneo (Rainboth, 1991). Such a pattern of faunal groups in the Borneon subregions has also been noted in the pioneering zoogeographical study on Sundaland (Molengraaff & Weber, 1919). Java is a relatively small but still a landbridge island connected with the large islands (Sumatra and Borneo) during the low sea level periods of the Pleistocene. The landbridge island with Borneo and its close proximity (about 100 km) is also indicated by the closely related avifaunal community (Thiollay, 1998).

Fossils found in Guangdong Province and Sumatra (Wang *et al.*, 1981) support the existence of Cyprinidae and Bagridae in the early Cenozoic age. The DNA sequences of Chinese (Xiao *et al.*, 2001) and South-east Asian (Dodson *et al.*, 1995) freshwater fishes are discussed in terms of biogeography and evolution, and to date, similar genetic information involving the conservative DNA sequences are needed and useful in revealing the evolutionary aspect of Southeast-East Asian ichthyofaunal geography in an objective manner.

ACKNOWLEDGMENTS

I am grateful to Prof. Liu Jiankang, Emeritius Director of the Institute of Hydrobiology, Chinese Academy of Sciences, for the use of the Institute's library facilities, Dr Zhang Ea for assistance with the Chinese documents and the *Third World Academy of Sciences* for a travel grant to China, as well as to Associate Professor Ng S. W for some stimulating discussion.

REFERENCES

Audley-Charles, M.G. (1983) Reconstruction of eastern Gondwanaland. *Nature*, **306**, 48–50.

Banarescu, P. (1972) The zoogeographical position of the east Asian freshwater fish fauna. *Review on Roumanian Biology, Zoological Section*, **17**, 315–323.

Banarescu, P. & Nalbant, T.T. (1982) New data about the Malayan–Indochinese affinities of the aquatic fauna of Western Ghat, South India. *Review on Roumanian Biology, Biology of Animal*, **27**, 23–27.

Beaufort, L.F. De (1951) *Zoogeography of the land and inland waters*. 208 pp. Sidgwick and Jackson, London.

Biswas, B. (1973) Quaternary changes in the sea-level in the South China Sea. *Bulletin of Geological Society, Malaysia*, **6**, 229–256.

Chen, Y. & He, S. (2001) Freshwater fishes distribution in Taiwan and continent of China and its biogeographical significance. *Progress in Natural Science*, **11**, 1–6.

Chu, Y. (1984) *The fishes of Fujian province*, Part I. 523 pp. Fujian Science and Technology Press, Fujian, China (Chinese).

Chu, Y. (1985) *The fishes of Fujian province*, Part II, 700 pp. Fujian Science and Technology Press, Fujian, China (Chinese).

Chu, X.L. (1986) Ichthyofauna and its geographical subdivisions in Yunnan, China. *Indo-Pacific fish biology* (eds T. Uyeno, *et al.*), pp. 471–476. *Proceeding of Second International Conference on Indo-Pacific Fishes.*

Cox, C.B. & Moore, P.D. (1993) *Biogeography: an ecological and evolutionary approach*, 326 pp. Blackwell Science Ltd, Cambridge, UK.

Darlington, P.J. (1957) *Zoogeography: the geographical distribution of animals*, 675 pp. Wiley, New York.

Dodson, J.J., Colombani, F. & Ng, P.K.L. (1995) Phylogeographic structure in mitochondrial DNA of a Southeast Asian fresh water fish, *Hemibagrus nemurus* (Siloroidei; Bagridae) and Pleistocene sea-level changes on the Sunda shelf. *Molecular Ecology*, **4**, 331–346.

Doi, A. (1997) A review of taxonomic studies of cypriniform fishes in Southeast Asia. *Japanese Journal of Ichthyology*, **44**, 1–33.

Emmel, F.J. & Curray, J.R. (1982) A submerged late Pleistocene delta and other features related to sea-level changes in the Malacca Strait. *Marine Geology*, **47**, 197–216.

Farris, J.S. (1988) *Hennig86 Reference*, Version 1.5. Mimeo, New York.

Gregory, J.W. (1925) The evolution of the river system of south-eastern Asia. *Scottish Geographical Journal*, **41**, 129–141.

Gregory, J.W. & Gregory, C.J. (1923) The alps of Chinese Tibet and their geographical relations. *Geographical Journal*, **61**, 153–179, 5 plates.

Kottelat, M. (1989) Zoogeography of the fishes from Indochinese inland waters with an annotated checklist. *Bulletin Zoologisch Musuem. Universiteit van Amsterdam*, **12**, 1–54.

Li, W.H. & Graur, D. (1991) *Fundamentals of molecular evolution*, p. 113. Sinauer Associates Inc. Publishers, Sunderland, MA.

Menon, A.G.K. (1987) *The fauna of India and the adjacent countries. Pisces, IV Teleostei-Cobitoidea, Part 1, Homalopteridae*, x + 259 pp, 16 plates. Zoological Survey of India, Calcutta.

Molengraaff, G.A.F. (1921) Modern deep-sea research in the East Indian *Archipelago Geogeographical Journal*, **59**, 95–121.

Molengraaff, G.A.F. & Weber, M. (1919) On the relation between the Pleistocene glacial period and the origin of the Sunda Sea (Java and South China-Sea), and its influence on the distribution of coral reefs and on the land and freshwater fauna. *Proc. K. A. Kad. Wetens Amsterdam*, **23**, 395–439, 2 plates.
Myers, G.S. (1951) Fresh-water fishes and East Indian zoogeography. *Stanford Ichthyological Bulletin*, **4**, 11–21.
Rainboth, W.J. (1991) Cyprinid fishes of Southeast Asia. *Cyprinid fishes: systematics, biology and exploitation* (eds I.J. Winfield and J.S. Nelson), pp. 156–210. Chapman & Hall, London.
Rainboth, W.J. (1996) *FAO species identification field guide for fishery purposes. Fishes of the Cambodian Mekong*, FAO, Rome.
Thiollay, J.M. (1998) Distribution patterns and insular biogeography of South Asian raptor communities. *Journal of Biogeography*, **25**, 57–72.
Wang, J.K., Li, G.F. & Wang, J.S. (1981) The early Tertiary fossil fishes from Sanshui and its adjacent basin, Guangdong. *Palaeontology of Sinica*, **160** (New Series C, 22), 1–90, 10 plates (Chinese, English summary).
Watrous, L.E. & Wheeler, Q.D. (1981) The out-group comparison method of character analysis. *Systematic Zoology*, **30**, 1–11.
Workman, D.R. (1975) Tectonic evolution of Indochina. *Journal of Geological Society, Thailand*, **1**, 3–19.
Xiao, W., Zhang, Y. & Liu, H. (2001) Molecular systematics of Xenocyprinae (Teleostei; Cyprinidae): Taxonomy, biogeography, and coevolution of a special group restricted in east Asia. *Molecular Phylogenetics and Evolution*, **18**, 163–173.
Xu, R. (1981) Vegetational changes in the past and the uplift of the Qinghai-Xizang Plateau. *Geological and ecological studies of Qinghai-Xizang plateau* (ed. D.S. Liu), pp. 139–144. Science Press, Beijing.
Yap, S.Y. (1999) Riverine and lacustrine fish communities in Southeast Asia. *Fish and fisheries of lakes and reservoirs in Southeast Asia and Africa* (eds W.L.T. van Densen and M.J. Morris), pp. 13–27. Westbury Publishing, Otley, UK.
Yap, S.Y., Ong, H.T. & Abdul Rahmid Kidam (1988) Formulation of aquaculture development at an ox-bow lake in Malaysia, I: Technical evaluations of site suitability. *Aquacultural Engineering*, **7**, 245–261.
Zakaria-Ismail, M. (1994) Zoogeography and biodiversity of the freshwater fishes of Southeast Asia. *Hydrobiologia*, **285**, 41–48.
Zhang, E., Liu, H. & He, C. (1996) Study of the fish fauna in Northern Jiangxi Province, China. *Chinese Journal of Zoology*, **31**, 3–12. (Chinese).

BIOSKETCH

Siaw-Yang Yap is an ecologist who has published on the ecology and biogeography of freshwater fish. She is now re-examining the biogeographical aspect from a combined ecological and evolutionary perspective.

Appendix 1 Distribution of fish genera (mainly cypriniformes, siluriformes and perciformes) in nineteen river basins of Southeast-East Asia. The river basins are: 1 Annam, 2 upper Mekong River, 3 mid-Mekong River, 4 lower Mekong River, 5 Chao Phraya, 6 southeastern Thailand and southwestern Kampuchea, 7 Salween, 8 Mae Khlong, 9 Malay Peninsula, 10 Sumatra, 11 Borneo, 12 Java, 13 Lantsangjiang, 14 Red River, 15 upper Yangtze River, 16 lower Yangtze River, 17 upper Pearl River, 18 lower Pearl River and 19 Minjiang-Jiulongjiang

Family/Genera		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Cyprinidae	*Barbodes*		+			+	+		+	+	+	+	+					+		+
	Barilius		+	+	+	+		+	+	+		+			+					
	Cirrhinus		+	+	+	+		+	+					+	+	+	+	+	+	+
	Garra	+	+	+	+	+	+	+	+	+		+		+	+	+	+	+	+	+
	Mystacoleucus	+	+	+	+	+	+	+	+	+	+	+							+	
	Osteochilus	+	+	+	+	+	+	+	+	+	+	+	+		+		+		+	+
	Puntius	+	+	+	+	+	+	+	+	+	+	+	+		+		+			+
	Rasbora		+	+	+	+	+	+	+	+	+	+	+		+		+	+		
	Tor	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+	+	+	+
Cobitidae	*Botia*		+	+	+	+		+	+	+	+	+	+	+	+	+	+	+		+
	Hemimyzon		+			+		+						+	+	+		+		+
	Homaloptera		+	+	+	+	+	+		+	+	+	+							+
	Schistura	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+			
Bagridae	*Leiocassis*		+	+	+	+			+	+	+	+	+			+	+	+	+	+
	Mystus		+	+	+	+	+	+	+	+	+	+	+		+	+	+	+	+	
Siluridae	*Silurus*		+		+	+	+	+	+	+		+		+	+	+	+	+	+	+
Sisoridae	*Glyptothorax*		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Clariidae	*Clarias*	+	+	+	+	+	+	+	+	+	+	+	+		+	+	+	+	+	+
Anabantidae	*Anabas*	+	+	+	+	+	+	+	+	+	+	+	+		+		+			
Channidae	*Channa*	+	+	+	+	+	+	+	+	+	+	+	+		+	+	+	+	+	+
Notopteridae	*Notopterus*		+	+	+	+	+	+	+	+	+	+	+			+	+			

Appendix 2 The distribution of cyprinid fishes in twenty-one river basins. The river basins are: 1 Annam, 2 Mekong River, 3 Chao Phraya, 4 southeastern Thailand and southwestern Kampuchea, 5 Salween, 6 Mae Khlong, 7 Malay Peninsula, 8 Sumatra, 9 west Borneo, 10 Sarawak, 11, north Borneo, 12 east Borneo, 13 south Borneo, 14 Java, 15 Lantsangjiang, 16 Red River, 17 upper Yangtze River, 18 lower Yangtze River, 19 upper Pearl River, 20 lower Pearl River and 21 Minjiang and Jiulongjiang

Genera	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Aaptosyax		+																			
Acheilognathus		+															+	+	+	+	+
Albulichthys		+	+			+		+	+				+								
Amblypharyngodon		+	+		+																
Amblyhynicthys		+	+				+	+	+				+								
Aspidoparia					+																
Balantiocheilos		+	+				+	+	+			+									
Bangana (= *Sinilabeo*)		+	+		+											+	+	+	+	+	
Barbichthys		+	+			+	+	+				+	+	+							
Barbodes		+	+	+		+	+	+	+	+	+	+	+	+					+		+
Barbus		+																			+
Barilius		+	+		+		+		+							+					
Boraras		+					+	+	+				+								
Brachydanio		+		+	+	+	+	+													
Catlocarpio		+	+																		
Chagnius					+																
Chanodichthys	+																				
Chela	+	+	+	+	+	+	+	+													
Cirrhinus		+	+		+	+									+	+	+		+	+	+
Cosmochilus		+	+						+	+											
Crossocheilus		+	+		+		+	+	+			+		+						+	+
Cyclocheilichthys	+	+	+	+		+	+	+	+	+		+	+	+		+					
Cyprinion		+	+		+											+					
Cyprinus		+			+										+	+	+	+	+	+	+
Danio		+	+		+		+														
Discherodontus		+	+			+															+
Eirmotus							+		+				+								
Epalzeorhynchos		+	+		+		+	+	+				+								
Esomus		+	+	+	+	+	+														
Garra		+	+	+	+	+	+		+	+	+	+			+	+	+	+	+	+	+
Hampala		+	+	+	+	+	+	+	+	+	+	+		+							
Hemiculter	+															+	+	+	+	+	+
Henicorhynchus		+	+																		
Hypsibarbus	+	+	+	+	+	+	+	+													
Inlecypris					+																
Kalimantania									+					+							
Labeo		+	+		+	+	+	+	+					+							+
Labiobarbus		+	+		+	+	+	+	+	+	+	+	+	+							
Leptobarbus	+	+	+	+		+	+		+		+	+	+								
Lobocheilos		+	+			+	+	+	+		+	+		+							
Longiculter			+																		
Luciosoma		+	+			+	+	+	+	+	+	+		+							
Macrochirichthys		+	+			+	+	+	+	+		+	+	+							
Mekongina		+																			
Microrasbora					+																
Mystacoleucus		+	+	+	+	+	+	+	+	+				+							+
Nematabramis										+	+	+									
Neobarynotus		+					+	+	+				+								
Neolissochilus		+			+		+	+						+							
Onychostoma	+	+													+	+	+	+			+
Oreichthys			+	+	+		+														
Osteobrama					+																
Osteochilus	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+		+		+	+
Oxygaster							+	+	+	+				+							
Parabarilius		+																			
Parachela		+	+				+	+	+	+	+	+									

Appendix 2 *continued*

Genera	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Paracrossochilus									+	+	+	+									
Paralaubuca		+	+				+														
Paraspnibarbus	+																				
Pectenocypris								+	+				+								
Poropuntius	+	+	+	+	+	+	+	+													
Probarbus		+	+			+	+														
Puntioplites		+	+			+	+	+	+	+		+	+	+							
Puntius	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+		+			+
Raiamas		+	+		+	+	+														
Rasbora		+	+	+	+	+	+	+	+	+	+	+	+	+		+		+	+		
Rasborichthys								+	+				+								
Rhodeus	+															+	+	+	+	+	+
Rohteichthys								+	+				+								
Salmostoma					+																
Sawbwa					+																
Schismatorhynchos								+	+		+	+									
Scaphognathops		+																			
Sikukia		+	+				+														
Thryssocypris		+							+												
Thynnichthys		+	+			+	+	+	+			+									
Tor	+	+	+		+	+	+	+	+	+		+		+	+		+	+	+	+	+
Opsariichthys		+														+	+	+	+	+	+
Abbottina																+	+	+	+	+	+
Acanthobrama																		+			
Acanthorhodeus															+	+		+			+
Acrossocheilus															+	+	+	+	+	+	+
Anabarilius																	+		+		
Ancherythroculter																	+				
Aphyocypris																	+	+	+		+
Aristichthys																	+	+		+	+
Atrilinea																		+		+	
Carassioides																		+			
Carassius																	+	+	+	+	+
Coreius																	+	+			
Ctenopharyngodon																	+	+		+	+
Culter																+	+	+			+
Diptychus																	+				
Discogobio																	+	+	+	+	
Distoechodon																	+	+		+	+
Elopichthys																+	+	+	+	+	+
Erythroculter																+	+		+	+	+
Folifer (= *Tor*)																+		+			+
Gnathopogon																+	+	+			+
Gobiobotia																+	+	+	+	+	+
Gymnocypris																	+				
Hemibarbus																+	+	+	+	+	+
Hemiculterella																	+	+		+	
Huigobio																	+			+	+
Hypophthalmichthys																	+	+		+	+
Ischikauia																+		+			
Luciobrama																+	+	+	+	+	+
Luciocyprinus															+	+		+	+	+	
Megalobrama																+	+	+		+	+
Microphysogobio																+	+	+		+	+
Mylopharyngodon																+	+	+		+	+
Nicholsicypris																+		+		+	
Ochetobius																+	+	+	+	+	+
Parabramis																	+	+		+	+

Appendix 2 *continued*

Genera	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Paracanthobrama																		+		+	
Paracheilognathus																	+	+		+	+
Parapelecus																+	+				+
Pararhodeus																+	+				
Parasinilabeo																		+		+	
Parator																+		+			
Parazacco																		+		+	
Percocypris															+	+	+		+		
Plagiognathops																+		+			
Platysmacheilus																	+	+		+	
Procypris																+	+		+		
Pseudogobio																		+		+	+
Pseudohemiculter																		+	+	+	+
Pseudolaubuca																	+	+		+	+
Pseudoperilampus																+		+			+
Pseudorasbora																+	+	+	+	+	+
Ptychidio																		+	+	+	
Racoma															+			+			
Rasborinus																+		+	+	+	+
Rectoris																+	+	+		+	
Rhinogobio																	+	+			+
Rhynchocypris																+					
Sarcocheilichthys																+	+	+	+	+	+
Saurogobio																+	+	+	+	+	+
Schizopygopsis																	+				
Schizothorax															+		+		+		
Semilabeo																+	+		+	+	
Sinibrama																+	+	+	+	+	+
Sinocrossocheilus																	+		+		
Sinocyclocheilus																	+		+	+	
Spinibarbus1																+	+	+	+	+	+
Spinibarbus'2																+					
Squaliobarbus																+	+	+	+	+	+
Toxabramis																+	+	+	+	+	
Typhlobarbus																	+		+		
Xenocypris																+	+	+	+	+	+
Yaoshanicus																		+		+	
Zacco																+	+	+	+	+	+
Belligobio																	+	+			+
Cultrichthys																	+	+		+	+
Gobiocypris																	+				
Gymnodiptychus																	+				
Herzensteinia																	+				
Phoxinus																	+	+			+
Pseudobrama																	+	+			
Capoeta		+															+		+	+	+
Squalidus																	+	+	+	+	+
Tanichthys																				+	
Varicorhinus																	+	+	+	+	+

Appendix 3 Numbers of cyprinid genera in twenty-one river basins of Southeast-East Asia. The river basins are numbered and defined similarly, as in Appendix 2

Genera	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Aaptosyax		1																			
Acheilognathus		1															7	8	1	4	4
Albulichthys		1	1			1		1	1				1								
Amblypharyngodon		1	1		1																
Amblyhynicthys		1	1				1	1	1				1								
Aspidoparia					1																
Balantiocheilos		1	1				1	1	1			1									
Bangana (= *Sinilabeo*)		1	1		2											1	1	1	4	2	
Barbichthys		1	1			1	1	1				1	1	1							
Barbodes		5	5	1		2	4	3	3	3	3	5	1	3	7				2		1
Barbus		1																			1
Barilius		2	3		1		2		1							1					
Boraras		1					1	2	1				2								
Brachydanio		1		1	5	1	2	1													
Catlocarpio		1	1																		
Chagnius					1																
Chanodichthys	1																				
Chela	1	2	2	1	1	1	2	2													
Cirrhinus		5	3		1	1									1	1	1		1	1	1
Cosmochilus		1	1						1	1											
Crossocheilus		3	3		1		5	5	2			3		2						1	1
Cyclocheilichthys	1	6	5	2		2	4	4	6	2		3	2	3		1					
Cyprinion		1	1		1											1					
Cyprinus		1			1										5	2	4	1	10	3	1
Danio		2	1		4		2														
Discherodontus		2	2			1															1
Eirmotus							1		1				1								
Epalzeorhynchos		2	2		1		1	1	1				1								
Esomus		2	2	2	2	1	2														
Garra		4	2	1	4	1	1		1	1	1	1			2	1	1	1	1	1	1
Hampala		2	1	1	1	1	1	2	3	2	1	2		1							
Hemiculter	2															2	3	2	1	1	2
Henicorhynchus		2	1																		
Hypsibarbus	3	4	3	1	1	4	5	2													
Inlecypris					1																
Kalimantania									1					1							
Labeo		2	4		5	1	1	3	1					2							1
Labiobarbus		2	2		2	1	4	2	3	1	2	3	2	1							
Leptobarbus	1	1	1	1		1	1		2		1	2	1								
Lobocheilos		8	8			1	5	3	3		1	4		4							
Longiculter			1																		
Luciosoma		1	1			2	2	3	3	1	1	1		1							
Macrochirichthys		1	1			1	1	1	1	1		1	1	1					1	1	
Mekongina		1																			
Microrasbora					2																
Mystacoleucus		3	1	1	1	2	2	2	1	1				1							1
Nematabramis										1	2	3									
Neobarynotus		1					1	1	1				1								
Neolissochilus		1			7		5	3						1							
Onychostoma	1	1													1	1	4	1		1	1
Oreichthys			1	1	1		1														
Osteobrama					3																
Osteochilus	3	5	6	3	1	5	9	13	14	8	4	6	6	4		1		1		1	1
Oxygaster							1	1	1	1				1							
Parabarilius		1																			
Parachela		4	3				4	3	3	1	1	2									
Paracrossochilus									1	2	1	1									
Paralaubuca		5	4				2														

Appendix 3 *continued*

Genera	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Paraspnibarbus	1																				
Pectenocypris								1	1				1								
Poropuntius	1	4	4	1	2	2	3	2													
Probarbus		3	1			1	1														
Puntioplites		3	1			1	2	2	1	2		2	1	1							
Puntius	2	8	6	5	7	4	9	8	12	6	3	3	5	5		1		1			1
Raiamas		1	1		1	1	1														
Rasbora		11	8	3	1	7	21	22	21	10	6	2	5	3		1		1	1		
Rasborichthys								1	1				1								
Rhodeus	1															2	3	4	2	4	3
Rohteichthys								1	1				1								
Salmostoma					1																
Sawbwa					1																
Schismatorhynchos								1	1		1	1									
Scaphognathops		2																			
Sikukia		2	2				1														
Thryssocypris		1							2												
Thynnichthys		1	1			1	1	2	2			1									
Tor	1	1	1		3	1	2	2	1	2		2		2	3		1	1	2	2	1
Opsariichthys		1														1	1	1	1	1	1
Abbottina																1	2	1	1	1	1
Acanthobrama																		1			
Acanthorhodeus	1														1	1		1			1
Acrossocheilus															1	1	2	3	4	7	6
Anabarilius																	12		9		
Ancherythroculter																	3				
Aphyocypris																	1	1	1		1
Aristichthys																	1	1		1	1
Atrilinea																		1		1	
Carassioides																		2			
Carassius																	2	1	2	2	1
Coreius																	2	1			
Ctenopharyngodon																	1	1		1	1
Culter																1	5	5			2
Diptychus																	3				
Discogobio																	1	1	3	1	
Distoechodon																	1	1		1	1
Elopichthys																1	1	1	1	1	1
Erythroculter																1	1		1	5	1
Folifer (= *Tor*)																1		1			1
Gnathopogon																1	2	1			2
Gobiobotia																1	6	4	1	3	2
Gymnocypris																	1				
Hemibarbus																1	1	3	1	4	2
Hemiculterella																	1	2		1	
Huigobio																	1			2	1
Hypophthalmichthys																	1	1		1	1
Ischikauia																1		1			
Luciobrama																1	1	1	1	1	1
Luciocyprinus															1	1		1	1	1	
Megalobrama																1	2	2		1	1
Microphysogobio																1	1	4		5	1
Mylopharyngodon																1	1	1		1	1
Nicholsicypris																1		1		1	
Ochetobius																1	1	1	1	1	1
Parabramis																	1	1		1	1
Paracanthobrama																		1		1	
Paracheilognathus																	1	2		1	1

Appendix 3 *continued*

Genera	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Parapelecus																1	1				1
Pararhodeus																1	1				
Parasinilabeo																		1		1	
Parator																1		1			
Parazacco																		1		1	
Percocypris		1													1	1	2		1		
Plagiognathops																1		1			
Platysmacheilus																	1	2		1	
Procypris																1	1		1		
Pseudogobio																		1		2	1
Pseudohemiculter																		1	2	2	1
Pseudolaubuca																	2	2		2	1
Pseudoperilampus																1		1			1
Pseudorasbora																2	1	2	1	2	1
Ptychidio																		1	1	1	
Racoma															1			1			
Rasborinus																1		1	1	2	1
Rectoris																1	1	1		1	
Rhinogobio																	3	2			1
Rhynchocypris																1					
Sarcocheilichthys																1	3	4	1	4	4
Saurogobio																1	3	5	1	1	1
Schizopygopsis																	4				
Schizothorax															5		17		1		
Semilabeo																1	2		2	3	
Sinibrama																1	2	1	1	2	1
Sinocrossocheilus																	1		1		
Sinocyclocheilus																	2		4	1	
Spinibarbus 1																1	2	2	4	2	1
Spinibarbus' 2																1					
Squaliobarbus																1	1	1	1	1	1
Toxabramis																1	1	1	1	2	
Typhlobarbus																	1		1		
Xenocypris																2	6	3	1	3	2
Yaoshanicus																		1		1	
Zacco																1	2	1	1	1	1
Belligobio																	2	1			1
Cultrichthys																	1	1		1	1
Gobiocypris																	1				
Gymnodiptychus																	2				
Herzensteinia																	1				
Phoxinus																	1	1			1
Pseudobrama																	1	1			
Capoeta		1															1		1	1	1
Squalidus																	3	2	1	3	2
Tanichthys																				1	
Varicorhinus																	1	6	2	8	1

These values were used to indicate the presence of cyprinids as scored in Appendix 2.
The scores were then converted into binary character (0 or 1) in a matrix.