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Geographic Distribution of Primary Freshwater Fishes in Four Principal Areas of Southeast Asia

by

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Introduction

Southeast Asia is one of the world's centers of abundance of freshwater fishes. The freshwater fish fauna of the region is characterized above all by the predominance of the Cyprinidae (carps and minnows) and their allies. The fauna is rather uniform in its composition throughout the region except for the Song Koi (=Song Hong) drainage, where the fish fauna closely resembles that of southern China including Hainan (Chevey and Lemasson, 1937), and there is a sharp distributional boundary along the Song Koi-Mekong watershed (Bănărescu, 1972). The fauna of Southeast Asia shares many genera with the fauna of India, and the fact led Hora (1937, 1944, 1949) and Menon (1953, 1955) to conclude that the Indian freshwater fish fauna in the main originated in and migrated from southeastern part of Asia.

There are marked affinities between the faunas of the Indochinese Peninsula and the Greater Sunda Islands and between the islands in spite of the geographic isolation of these places, which has attracted the attention of many ichthyologists and zoogeographists, such as Krempf and Chevey (1936), de Beaufort (1951) and Darlington (1957). They all explain the affinities by land connections existed during geological times between the mainland and the islands and between the islands, referring to the Sundaland.

The general and fundamental characters of the freshwater fish fauna of Southeast Asia are thus rather clearly delineated, but the detailed structure of local fauna of each subarea composing the region and the origin and dispersal of the fauna still require further elucidation on an extensive basis.

The present paper deals with the primary freshwater fish fauna in four principal areas of Southeast Asia, i.e. the Irrawaddy–Salwin basins, the Greater Sunda Islands, the Mekong-Chao Phya basins, and the Song Koi basin, in order to clarify and compare characteristics of the fauna of each the area and investigate the origin and dispersal of freshwater fishes in the

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region. By Southeast Asia I mean the area from Burma and Thailand east to North Vietnam and south to Indonesia. The Philippine Archipelago is included, but Celebes and New Guinea are not. The Sunda and the Mekong-Chao Phya areas are regarded as constituting together a faunal district, which is called in this paper Indosinian district. The Malayan Peninsula, though not dealt with here, is included in the district.

Arguments in this paper are restricted to primary-division freshwater fishes according to the ecological classification by Myers (1938), that is, fishes strictly confined to freshwater, and those of the secondary division and the so-called vicarious freshwater fishes, or fishes of strict freshwater genera derived from primary marine families, are precluded. The geographic ranges of fishes are based primarily on Day (1878) and Tint Hlaing (1971) for Burmese fishes, Weber and de Beaufort (1911–1962) for Sunda fishes, Smith (1945) and Taki (1974, 1975) for Mekong-Chao Phya fishes, and Chevey and Lemasson (1937) for Song Koi fishes. The Cypriniformes and Siluriformes are regarded as distinct groups of order rank. The subdivision of the Cyprinidae and of the Cobitidae is that of Bănărescu (1968, 1972).

I Review of primary freshwater fishes in the four principal areas

So far as I am aware, there are 714 species falling into 175 primary freshwater genera known from the four principal areas. Summary of geographic distribution of these fishes is presented in Table 1.

Fishes belonging to the order Cypriniformes form 63% of total fishes occurring in the areas in terms of number of genera and 72% in terms of number of species. The Siluriformes (catfishes), another component of the superorder Ostaryophysi, are moderately rich in the areas, forming 25% in number of genera and 21% in that of species. The remainders are members of three orders, Osteoglossiformes, Perciformes and Mastacembeliformes. While the Osteoglossiformes are archaic teleosteans, the other two belong to the much more advanced superorder Actinopterygii (spiny-rayed fishes). These non-ostaryophysans are also well represented in the study area.

According to the present geographic range, all the genera in the study area can be classified into several groups, viz. those occurring mainly in India, those distributed evenly in India and main part of Southeast Asia, especially the Indosinian district, those having main range in the Indosinian district, those found chiefly in Chinese freshwaters, and those widely spread from Africa or West Asia to China or East Asia. They are termed in this paper Indian element, Indo-Indosinian element, Indosinian element, Chinese element, and Widespread element, respectively. Table 2 shows the distributional classification of all Southeast Asian genera. Some of the Indo-Indosinian and Indosinian genera extend their range eastward to southern China. Outlines of the distribution of Southeast Asian freshwater fishes are as follows:

Table 1 List of primary freshwater fish orders and families found in the four principal areas of Southeast Asia, with number of genera and species in each category. Number of genera is presented first followed in parentheses by that of species. Abbreviations: IS, Irrawaddy-Salwin basins; SI, Greater Sunda Islands; MC, Mekong-Chao Phya basins; SK, Song Koi (Song Hong) basin.

Classification	Number of genera and species				
	IS	SI	MC	SK	Total area
1. Osteoglossiformes	1(2)	2(4)	2(4)		2(4)
Osteoglossidae		1(1)	1(1)		1(1)
Notopteridae	1(2)	1(3)	1(3)		1(3)
2. Cypriniformes	33(94)	49(201)	63(237)	37(60)	111(510)
Cyprinidae	25(74)	34(156)	52(195)	31(53)	85(410)
Gyrinocheilidae		1(1)	1(1)		1(1)
Homalopteridae	2(5)	7(25)	3(7)	2(2)	11(38)
Cobitidae	6(15)	7(19)	7(34)	4(5)	14(62)
3. Siluriformes	16(34)	27(84)	23(69)	8 (10)	43(149)
Siluridae	2(4)	8(23)	7(18)	1(1)	9(32)
Clariidae	1(1)	3(6)	1(3)	1(1)	3(8)
Pangasiidae	3(7)	4(12)	6(21)		10(31)
Amblycipitidae	1(1)	1(1)			1(1)
Sisoridae	3(5)	3(6)	3(7)	3(3)	6(17)
Bagridae	3(13)	4(28)	4(15)	2(4)	8(46)
Chacidae	1(1)	1(1)			1(2)
Cranoglanididae				1(1)	1(1)
Olyridae	1(1)				1(1)
Akysidae		3(7)	1(4)		3(9)
Heteropneustidae	1(1)		1(1)		1(1)
4. Perciformes	10(15)	13(25)	10(20)	3(5)	16(36)
Channidae	1(5)	1(9)	1(7)	1(3)	1(15)
Anabantidae	1(1)	1(1)	1(1)	1(1)	1(1)
Osphronemidae	1(1)	1(1)	1(1)		1(1)
Helostomidae		1(1)	1(1)		1(1)
Belontiidae	4(5)	6(10)	4(8)	1(1)	8(14)
Luciocephalidae		1(1)			1(1)
Nandidae	1(1)	1(1)	1(1)		1(1)
Pristolepidae	1(1)	1(1)	1(1)		1(1)
Badidae	1(1)				1(1)
5. Mastacembeliformes	3(7)	2(7)	2(7)	1(1)	3(14)
Mastacembelidae	2(6)	2(7)	2(7)	1(1)	2(13)
Chaudhriidae	1(1)				1(1)
Total Ostaryophysi (2+3)	49(128)	76(285)	86(306)	45(70)	154(660)
Total non-Ostaryophysi (1+4+5)	14(24)	17(36)	14(31)	4(6)	21(54)
Total primary freshwater fish	63(152)	93(321)	100(337)	49(76)	175(714)

1. Ostaryophysans

(1) Cypriniformes

This order of carps and loaches is represented in the study area by four families: Cyprinidae, Gyrinocheilidae, Homalopteridae (including Gastromyzonidae as subfamily), and Cobitidae.

Compared with Chinese and High Asian forms, cypriniform fishes in Southeast Asia exhibit less remarkable specialization, but have reached the highest stage of development as regards number of genera and species. Eight subfamilies are recognized in the four areas: Barbinae, Danioinae, Cultrinae, Gobioinae, Acheilognathinae, Xenocyprininae, Hypophthalmichtyinae, and Leuciscinae. I am unable to determine exact status of the highly specialized Burmese genus *Sawbwa,* which is therefore excluded from the numerical analysis given below.

The Barbinae predominate in the cyprinids of the area. Of the 50 genera in the subfamily found in the areas, six are referrable to the Chinese element, three are to the Widespread element, and 41 are to the Indian, Indo-Indosinian, or Indosinian element. The Danioinae and the Cultrinae have main ranges in temperate as well as tropical zones. Five of the 13 danioine genera and six of the 15 cultrine genera are Chinese. The remaining five subfamilies have their main ranges in China, wherefrom the Leuciscinae extend to the Holarctic region. Outside the Song Koi drainage, the Chinese genera occur only in the Mekong basin.

The Gyrinocheilidae are strictly Indosinian. In the Homalopteridae, the Gastromyzoninae do not occur in western Southeast Asia, while the Homalopterinae are found throughout the region. The Cobitidae are subdivided into the Botiinae, Cobitinae and Noemacheilinae. The Botiinae are common fishes in all the regions except the Song Koi area where they are absent. Some species of the subfamily reach the Yangtze. The Cobitidae are represented in the areas under study by as many as 12 genera, of which three occur solely in the Song Koi basin. The Noemacheilinae are represented only by the Indosinian *Noemacheilus*.

(2) Siluriformes

Eleven families occur in the four areas (Table 1). *Euchiloglanis* and *Parapseudecheneis* in the Sisoridae and *Pseudobagrus* in the Bagridae have their main ranges in China, and *Silurus* (including *Parasilurus*) is known from northeastern Asia as well. *Clarias* in the Clariidae occur widely from Africa through to the Yangtze, and *Heterobranchus* in the same family inhabits tropical freshwaters of Asia and Africa. All other genera occur mainly in South and Southeast Asia, but some reach China or even further north.

2. Non-ostaryophysans.

(1) Osteoglossiformes

Two families occur in Southeast Asia; each of them is represented there by a single genus. The Notopteridae are not recorded from the Song Koi basin. *Scleropages* in the Osteoglossidae inhabits the Cambodian Mekong, the Malayan Peninsula, the Greater Sunda

Table 2 List of primary freshwater fish genera known from the four principal areas of Southeast Asia, classified into different elements according to geographic range. For main range of each element, see the text. * Endemic to Burma; ** occurs also in Australia.

Family	Element	Genus
Osteoglossidae	Indosinian**	*Scleropages*
Notopteridae	Widespread	*Notopterus*
Cyprinidae	Indian	*Rohtee, Chagunius, Amblypharyngodon, Catla, Aspidoparia, Semiplotus*
	Indo-Indosinian	*Sawbwa**, *Catlocarpio, Mystacoleucus, Tor, Lissochilus, Oreichthys, Thynnichthys, Puntius, Osteochilus, Schismatorhynchus, Crossochilus, Danio, Esomus, Rasbora, Oxygaster, Chela*
	Indosinian	*Cyclocheilichthys, Albulichthys, Sikukia, Cosmochilus, Hampala, Probarbus, Rohteichthys, Puntioplites, Balantiocheilus, Leptobarbus, Labiobarbus, Amblyrhynchichthys, Xenocheilichthys, Barynotus, Papillocheilus, Barbichthys, Scaphiodonichthys, Scapgognathops, Tylognathus, Holotylognathus, Morulius, Henichorhynchus, Epalzeorhynchos, Mekongina, Paracrossocheilus, Luciosoma, Parabarilius, Daniops, Filirasbora, Macrochirichthys, Longiculter, Paralaubuca, Cultrops, Parachela, Nematabramis, Rasborichthys*
	Chinese	*Spinibarbus, Gymnostomus* (incld. *Varicorhinus*), *Onychostoma, Acrossocheilus, Pseudogyrinocheilus, Hemibarbus, Luciobrama, Opsariichthys, Elopichthys, Squalidobarbus, Ochetobius, Toxabramis, Hemiculter, Erythroculter, Culter, Megalobrama, Rasborinus, Xenocypris, Acanthorhodeus, Sarcocheilichthys, Hypophthalmichthys, Mylopharyngodon, Ctenopharyngodon*
	Widespread	*Cirrhinus, Labeo, Garra, Barilius*
Gyrinocheilidae	Indosinian	*Gyrinocheilus*
Homalopteridae	Indo-Indosinian	*Balitora*
	Indosinian	*Homaloptera, Pseudohomaloptera, Glaniopsis, Annamia, Parhomaloptera, Protomyzon, Progastromyzon, Sewellia, Gastromyzon*
	Chinese	*Sinogastromyzon*
Cobitidae	Indian	*Lepidocephalichthys*
	Indo-Indosinian	*Apua**, *Lepidocephalus, Acanthophthalmus*
	Indosinian	*Acanthopsis, Acanthopsoides* (=*Neacanthopsis*), *Cobitophis, Elexis, Vaillantella, Noemacheilus*
	Chinese	*Cobitis, Misgurnus, Homatula*
	Widespread	*Botia*
Siluridae	Indo-Indosinian	*Wallagonia, Ompok*
	Indosinian	*Apodoglanis, Silurichthys, Wallago* (=*Belodontichthys*), *Silurodes, Kryptopterus, Hemisilurus, Silurus* (incld. *Parasilurus*)
Clariidae	Indosinian	*Prophagorus*
	Widespread	*Clarias, Heterobranchus*

Pangasiidae	Indian	*Eutropiichthys, Silonia*
	Indo-Indosinian	*Pseudotropius*
	Indosinian	*Platytropius, Laides, Helicophagus, Pangasianodon, Pangasius, Pteropangasius*
Amblycipitidae	Indo-Indosinian	*Amblyceps*
Sisoridae	Indo-Indosinian	*Bagarius, Gagata, Glyptothorax*
	Indosinian	*Oreoglanis*
	Chinese	*Euchiloglanis, Parapseudecheneis*
Bagridae	Indian	*Erethistes, Rita*
	Indo-Indosinian	*Mystus*
	Indosinian	*Bagroides, Leiocassis* (s. str.), *Heterobagrus, Bagrichthys*
	Chinese	*Pseudobagrus*
Chacidae	Indo-Indosinian	*Chaca*
Cranoglanididae	Chinese	*Cranoglanis*
Olyridae	Indian	*Olyra*
Akysidae	Indosinian	*Akysis, Acrochordonichthys, Breitensteinia*
Heteropneustidae	Indo-Indosinian	*Heteropneustes*
Channidae	Widespread	*Channa*
Anabantidae	Widespread	*Anabas*
Osphronemidae	Indosinian	*Osphronemus*
Helostomidae	Indosinian	*Helostomus*
Belontiidae	Indian	*Belontia, Colisa*
	Indosinian	*Betta, Parosphronemus, Trichopsis, Trichogaster, Sphaerichthys*
	Widespread	*Macropodus*
Luciocephalidae	Indosinian	*Luciocephalus*
Nandidae	Indo-Indosinian	*Nandus*
Pristolepidae	Indosinian	*Pristolepis*
Badidae	Indian	*Badis*
Mastacembelidae	Indo-Indosinian	*Macrognathus*
	Widespread	*Mastacembelus*
Chaudhriidae	Indo-Indosinian	*Chaudhria**

Islands, and Australia.

(2) Perciformes

Fishes in this order are relatively numerous in the study area except the Song Koi basin. Main ranges of these fishes are Asian tropics; all the genera found in the study area are confined in Southeast Asia, except for the following three genera. *Channa* shows a wide range from Africa through tropical Asia north to the Amur drainage. *Anabas* extends from tropical Asia to the Yangtze. *Macropodus* is known from India and Ceylon north to China and Korea.

(3) Mastacembelidae

This order is made up of the Mastacembelidae and Chaudhriidae; both are found in the study area. *Mastacembelus* is known from Africa to China; *Macrognathus* occurs in tropical Asia; *Chaudhria* is endemic to Burma.

II Composition and relationships of primary freshwater fish faunas of the four areas

1. Irrawaddy-Salwin basins

Of the 63 genera of primary freshwater fishes known from the area, 15 genera (24% of the total number) belong to the Indian element, 26 (41%) to the Indo-Indosinian, 8 (13%) to the Indosinian, and 11 (17%) to the Widespread. The remaining three are endemic to the area. No Chinese element is found there, though the Indo-Burmese cyprinid *Semiplotus* is most probably closely related to the Chinese *Onychostoma*. Analysis to species level reveals that the Burmese fauna shares more species with the Indian fauna than with the Indosinian.

It is evident from the above that the primary freshwater fish fauna of the Irrawaddy-Salwin basins is a transitional and more or less intermediate one between the Indian and Indosinian fuanas, but closer to the Indian than to the Indosinian. The fauna appears a little more closely allied to that of the Mekong-Chao Phya area than that of the Greater Sunda Islands (Fig. 1).

With the exception of *Chaudhria, Sawbwa* and *Apua*, endemism in this fauna has reached only species level. Difference in the composition of fauna between the Irrawaddy and the Salwin is not known very clearly.

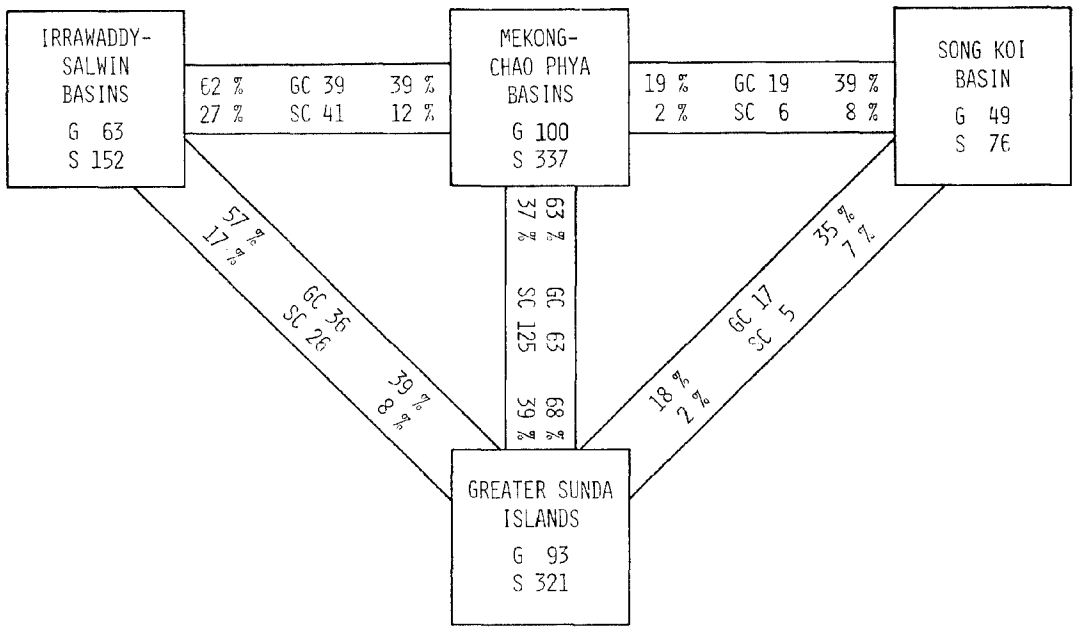

Fig. 1 Numerical relationships between the primary freshwater fish faunas of the four principal areas of Southeast Asia. Total number of genera (G) and of species (S) is given in square box, number of common genera (GC) and species (SC) between two areas is presented in the center of belt connecting two areas, and rate of common genera and species is expressed as percentage of total number of fish in either of the two areas concerned.

2. Greater Sunda Islands

The Greater Sunda Islands have a large freshwater fauna which is particularly rich in siluriform and perciform fishes. The fauna consists of 26 Indo-Indosinian, 56 Indosinian and 11 Widespread genera. Neither Indian nor Chinese genera occur there.

The fauna of the area shows a close similarity to that of the Mekong-Chao Phya basins, with a number of species occuring in both the areas (Fig. 1). Yet there are a few endemic genera such as *Barynotus, Elexis* and *Vaillantella* on the one hand and rather many mainland forms are absent from the islands on the other hand. Large-sized lowland fishes of the Mekong and the Menam Chao Phya such as *Catlocarpio* and *Probarbus* do not occur on the islands. The Widespread element is also rather poorly represented: *Cirrhinus* and *Barilius* are absent and *Labeo* and *Garra* comprise few species there. Upland forms such as *Scaphiodonichthys* and *Onychostoma* are absent too.

3. Mekong-Chao Phya basins.

In the Mekong basin from its estuary up to Chiengsen, Thailand, 87 genera including 237 species of primary freshwater fish have been recorded. Of these, 60 genera and 106 species are common to the middle course above the Khong Falls and the lower course below the falls. In the Chao Phya drainage 88 genera containing 266 species are known. There are 74 common genera (84% of the total Chao Phya genera and 87% of the total middle Mekong genera) between the Chao Phya and the middle Mekong, and 58 common genera (66% and 94%) between the Chao Phya and the lower Mekong. The faunas of the two rivers thus show a striking resemblance, and therefore the two drainages can be regarded as one and the same faunal area.

The Mekong-Chao Phya fauna as a whole is particularly rich in cyprinid fishes and their allied forms (Table 1). Naturally, fishes of the Indosinian element predominate in the fauna, comprising 61 of the 99 known genera in the area. The Indo-Indosinian element includes 23 genera. Widespread genera, especially those belonging to the Cyprinidae, are represented by many species. There are three Chinese genera in the Mekong basin: *Acanthorhodeus, Onychostoma* and *Elopichthys* (the latter two are based on my recent collection in Laos).

4. Song Koi basin

The freshwater fish fauna of the Song Koi basin is the smallest of the four and quite distinctive. There are only four non-ostaryophysan genera, *Channa, Anabas, Macropodus* and *Mastacembelus*. All of them extend further north to the Yangtze or East Asia. As to ostaryophysans, only nine genera and 10 species are Indosinian or Indo-Indosinian, and four genera and eight species are of Widespread element. All other cypriniform and siluriform fishes have their main ranges in Chinese freshwaters.

In the Cyprinidae, the Barbinae predominate, but not to the extent that they do in other part of Southeast Asia. Four genera and five species are Indo-Indosinian, three genera and four species are Indosinian, two genera and six species are Widespread, and six genera and 12 species are Chinese. There are five Chinese and/or East Asian cyprinid subfamilies:

Xenocyprininae, Acheilognathinae, Gobioinae, Hypophthalmichthyinae, and Leuciscinae. Cobitids are not numerous; neither the widespread *Botia* nor its Chinese relative, *Leptobotia,* inhabits the Song Koi drainage. The siluriform fishes are represented by only eight genera, of which *Bagarius* and *Mystus* are Indo-Indosinian.

It is obvious that the fauna has derived mainly from Chinese stock.

III Origin and dispersal of the cyprinid fishes of Southeast Asia

As briefly referred to before, Hora and Menon are of the opinion that a large part of the freshwater fish fauna of India originated in and migrated from the eastern countries. Hora (1937) states that the freshwater fishes of India have their origin in southeastern Asia, most probably in Indochina, wherefrom they spread westward to India and then to Africa. He also attempts to explain the strong Malayan affinities recognized in the fauna of peninsular India by the 'Satpura Hypothesis' (Hora, 1944, 1949). He hypothesizes that Malayan hill-stream fishes migrated to peninsular India during the late Tertiary via Thailand, Burma, and Assam, and then along the Satpura range which was then a continuous extention of hills running from Assam to the West Ghats.

Menon (1955) considers that the freshwater fishes of India originated in South China and they spread toward west by way of two routes, one along the Himalayas to India and then to West Asia and Africa during the Pliocene and Pleistocene, and the other along the Burma-Malaya arc and the Indo-Malayan mountains and then southward to peninsular India via the Satpura trend of mountains during the Pleistocene.

Hora and Menon's view on the distribution of the Malayan stock to the Indian Peninsula, reinforced with geological and climatological evidences, may be the best and only possible explanation for certain fishes that are strictly mountain-torrennt dwellers. For other kinds of fish, however, the hypothesis seems of minor importance. And the cyprinid *Osteochilus, Mystacoleucus* and *Thynnichthys* which are cited by Hora (1949) as examples of hill-stream fishes are in fact inhabitants of lowland flowing waters and do not occur in swift-running hill streams at least in Southeast Asia.

The distribution of fishes on Borneo offers a clue to distinguish old and new elements of fish occurring in the Sunda area. The fish fauna of the Kapuas of western Borneo closely resembles that of the rivers of eastern Sumatra. This similarity is generally attributed to the connection of the river systems of western Borneo and eastern Sumatra during the glacial times. On the contrary the fauna of the Mahakam of eastern Borneo has developed many endemic forms, and shows much less affinity with the fauna of Sumatra than that of Kapuas does. Based on such observations and that the watershed between the Kapuas and the Mahakam has long been the same as it is now, de Beaufort (1951) concludes that the fishes common to eastern Sumatra and the Kapuas and not found in the Mahakam are new or

Pleistcene migrants to the islands, and those also occur in the Mahakam are of an older invasion.

On the basis of the present-day distribution and fossil records as well as morphological features of the fishes, we can distinguish fairly clearly several groups of cyprinid fish that differ in the mode and period of migration to or origination in Southeast Asia.

The first group is composed of *Tor, Crossochilus, Puntius, Thynnichthys, Osteochilus, Cyclocheilichthys* genus-group (including *Cyclocheilichthys, Oriechthys, Albulichthys* and *Barynotus*), *Labiobarbus, Mystacoleucus-Spinibarbus* group (perhaps congeneric), *Tylognathus, Rasbora, Oxygaster,* and *Chela.* They occur mostly from India or rarely from Burma throughout the Indochinese Peninsula and the Greater Sunda Islands east to South China. They are generally abundant and common in Indian freshwaters, but their distribution appears to center in Southeast Asia. Subgeneric or almost generic differentiation is recognized between many Indian and Southeast Asian groups. All but one (*Chela*) are found in the Mahakam. *Puntius, Osteochilus, Thynnichthys* and *Rasbora* are represented in the Eocene Sipang fauna in central Sumatra (Sanders, 1934). A *Puntius* is known from the Miocene Mae Sot deposites in northwestern Thailand near the Burmese border (Uyeno, 1969).

All these observations indicate that the fishes are old occupants of Southeast Asia. Their ancestral forms may have been well established there, perhaps with wide ranges, already during the Eocene or even earlier times, and their dispersal to India may not be a recent event. Although their present ranges extend to a part of China, and the Barbinae were fairly more numerous than now during Tertiary times in East Asia (Bănărescu, 1972), the center of speciation should probably have included the Indosinian district which was probably a continuous dry land during certain periods of the Tertiary.

Fishes in the second group are those found in the Mahakam but not in India and Burma. *Leptobarbus, Hampala* and *Macrochirichthys* belong to this group. *Leptobarbus* occurs also in South China and North Vietnam, but the other two are known only from the Indosinian district. They, especially the latter two, may be remnants of old and primitive stock existed in the old-time Indosinian land.

The third is the Widespread element defined above, made up of *Cirrhinus, Labeo, Garra* and *Barilius.* Despite their wide distribution, they are only poorly represented in the Sunda area. Only *Garra* is known from the Mahakam. These patterns of distribution suggest that they may have originated in deep inland, and performed a long journey toward Africa and to the south. Their spread to the Sunda area seems to date back to certain periods when segregation of the Mahakam fauna had almost been completed.

The fourth group includes *Lissochilus, Epalzeorhynchos, Danio* and *Esomus.* Their origination in rather western part of Asia and relatively young history on the Sunda Islands are suggested by the abundance of these fishes in the Indian region, the scantiness in the Sunda area, and the absence from the Mahakam and from China.

The fifth group is made up of a few cyprinids inhiabting mainly mountain streams: *Onychostoma, Scaphiodonichthys, Scaphognathops* and *Semiplotus*. They and their Chinese relative, *Gymnostomus* (=*Varicorhinus* by some authors), show overlapped or not distantly separated ranges. *Gymnostomus* extends to northwestern China. They are hardly distinguishable from the West Asian *Scaphiodon* and some species of *Barbus* and *Varicorhinus* of Africa. These facts strongly suggest the initial occurrence of this group in rather northern part of mainland and subsequent spread down over continental Southeast Asia and South China on the one hand and toward West Asia on the other hand. The African and European *Barbus, Varicorhinus* and other related forms may be close to this group in phylogenetic origin. None of them occur on the Sunda Islands.

The sixth group is strictly Indosinian in distribution. This group includes a large number of genera, but many of them contain only small number of species. This group includes all of the remaining genera except the undermentioned Indian and Chinese elements. They have limited ranges, and are often endemic to either the mainland portion or the insular part. No genus of this group occurs in the Mahakam. Many exhibit close morphological similarities to other larger and more widely distributed genera. These facts evidence that

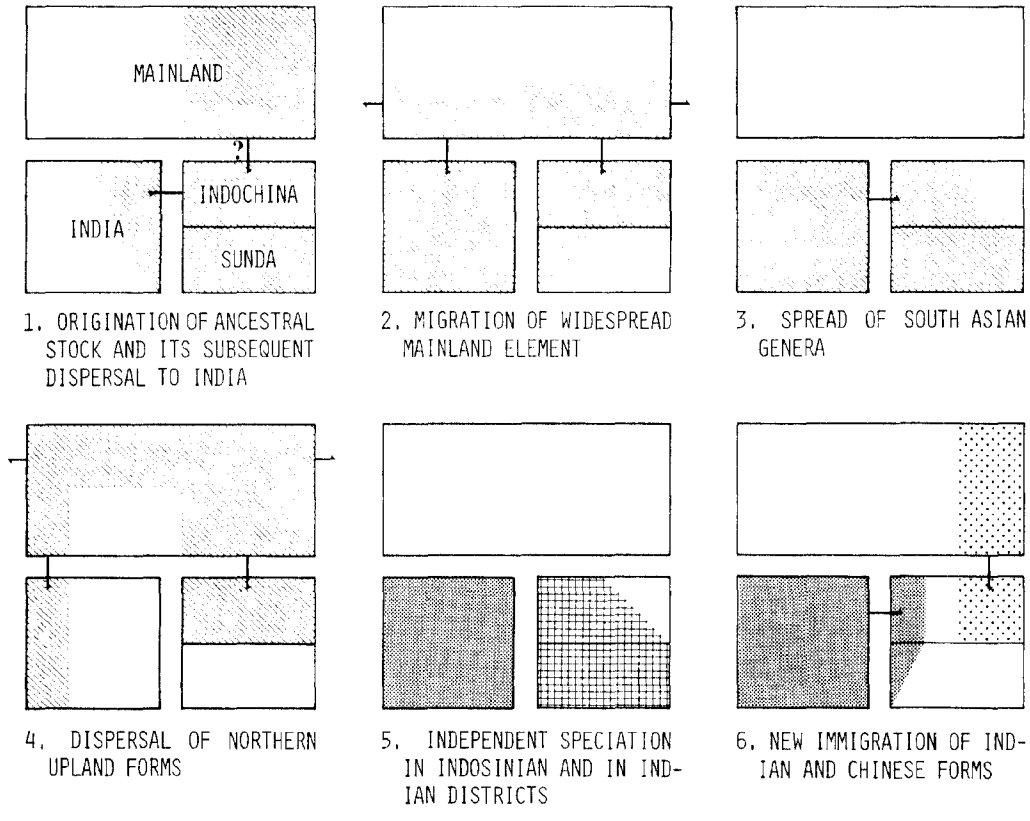

Fig. 2 Diagrammatic representation of the postulated dispersal patterns of the cyprinid fishes in Southeast Asia and adjacent areas. The serial numbers show in general the sequence of the events, but some patterns may be partially contemporaneous. Arrow represents migration of fish.

many of them, if not all, have been derived from older Indosinian stocks, and their evolutionary history is of relatively young age. The *Garra*-like *Mekongina,* the *Danio*-like *Daniops*, and many other forms exemplify the derivative origin of this type.

The seventh and the eighth are the Indian and Chinese elements, respectively, except for the Indian *Semiplotus* which is referred to the group 5. The Indian forms in strict sense show only marginal distribution in Southeast Asia, and hence of little importance in discussing Southeast Asian fishes. The Chinese genera do not penetrate deep into Southeast Asia. They should certainly have old evolutionary history in China, but may probably have not gained access to Southeast Asia until recent times, blocked by certain barriers existed between the two regions.

The postulated successive waves of dispersal of the cyprinid fishes in Southeast Asia and in India are schematically illustrated in Fig. 2. The distribution of the cyprinids of India seems to date from older times than as assumed by Hora and Menon. Brittan (1954) has shown that *Rasbora* may have reached India during the early Tertiary.

In addition to the rather numerous Chinese cyprinid genera, the fauna of the Song Koi basin includes the old Indosinian genera of the groups 1 and 2, the widespread continental forms of the group 3, and the mountain-stream cyprinids of the group 5. All of the North Vietnamese representatives of these groups extend further east to China. But none of the Indosinian genera of the group 6 occurs in the river basin. In other words, the basin received older Indosinian forms from the south and continental forms from the north and east, but subsequent migration of Indosinian and Indo-Indosinian forms from the south and southwest has been blocked since long time ago (Fig. 2). The mountains between the Song Koi and the Mekong basins are relatively low and not steep at least at present, and do not seem to be an effective and long-lasting barrier. The decided gap in the composition of fauna may indicate the former existence of more effective barriers, a sea for example, lying from the Bay of Tonkin nearly to Yunnan.

On the west of Borneo and Java cyprinid fauna diminishes abruptly. Only a *Puntius* and a *Resbora* extend to western part of the Lesser Sunda Islands, crossing Wallace's Line. On Mindanao of the Philippines there are *Rasbora, Nematabramis,* a species flock of *Puntius* and four endemic cyprinid genera. But all of the four endemic genera are immediate derivatives from *Puntius* within Lake Lanao, and all of the endemic species of *Puntius* are also derivatives from a single species, *P. binotatus,* which is widely distributed in Southeast Asia (Myers, 1960). It is interesting that both *Puntius* and *Rasbora* are members of the old cyprinid group of the Indosinian district. Cyprinids are absent from the northern Philippines.

IV Zoogeographical division of Southeast Asia

Zoogeographical division of Southeast Asia and adjacent areas reached upon the distribution of the primary freshwater fishes is shown in Fig. 3. Southeast Asia is totally included in

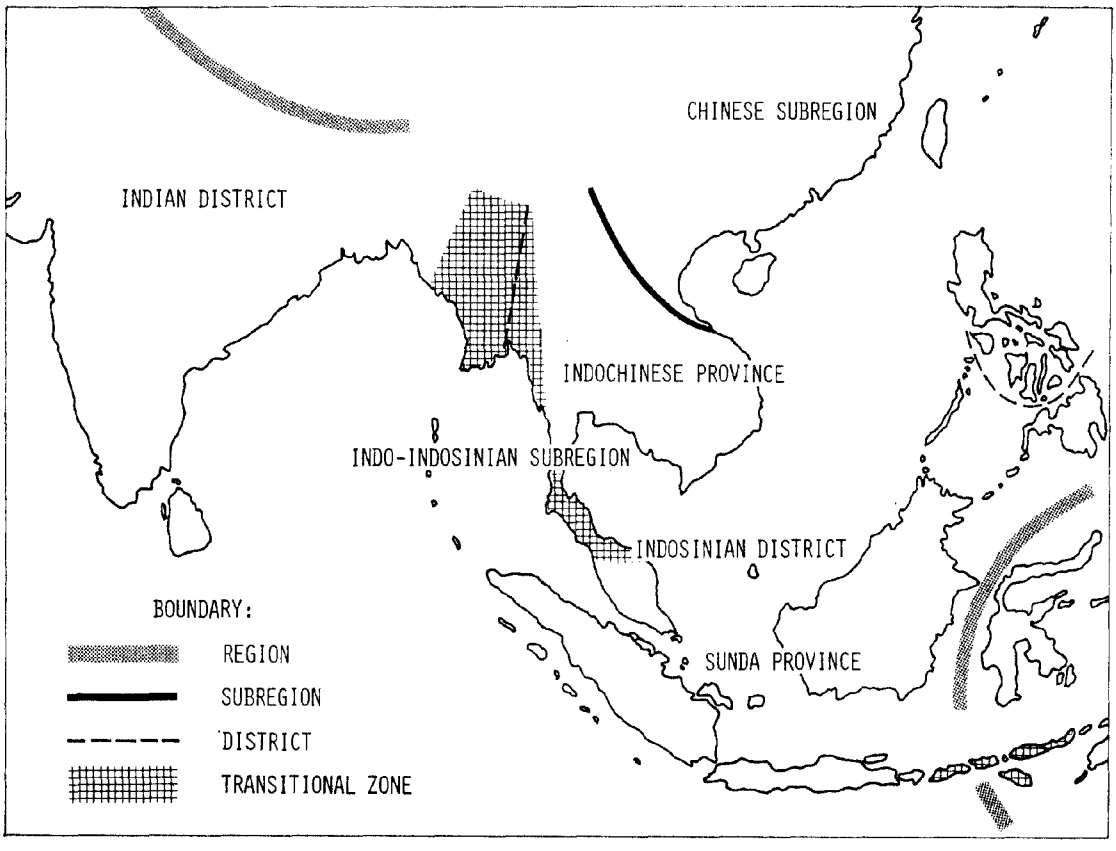

Fig. 3 Zoogeographical division of Southeast Asia and adjacent areas based on the distribution of primary freshwater fishes.

the Oriental or Sino-Indian faunal region, and sharply subdivided into two sections. The western and main section belongs to the so-called Indo-Malayan or, in my terminology, Indo-Indosinian subregion. The eastern section is a part of the Chinese subregion, which occupies North Vietnam, entire China and a part of East Asia. The boundary between the two subregions can be drawn very sharply so far as lowland forms are concerned. Many mountain stream fishes spread over both sides of the boundary.

Within the Indo-Indosinian subregion, Indian and Indosinian faunas show differentiation to some extent. The two areas are therefore considered to constitute different faunal districts. The two faunas overlap each other in Burma, thus forming a broad transitional zone.

In view of the absence of a number of mainland forms from the Greater Sunda Islands and the occurrence of endemic genera on the islands, the Indosinian district may be split into two sections, Indochinese and Sunda provinces.

Summary

Analysis of the primary freshwater fish faunas of the four principal areas of Southeast Asia shows that 1) the fauna of the Irrawaddy-Salwin basins, while including endemic forms,

is as a whole intermediate between th faunas of India and the Indosinian district, 2) the faunas of the Greater Sunda Islands and the Mekong-Chao Phya basins have a close resemblance, but rather many mainland genera do not occur on the islands and some endemic forms are found in each the area, and 3) the fauna of the Song-Koi basin is similar to that of southern China and distinct from those of other part of Southeast Asia. In the cyprinid fishes there are several groups which differ in the evolutionary history and pattern of dispersal. Their ancestral stock may have been well established geographically in main part of Southeast Asia during the early Tertiary. The sharp boundary separating the Chinese and the Indo-Indosinian subregions suggests the former existence of a certain effective and long-lasting barrier extending from the Bay of Tonkin nearly to Yunnan.

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