SPECIATION AMONG THE FRESHWATER FISHES OF CEYLON

BY

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[SUMMARY]

According to age, the freshwater fish fauna of Ceylon is divisible into two elements—the Eocene element and the Quaternary and Sub-Recent element—which, with one exception (*Etroplus* Cuvier, *see page* 251), have been derived from the Indian Peninsula. All the endemic freshwater fishes of Ceylon belong essentially to the *Primary division* (page 250). On the bases of their ecological tolerance, the endemic element is grouped under three ecological associations, and the probable time and rate of speciation of the different species complexes are determined. The factors leading to the evolutionary divergences and their nature are discussed in detail. Further, it is shown that different systematic categories, ranging from unchanged populations to polytypic species and superspecies exist on the island, especially in relation to the mainland fauna. In addition based on the mode of differentiation of the endemic element on the island, two categories of divergences, are recognized here. The present study also shows that environmental changes coupled with a number of other factors have been responsible for bringing about a fairly fast rate of speciation in the Ceylon fishes.

INTRODUCTION

Organic evolution, or descent with modification from previously existing stocks, is now universally accepted. This phenomenon, of which speciation is a phase, whereby a single species differentiates into two or more populations, through the elimination of certain traits and the addition of new ones, is a continuous operation. It is not confined to past geological ages, but is actually at work even during the present era.

Geographical as well as biological (physiological or reproductive) isolation, both complementary or partly interdependent in their action, are considered to be the most potent factors in this process of animal speciation. Insular isolation or isolation of populations on islands has, in fact, attracted the attention of many workers, and so far the greatest progress in this direction has been achieved in the field of ornithology, where variations of the mainland, continental island and oceanic island species have been studied more extensively than in any other group of animals. But, though much has been written about insular speciation, little is known regarding the actual causes, or the mechanism at work, in bringing about the spread of evolutionary divergences among the insular fauna. In tackling such a problem, it would be worthwhile if equal consideration is also given to allied subjects, like the geological, palaeontological and biological histories of the insular areas and the adjoining continents; for, with concerted effort, one could arrive much nearer the truth.

The term biological histories is mentioned because it would be profitable, when the field of investigation involves only one group, to balance the data obtained with relevant collateral evidence as discernible in other species complexes of the same area. Also, it is essential that importance should be attached to the 'ecological tolerance' and the 'habitat preference' of the species complex dealt with, as evolutionary rates are apt to differ in the different groups, under the same or varied environmental conditions.

I have recently studied this problem of evolutionary divergences with special reference to torrential fishes in Peninsular India (Silas, 1952)[1], and have found

[1] Most of the species studied are hill-stream forms, though a few lowland species are included in the list as they occur as isolates.

in that comparatively young group of fishes (for in Peninsular India, they do not seem to date back to earlier than the Pliocene) the fluctuations in climatic conditions in the form of abundant rainfall, aridity and changes in temperature during the Quaternary and Sub-Recent periods, and the orogenic movements which rejuvenated the streams of the Western Ghats of the Peninsula during the Pleistocene, are primarily responsible for bringing about considerable divergences. Here I make an attempt to see what light the freshwater fish fauna of Ceylon, which is a typical insular fauna at present, throws on this problem of speciation and evolutionary divergences.

GEOLOGICAL HISTORY OF CEYLON AND THE SOURCE OF ITS FRESHWATER FISH FAUNA

The works of Wayland (1919), Wayland and Davis (1923), Wadia (1941), Deraniyagala (1939, 1945), Jacob (1949), and others give us some idea of the palaeo history of Ceylon. It is inferred that Ceylon was part of the Indian Peninsula from the dawn of geological history up to the Miocene, when the North West of Ceylon was depressed several hundred feet below the sea, thus being severed from the mainland for the first time. Subsequent to this, due to minor oscillations and eustatic movements, Ceylon seems to have been intermittently connected with the mainland during the Quaternary Period, and even during the Holocene; for its last severance from the mainland is said to have taken place only about 10,000 years back, with the end of the last 'Pluvial Period'.

TABLE I

TABLE SHOWING THE AFFINITIES AND THE SOURCE OF THE FRESHWATER FISHES OF CEYLON

	Species and subspecies	*Genera*
1. Total number of freshwater fishes found in Peninsular India and Ceylon.	295	91
2. Total number of freshwater fishes found in Ceylon.	57	30
	Expressed as percentages of the total number given in row 1.	
3. Freshwater fishes of Ceylon.	19.322	32.975
4. Freshwater fishes endemic in Ceylon.	7.457	2.197
5. Fishes common to Peninsular India as a whole and Ceylon.	11.864	29.670
6. Fishes common to 'Malabar' and Ceylon.	11.864	29.670
7. Freshwater fishes found in Ceylon on the one hand and the Chinese or the Malayan Sub-Regions on the other, but not present in Peninsular India.	0.338	1.098
8. Freshwater fishes endemic in Peninsular India.	40.678	12.087

The very great similarity of the present-day freshwater fish fauna of Ceylon to that of Peninsular India, especially to the 'Malabar' (as is shown in Table I, given above), leads one to the inevitable conclusion that the island received its fish fauna from the mainland; and that this was possible through former land connections. Thus, as on the Indian Peninsula, the influx of the bulk of this fauna to Ceylon would date back to not earlier than the Pliocene. However, paleontological evidence indicates that a small element of the present-day freshwater fish fauna of Ceylon could belong to the early Eocene Period (*vide infra*). The fossil remains of extinct mammals, as well as the occurrence of certain living vertebrates, both in Ceylon and in India, and the past history of human civilization on the island, amply show that former land connections during the Quaternary and Sub-Recent Periods definitely acted as highways of migration from the mainland to the island. Therefore, during these periods, continuity in the watersheds between the mainland and the island would also have favoured the migration of aquatic animals.

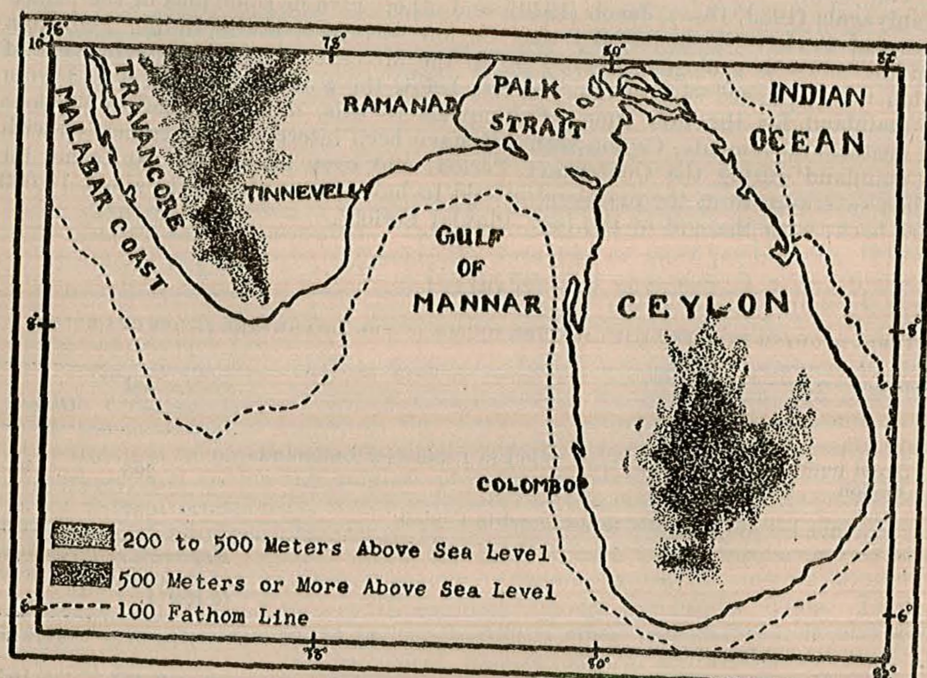

Fig. 1. Map showing part of Peninsular India and Ceylon.

Freshwater Fish Fauna of Ceylon

In using the term 'Freshwater Fishes', I have taken into consideration all those fishes which belong, according to Myer's terminology (Myers, 1937), to the *Primary division* (consisting of fishes physiologically restricted to freshwater throughout their life cycle) and the *Secondary division* (fishes which may spend part of their life cycle in a marine habitat). A list of the freshwater fishes (thus defined) of Ceylon is given below:

List of the Freshwater Fishes of Ceylon[1]

Chela laubuca (Hamilton)
Puntius amphibius (Valenciennes)
**Puntius bimaculatus* (Bleeker)
Puntius chola (Hamilton)
Puntius sarana (Hamilton)
Puntius dorsalis (Jerdon)
Puntius filamentosus (Valenciennes)
**Puntius nigrofasciatus* (Günther)
Puntius pleurotania Bleeker
**Puntius cumingi* (Günther)
**Puntius sinhala* (Duncker)
Puntius ticto Hamilton
Puntius vittatus Day
**Puntius titteya* Deraniyagala
†*Tor khudree longispinis* (Günther)
†*Garra lamta ceylonensis* Bleeker
Labeo dussumieri (Valenciennes)
†*Labeo porcellus lankae* Deraniyagala
**Labeo fisheri* (Jordan & Starks)
Rasbora daniconius (Hamilton)
**Rasbora vaterifloris* Deraniyagala
Amblypharyngodon melettinus (Valenciennes)
***Horadandia atukorali* Deraniyagala
†*Esomus barbatus thermoicus* (Valenciennes)
Danio aequipinnatus (McClelland)
Barilius bendelisis (Hamilton)
Barilius vagra (Hamilton)
Lepidocephalus thermalis (Valenciennes)
Noemacheilus botia botia (Hamilton)
Noemacheilus botia aureus Day
**Noemacheilus notostigma* Bleeker
†*Wallago attu valeya* Deraniyagala
Ompok bimaculatus (Bloch)
Mystus keletius (Valenciennes)
Mystus gulio (Hamilton)
Mystus vittatus (Bloch)
†*Clarias dussumieri brachysoma* (Günther)
Heteropneustes fossilis (Bloch)
**Heteropneustes microps* (Günther)
Anguilla bengalensis (Gray & Hardwick)
Anguilla australis (Richard)

[1] In the above list slight changes in the nomenclature have been advocated wherever found necessary. For instance *Anguilla bengalensis* (Gray & Hardwick) will be found as *Anguilla bicolor bicolor* McClelland in Deraniyagala (1952). The subspecies *Garra ceylonensis phillipsi* Deraniyagala is considered here a synonym of *Garra lamta ceylonensis* Bleeker.

Exotic or introduced species like *Osphronemus gourami* (Lacépède), *Cyprinus carpio* var., *etc.*, are left out in the above list, as they serve no useful purpose in the present study. So also are some of the imperfectly known species, like *Ambassis thermalis* Cuvier, *etc.* *Etroplus* Cuvier, which represents the 'African element' in the fish fauna of Peninsular India and Ceylon, is also omitted for the same reason. The latter with two species, *E. suratensis* (Bloch) and *E. maculatus* (Bloch), has its nearest related form in *Paretroplus* Bleeker of Madagascar. It is probable that this 'African element' reached Peninsular India by sea, *via* the Seychelles—Chagos—Maldive Chain. They are *Secondary division* fishes and their salt-tolerance indicates that sea barriers can be crossed.

†_Aplocheilus lineatus dayi_ (Steindachner)
Aplocheilus panchax (Hamilton)
Xenentodon cancila (Hamilton)
†_Anabas testudienus kavaiya_ Deraniyagala
*_Belontia signata_ (Günther)
Macropodus cupanus (Cuvier)
**_Malpalutta kretseri_ Deraniyagala
Glossogobius giuris (Hamilton)
Channa striatus (Bloch)
Channa punctatus (Bloch)
†_Channa marulius ara_ (Deraniyagala)
†_Channa gachua kelaarti_ (Günther)
Channa orientalis Schneider
Macrognathus aculeatus (Bloch)
Mastocembelus armatus (Lacépède)
Synbranchus bengalensis (McClelland)

**Generic Divergence. *Specific Divergence. †Subspecific Divergence.[1]

Endemic Fishes and their Ecological Tolerance

Out of the 57 species and subspecies listed above, as many as 21 are endemic in Ceylon. A noteworthy feature is that all the endemic fishes belong to the _Primary division_, and are essentially confined to freshwaters. They are not of the 'migratory type', though some hill-steam fishes, like species of _Garra_ Hamilton and _Tor_ Gray, are known to travel short distances seeking quiet waters during the breeding season. Fishes occurring in the estuaries and lowlands do not generally move to the upper reaches of the stream, where the current is much swifter, the water cooler and the food almost entirely different. Even physiological factors may tend to play a part in the 'habitat preference' of certain fishes. For instance, in stagnant waters and swamps, the oxygen content of the water is low enough to make normal aquatic respiration inadequate for the needs of the fish, unless the blood has become modified to function at very low oxygen tension.

The works of Carter and Beadle (1930), Carter (1931), Wilmer (1934), and others are very suggestive in this respect, as they have shown that under normal circumstances fishes of clear and fast flowing waters will not survive for long in stagnant waters with very low oxygen tension, unless their blood is modified to counteract the effects of excess of carbon dioxide (carbon dioxide insensitiveness), or they have developed accessory respiratory organs, etc.

Therefore, as a rule, fishes of the _Primary division_, living in hill-streams, lakes, rivers, estuaries and marshes are prone to remain in their respective habitats. On this basis, as many as three principal ecological zones can be recognized in the drainage system in Ceylon, which may be classified as follows:

1. Sluggish streams of the coastal tract, estuaries, marshes and swamps (sluggish waters).
2. Clear waters of rivers, lakes and tanks (fluviatile and lacustrine waters).
3. Hill-streams (rapid running waters).

The endemic species and subspecies mentioned under the above three zones in the following table, are not strictly stenozonal; but, as already pointed out are primarily to be met with in their respective habitats.

[1]The term 'Subspecific Divergence' is used here to denote all infra-specific categories of divergences. The absence of any work for delimiting subspecies, races and varieties of Ceylon fishes has made it necessary to follow such a course.

TABLE II

Zone 1 Sluggish waters	Zone 2 Fluviatile or Lacustrine waters	Zone 3 Rapid running waters
†_Clarias dussumieri brachysoma_ (Günther)	*_Puntius bimaculatus_ Bleeker	†_Garra lamta ceylonensis_ Bleeker
*_Heteropneustes microps_ (Günther)	*_Puntius nigrofasciatus_ (Günther)	†_Tor khudree longispinis_ (Günther)
†_Anabas testudienus kavaiya_ Deraniyagala	*_Puntius sinhala_ (Duncker)	*_Noemacheilus notostigma_ Bleeker
*_Belontia signatus_ (Günther)	*_Puntius cumingi_ (Günther)	
**_Malpulutta kretseri_ Deraniyagala	*_Puntius titteya_ Deraniyagala	
†_Channa marulius ara_ Deraniyagala	†_Labeo porcellus lankae_ Deraniyagala	
†_Channa gachua kelaarti_ (Günther)	*_Labeo fisheri_ Jordan & Starks	
	*_Rasbora vaterifloris_ Deraniyagala	
	**_Horadandia attukorali_ Deraniyagala	
	†_Esomus barbatus thermoicus_ (Valenciennes)	
	†_Wallago attu valeya_ Deraniyagala	
	†_Aplocheilus lineatus dayi_ (Steindachner)	

**Generic Divergence. *Specific Divergence. †Subspecific Divergence.

Of the non-endemic element, species of _Channa_, _Macropodus_, _Glossogobius_, _Synbranchus_ and _Mystus gulio_, occur in Zone 1; while species of _Noemacheilus_, _Danio_ and _Barilius_ occur in Zone 3. The rest are generally found in Zone 2.

Factors Leading to Evolutionary Divergences

A treatment of the evolutionary divergences of these fishes on the bases of their ecological tolerance is given below:

Zone 1. _Fishes found in the sluggish streams of the coastal tract, estuaries, marshes and swamps._ Up to now, there have been no reports of fossil remains of freshwater Acanthopterygians from Ceylon; but, from their past history, as well as their present-day distribution, it can be reasonably inferred that the Anabantidae and kindred fishes were the earliest Acanthopterygians to reach Ceylon from the Indian Peninsula. In age, this element dates back to the early Tertiary, as remains of a variety of _Macropodus_ Lacépède, and other allied fishes of the famili s Nandidae and Pristolepidae (_Nandus_ Valenciennes and _Pristolepis_ Jordon), known from the Inter-Trappean beds of the Deccan, testify. As Ceylon was part of the mainland during the Eocene, the distribution of these fishes from India further south to Ceylon, would have been uninterrupted. Contemporaneous with the spread of _Macropodus_ to Ceylon, would also have been the distribution of _Belontia_ Myers, another Anabantid, which is at present represented in Ceylon and the Malayan Archipelago by different species. Its extinction on the Indian Peninsula might have been brought about by the lava-flows of the Deccan Trap eruptions during the later part of the Eocene. The influx of _Anabas_ from the mainland to Ceylon may also date back to this period.

All the above mentioned species are marsh-loving forms, and _Malpulutta_ Deraniyagala, another Anabantid genus, which is endemic in Ceylon, probably evolved due to long isolation from the Macropodid stock on the island with which it shows considerable affinities. The survival of this Eocene element in Ceylon, and its proliferation there, indicates that Ceylon was part of the mainland during the Eocene; the Deccan Trap eruptions, which brought about the extermination of a greater part of the fauna of the Peninsula, did not in any way affect it. Geological data seem to confirm this conclusion.

The Quaternary and Recent physiography of Ceylon suggest that the intermittent land connections of the island during this period were established only with the Indian Peninsula. These land connections would no doubt have facilitated the further influx of the Anabantidae and allied fishes from the mainland. The spread of air-breathing fishes, like *Clarias* Gronovius, *Heteropneustes* Müller and *Channa* Scopoli, to Ceylon can also be dated back to this period, probably to the early or middle Pliocene, as prior to this their spread from the north to the Peninsula itself was prevented by the existence of an arm of the sea. Fossil remains of *Clarias* and *Channa* are known from the Siwalik deposits of Northern India.

Though these fishes do not belong to the *Secondary division*, their occasional presence in very slightly brackishwater situations indicates their slight 'salt-water tolerance'. This, in addition to the fact that they possess accessory respiratory organs, increases their powers of vagility, so much so that, among these fishes, we can expect a much faster rate of distribution than among those confined to hill-streams, rivers and lakes. Only infra-specific levels of divergences seem to have taken place in *Clarias* and *Channa*, while one species of *Heteropneustes* has evolved on the island, which on the whole is indeed a relatively 'slow rate' of speciation as compared to fishes belonging to the other ecological associations on the island. That more than one factor could have been responsible for this is shown below.

1. *Isolation:* First of all, though geographical isolation of the stock on the island was effected from time to time during the Pliocene-Pleistocene and Post-Pleistocene, the periods of isolation were probably not long enough to bring into play complete biological isolation. Also, in comparing the endemic and non-endemic species of the island, the fact that many of the unchanged populations of the island could be recent migrants should not be lost sight of. This being so, it would be erroneous to base the rate of speciaton of a particular genus or species complex of the island on the mere grounds of subspecific speciation. However, in the present context, the term 'slow rate' is not used to mean 'bradytelic' (Simpson, 1944); but for a relative comparison of the speed of speciation shown by species belonging to the different ecological associations on the island.

2. *Phenotypic plasticity:* Plasticity will indirectly influence the speed of speciation. Fishes capable of surviving in given environmental extremes in nature should theoretically be less subject to the action of natural selection, especially if they are able to adjust themselves physiologically to such varied conditions. Marsh-loving fishes, unlike other species which tolerate no alteration of external conditions and live in an almost unvarying niche, show much greater vagility and powers of adjustability to a wider set of environmental factors. Thus, their rate of speciation may seem to be relatively slow.

3. *Environmental influences:* Environment influences the rate of speciation through natural selection and other means. Greater phenotypic plasticity may also be associated with a relatively low mutation rate, and subsequently a slow rate of speciation. But even in such cases, if localized dynamic environmental conditions are present, the speed of speciation will be accelerated, sometimes to the point of bringing about tachytelic tendencies in the group. In Ceylon, the habitats of fishes like *Clarias* and *Channa* seem not to have been subjected to such dynamic environmental changes.

Thus, as already indicated, the evolutionary rates of marsh-loving fishes on the island, both of the Eocene as well as the Quaternary, are more or less normal or horotelic (Simpson, *op. cit.*), as far as the group by itself is concerned; but is relatively slow, as will be seen presently, when compared to fishes of other ecological associations on the island.

ZONE 2. *Fishes living in clear waters of rivers, lakes and tanks.* The bulk of this ecological association include fishes like the Cypriniformes and Siluriformes which in their spread to Ceylon are also contemporaneous with *Clarias* and *Channa*. Genera like *Puntius* Hamilton, *Labeo* Cuvier, *Rasbora* Bleeker and *Esomus* Swainson have diverged into numerous species and subspecies in Peninsular India. On the other hand, in Ceylon, a genus and as many as six species and five subspecies have evolved from the Pliocene to the present-day. Thus, it is interesting to note that, as normal aquatic breathers, they show a much faster rate of speciation than air-breathing fishes, such as *Clarias*.

It is further evident, from their levels of divergences on the island, that their evolution was not synchronic, but took place probably at different phases of isolation from the mainland during this period. Isolation, both geographical and biological, and cyclic environmental changes (alternate effects of Pluvials and Arid Phases), would have definitely aided speciation. Moreover, there is ample evidence to show that a still more dynamic factor was at work, which would have been responsible for accelerating the speed of speciation of these fishes.

Wadia (1941) provides evidence that the waterfalls of the highlands of central Ceylon are not accidental features, but are connected with earth-movements which have lately disturbed the island's structural framework and have generally accentuated its relief. According to him "The occurrence of so many falls and steep cascades bespeaks of Sub-Recent or Pleistocene rejuvenation of the streams after they had acquired the maturity of an ancient drainage system............this is due to the introduction of an abrupt inequality in the channels by fault dislocation. *The faulting has raised the headwaters relatively to the lower courses of the rivers by an upheaval of considerable magnitude* and the upheaval was so late that the rivers have had no time to adjust their gradients by cutting through the precipices so interposed and replacing them by gorges." (Italics mine.)

It may well be asked what effect the rejuvenation of a stream could have on its fish fauna? For fishes with a *limited ecological tolerance* sudden changes in the habitat, such as the creation of more torrential conditions, would naturally leave open only two alternatives: rapid evolution to suit the changed environmental conditions; or, if non-adaptive, either sudden or gradual extinction may be the result. Both in the region of the Himalayas (Hora, 1953), as well as in the Western Ghats of Peninsular India (Silas, 1952), such rejuvenation of hill-streams and rivers are known to have been responsible for the evolution of new species and even genera of fishes; and it is difficult to resist the conclusion that in Ceylon, too, this phenomenon could have had some effect on the evolutionary divergences of certain fishes, with consequent effects on their rate of speciation.

Taking into account the periods of isolation, the average length of the generations of each species, and the environmental changes in the insular area during this period, it would be reasonable to place subspecific levels of divergences offishes like *Puntius*, *Labeo* and *Esomus* as having taken place during the past 10,000 to 15,000 years of isolation of the island from the mainland. Generic and specific levels of divergences among this group of fishes may date back to earlier periods of isolation during the Pliocene-Pleistocene.

ZONE 3. *Hill-stream fishes.* Though the influx of hill-stream fishes, such as *Garra* Hamilton, *Tor* Gray and *Noemacheilus* van Hasselt, to the Peninsula and Ceylon dates to the same period as *Puntius* and allied fishes during the Quaternary, in Ceylon they have not evolved as many species and subspecies as their allies of the mainland. However, it is likely that this migrant element had already attained a certain amount of specialization or in other words was 'preadapted', which made further divergences unnecessary for some time; and this evolutionary pause was aided by the absence of complete biological isolation. Other factors being the same, as in the previous group, the rejuvenation of the hill-streams during the Pleistocene, and Sub-Recent periods, would have been directly responsible for bringing about divergences in fishes of this ecological association, which at present have attained specific and subspecific levels of differentiation from the mainland-stock.

Nature of Evolutionary Divergences and Problems of Speciation

As already seen, after their migration to Ceylon, these fishes have proceeded to diverge and have attained varying degrees of differentiation from the mainland stock, ranging from generic to subspecific levels as follows: generic divergences (2); specific divergences (10) and subspecific divergences (10). In other words, specific and infra-specific levels of divergence seem to predominate, while generic-divergence amounts to only about 9.09 per cent of the total endemic element in the freshwater fish fauna of Ceylon. All the non-endemic species, with two exceptions,[1] are found in Peninsular India. The absence of any endemic family of freshwater fishes in Ceylon once again points to the conclusion that the complete isolation of the fish fauna there is a recent phenomenon.

It may be noted here that the concepts of polytypic species and other systematic categories have not been fully extended to Indian fishes. The present study shows that, when the Indian and Ceylon species are considered as a whole, different types or a series of systematic categories can be recognized, an evaluation of which would further the understanding of the evolutionary divergences of the insular fish fauna. They range from (*i*) widespread and variable species which have not yet differentiated into distinguishable forms on the island (*e.g.*, *Danio aequipinnatus*, *Puntius ticto*), to (*ii*) scarcely diverged forms, involving only subspecific divergence (probably varieties or races, *e.g.*, *Channa marulius ara*), to (*iii*) polytypic species or *Rassenkreise* (Rensch, 1929) which have closely allied subspecies on the mainland or on the island itself (*e.g.*, *Esomus barbatus thermoicus*), to (*iv*) superspecies or *Artenkreise* (Rensch, 1929) which include groups of allopatric species or semispecies[2] *e.g.* *Puntius spp.*, and *Noemacheilus notostigma*, having closely allied species on the mainland.

But these systematic categories do not fully explain certain aspects of speciation or, to be more precise, the mode of divergences of the insular fauna in relation to the mainland stock. Cain (1953) speaking of geographical and ecological species concepts in relation to coexistence, and in this connexion the usage of the terms *sympatry* and *allopatry* emphasizes Mayr's view (Mayr, 1942, p. 227) that *geographical* and *ecological* 'ranges' are not exclusive, but overlap to a great extent. Hence, unless properly understood, there is apt to be some confusion in the normal usage of these terms. However, *sympatry* and *allopatry* may be used with advantage in reference to spatial distribution (geographical), for the principal criterion distinguishing them is considered to be the 'breeding range' of the population. On this basis, in the case of Peninsular India and Ceylon, fundamentally two types of divergences can be made out. The first category would involve fishes, which exhibit spatially a *sympatric pattern of distribution*. Here, the mainland stock, which for convenience may be called the 'parent stock' ('X' in Figure 2, *a–f*), is also present on the island. *Malpulutta kretseri*, to cite one example, may be said to belong to this group, as it has undoubtedly evolved from the Macropodid stock on the island. Other instances are to be found in the genera *Heteropneustes* and *Rasbora* on the island. From the point of view of geographical speciation, it is likely that some of these forms originally differentiated on the same lines as that given below for the second category. The secondary invasion of the island by the 'parent stock' at some later date will also tend to bring about the same condition as that given for the first category. Hence a delimitation of the first category of divergents in an insular area is more difficult since it needs an intimate knowledge of the phylogenetic affinities.

[1] *Channa orientalis* Schneider, and the genus *Belontia* Myers, are represented elsewhere in the Malayan Sub-Region and further east.

[2] Semispecies (Mayr, 1942, p. 165) is used to indicate taxonomically distinct and wholly allopatric, but closely related species.

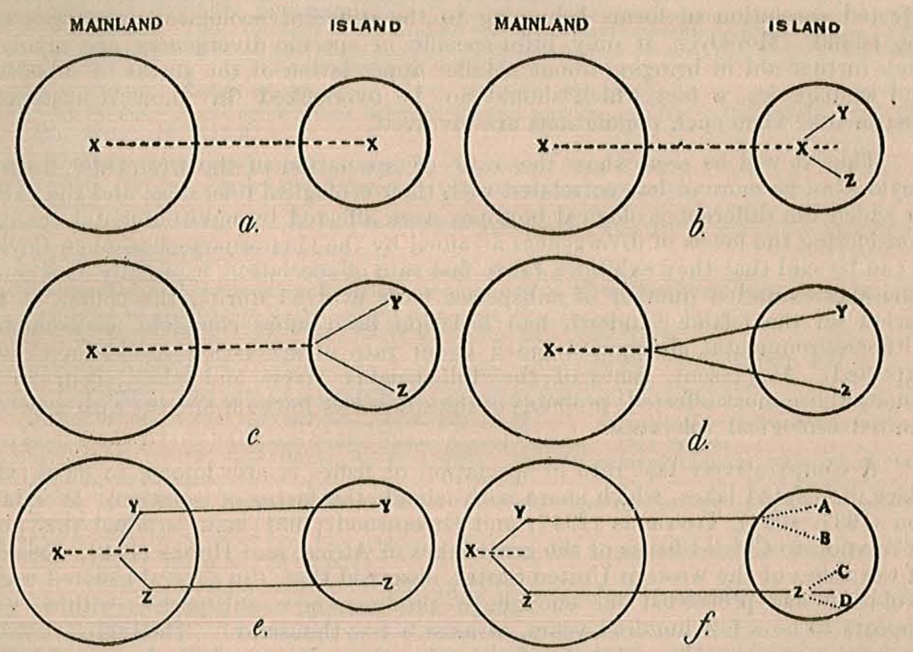

Fig. 2, *a–f*. Figures showing different types of divergences of fishes of the insular area. An 'X' represents the 'parentstock' of the mainland, while 'Y, Z, A, B, C, D' represent divergents. Figure (*a*) shows unchanged populations on the mainland and the island; (*b*) The first category: the divergence into 'Y' and 'Z' having taken place from the 'parentstock' 'X' present on the island itself; (*c*) The second category: the divergence into 'Y' and 'Z' having taken place from the 'parentstock' 'X' of the mainland on reaching the island; (*d*) Same as in figure *c*; (*e*) 'Y' and 'Z' stocks on the island represent unchanged populations as 'X' in figure *a*; (*f*) The divergence of 'Y' stock into 'A' and 'B' is the same condition as in figures *c* and *d*, while 'Z' stock into 'C' and 'D' represents divergences as seen in figure *b*. Figures *e* and *f* also show diagramatic representations of polytypic species and superspecies.

The second category will include fishes which have undergone differentiation from the 'parent stock' of the mainland on their arrival on the island, to the extent that the two populations are different, though not distinct. They may belong to a polytypic species or even a superspecies, but geographically they occupy two different areas (mainland and island), in which each strain amounts to 100 per cent of the population. This category will include fishes like *Puntius* *sinhala*, and *Tor khudree longispinis*, which replace, so to say, the mainland 'parent stock' of *Puntius melanampyx* (Day) and *Tor khudree khudree* (Sykes), and other fishes on the island. Spatially they exhibit an *allopatric pattern of distribution*; and, as already indicated, are members of a polytypic species or other systematic categories; but, neither the term allopatric, nor the connotations used above, will fully signify this mode of insular divergence from the 'parent stock' of the mainland.

Therefore, the distinction of endemic insular species into the above mentioned two categories of divergents, based principally on spatial distribution, will be useful as it may help in making clear a number of problems, such as whether single, double or more invasions have taken place from the mainland to the island; the periods of migration and the probable duration of isolation (both geographical and biological) of the different species complexes; and as to how far environmental changes affected speciation of forms belonging to the different ecological associations on the island. Moreover, if only infra-specific or specific divergences are involved, they further aid in bringing about a fuller appreciation of the status of subspecies and semispecies, a fact which should not be overlooked in modern systematic treatments, when such populations are involved.

Thus it will be seen that the rate of speciation of the freshwater fishes of Ceylon can be more or less correlated with their ecological tolerance, and the extent to which the different ecological biotopes were affected by environmental changes. Considering the levels of divergences attained by the Quaternary element in Ceylon, it can be said that they exhibit a fairly fast rate of speciation, especially as a genus, nine species and a number of subspecies have evolved during the course of this period on the island. Indeed, had isolation been more complete, concomittant with environmental changes, a much faster rate of speciation would have been expected. At present, fishes of the hill-streams, rivers and lakes seem to be among those most affected, probably as these habitats harbour species with generally limited ecological tolerance.

A comparatively fast rate of speciation of fishes is also known to have taken place in isolated lakes, which share with islands the factor of isolation. Worthington (1937, 1940), Trewavas (1947) and Greenwood (1951) have studied this point in relation to Chiclid fishes of the great lakes of Africa, and Hubbs (1940), speaking of the fishes of the western United States, observed that "in several isolated waters evolution has proceeded far enough to produce new subspecies within what appears to be a few hundred years, at most a few thousand." Therefore, it would be only a conservative estimate if the rate of speciation of Ceylonese fishes is compared with the estimated normal rate of 500,000 years as given for the evolution of new species of mammals (Zeuner, 1946). The point gains emphasis when we remember that freshwater fishes, unlike mammals, are more susceptible to environmental changes.

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