Geographical Distribution of Indian Freshwater Fishes and Its Bearing on the Probable Land Connections between India and the Adjacent Countries.*

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THE relationships and the geographical distribution of the freshwater fishes of India were discussed by two of the leading ichthyologists, Day[3,4]† and Günther[7], of the last century. The former advocated Malayan affinities for the Indian fauna, while the latter, though admitting the migration of several Oriental freshwater fishes to Africa, laid special stress on the African affinities of this fauna. Beyond some casual references[1,2] very little work has since been done on this aspect of the Indian freshwater fishes, and in view of the advances that have been made in our knowledge of the paleogeography and systematics of fishes it seems opportune to review the whole subject in the light of recently discovered facts.

A freshwater fish lives entirely in freshwater, both in the young and adult stages, and never descends to the sea. The above definition excludes all anadromous fishes which are essentially marine but ascend freshwaters for breeding, and the catadromous fishes which are essentially freshwater forms but descend into the sea for similar purposes. As the freshwater fishes are generally restricted to the water courses in which they live, they form a very important group for the elucidation of the paleohydrographical relationships of adjacent lands. Watersheds in the case of these fishes form effective barriers so long as their positions remain unchanged; the process of river-capture, however, may facilitate their migration in one direction but not in the other. There is an unfortunate impression, mainly among geologists, that in the case of fishes dispersal may be effected through the agency of birds, chiefly aquatic species, which may carry the eggs attached to their feet from one watershed to another. Those, who have paid particular attention to this matter, however, are definitely of the opinion that such a mode of dispersal of freshwater fishes is normally highly improbable, even though there may be records of such fortuitous dispersal in practically all groups of animals including freshwater fishes.

In connection with my work on the Siluroid fishes of India for a revised edition of "Fishes" in the *Fauna of British India* series, I have been greatly struck by the close similarity of the Indian forms to those found towards the east in Indo-China, Siam, and the Malay Archipelago. As a result of a detailed study of the genera and species inhabiting these regions I am definitely of the opinion that the freshwater fish fauna of India in the main originated in South-eastern Asia, most probably in Indo-China, and spread westwards by successive waves of migration to India and later to Africa while the two masses of land were connected with each other. Gregory's researches[5,6] on the evolution of the mountain and river systems of South-eastern Asia have shown that in this region there were extensive river captures—the rivers on the west beheading the rivers on the east; these changes made possible the migrations of aquatic animals from the east to the west but not in the reverse direction. Gregory's researches have further shown that all the rivers of Eastern Tibet drained into the Gulf of Siam or the South China Sea before the present river systems became established, and this bears out Pelseneer's view.[12,13] The freshwater fauna of Eastern Asia at least may have originated along the coasts of Indo-China, when the ocean water in this area was greatly diluted by the drainage into it of several river systems.

Professor Gregory's views about the capture of the eastern rivers by the western rivers are, however, not accepted by all geologists, for there is a general belief that the Brahmaputra and the Irrawaddy-Salween systems were separated in the Pre-Eocene period by the Tethys Sea and in the Post-Eocene days by the newly upheaved Himalayas, the

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† Numerals refer to the corresponding numbers in the list of references at the end of the article.

Patkoi Range and the Arakan Yomas. According to these views there could not be any migration of freshwater faunas by a system of river-captures, except perhaps during the transition periods, between the Indo-Chinese rivers and the Indian rivers. Further there is no geological evidence for the Indian rivers having originated in Burma. Some of the peculiarities in the distribution of Indian freshwater fishes may be explained on the supposed existence of the Siwalik or the Indo-Brahm River,[11,14,18] but a considerable mass of evidence bearing on the close relationship and distribution of the fishes of South-eastern Asia demands for its explanation a hypothesis similar to that worked out by Gregory. This mass of evidence is so striking and convincing that it may be worth-while for the geologists to re-examine their data regarding the Cretaceous-Tertiary land connections between India and the Far East.

Mori[10] has recently stressed the Oriental affinities of the fish-fauna of the Upper Yangtse-Kiang which comprises an abundance of the Siluroidea, the Homalopteridæ, the Ophicephalidæ and a large number of Indian genera of the Cyprinidæ. These results fully support Gregory's work according to which the Upper Yangtse-Kiang at first drained into the Red River but later turned northeastwards across Central China to the East China Sea. Only such a course of events could account for the presence of Oriental genera in the Upper Yangtse-Kiang and the Palæarctic genera in its middle and lower portions. According to Mori's researches the Nan Shan Mountain Range divides China into the northern Palæarctic subregion and the southern Oriental subregion.

As a comprehensive example of the east to west migration of the aquatic fauna, one may consider the evolution and distribution of the family Schilbeidæ* which is represented both in the Oriental and the Ethiopian regions by a number of genera. Of the 19 or 20 genera of the family that can be recognised at the present day there is not one that is common to the two regions. If it be conceded that the ancestors of the Schilbeidæ were devoid of barbels and teeth in the jaws, it naturally follows that the African genera, usually with eight barbels and a well-developed dentition, represent a fairly specialised and more highly evolved branch of the family; African genera such as *Ansorgia* Boulenger, with only one pair of mandibular barbels, and *Siluranodon* Bleeker, with no teeth in the jaws, are retrogressive forms as compared with the primitive genera found in the Far East. I believe that *Pangasianodon* Chevey, represents the least specialised form of the family; this genus is found in Indo-China and is characterised by the possession of two minute maxillary barbels, a large air-bladder and no teeth. *Silonia* Swainson, of the Indian waters, also possesses two minute barbels, but owing to its highly predaceous habits, it has developed large caniniform teeth both in the jaws and on the palate. Due to the reduction of its body cavity by the greater development of the caudal region and the lateral compression of the body the air-bladder is greatly reduced. In Peninsular India some less specialised, *Silonia*-like fishes became further modified and developed two additional mandibular barbels; they possess caniniform teeth and a long anal fin but the air-bladder is not so greatly reduced as in *Silonia*. For this new type I have proposed the name *Silonopangasius*.† So far as can be judged at present this line of specialisation only extended as far as the extreme west of Peninsular India.

Pangasianodon-like ancestors also gave rise to forms like *Helicophagus* Bleeker and *Pangasius* Cuvier and Valenciennes; the latter is found from Indo-China to India, while the former, in which the dentition is only partially developed, is found only in the Far East and is absent from Burma and India. Though there are several species of *Pangasius* in Indo-China, Siam and the Malay Archipelago, in Indian waters it is represented by a single, very highly specialised form. Here again the specialisation in form occurs as one proceeds from the east to the west.

In Siam and the Malay Archipelago *Helicophagus* gave rise to the genus *Laides* Jordan (= *Lais*, 6 barbels); possibly *Laides* evolved into *Pseudeutropius* Bleeker (8 barbels) in the Malay Archipelago; the latter genus is also found in India. Certain members of *Pangasius*, probably more specialised as regards dentition, gave rise in

* For a detailed treatment of the classification, distribution, ecology and evolution of the Schilbeidæ reference may be made to my paper, shortly to be published in the *Records of the Indian Museum*.

† Genotype: *Ageneiosus childreni* Sykes, 1841.

Siam to *Platytropius*,* a new genus with extensive patches of vomero-palatine teeth, and with a flattened head and air-bladder, and in India to *Proeutropiichthys*,† a new genus for species of *Pseudeutropius* with four patches of teeth on the palate. In the Indian waters *Pseudeutropius* gave rise to *Ailia* Gray and *Proeutropiichthys* to *Eutropiichthys* Bleeker, the latter genus is also known from Siam. Probably *Platytropius* gave rise to *Clupisoma* Swainson of the Indian Waters. From the primitive stock that gave rise to *Proeutropiichthys*, probably developed all the Schilbeid genera of Africa, at a stage when the mandibular barbels were considerably behind the tip of the lower jaw and were not situated in a straight line. So far no intermediate forms have been discovered between the Indian *Pseudeutropius* (*sensu lato*) and the African *Eutropius*. As the difference in the two forms consists mainly in the position of the mandibular barbels, no palæontological records will ever be able to bridge the gulf between the Indian and the African Schilbeidæ. There is, however, little doubt about the close genetic affinities of the Indian and the African genera of the Schilbeidæ.

According to Regan[16] "The distinctness of the African and the Indian Schilbeidæ makes it probable that this family was established in both regions in pre-tertiary times." The probable history of the dispersal of the Schilbeidæ as understood by me makes it clear that this family must have extended its range to Africa before the two continents became disconnected, probably during or after the Eocene.

The facts detailed above concerning the geographical distribution of the Schilbeidæ are opposed to the theory of permanence of oceans and continents, as they can only be explained by the existence of connected water courses, through either river-captures, commingling or otherwise, over a land connection between India and Africa. Whether this connection was in the form of a "land-bridge" between the two continents, or the two land-masses were merely juxtaposed at some remote period and later drifted apart, it is very difficult to decide. It seems clear, however, that even during the Eocene South India and Africa had land-connections which permitted a dispersal of the freshwater fishes from the former to the latter country. The abrupt change in the African and the Indian Schilbeidæ is certainly the result of some form of isolation since a fairly remote period, and before this occurred presumably the Indian forms were of the same type as those now found in Africa. The higher specialisation of the Indian genera can be accounted for by the fact that India was a centre of great disturbance during the Tertiary period owing to the earth-movements that gave rise to the Himalayas, whereas Tropical Africa with its large lakes provided a stable environment for its fauna and the specialisations of the Schilbeidæ of this region can definitely be correlated with life in comparatively calm and clear waters.

There is also a belief that the Ostariophysi, the class to which Catfishes and Carps belong, originated in the north and spread southward to different continents. This hypothesis would explain the occurrence of allied genera both in India and Africa without the aid of a land connection between the two countries. Regan[16] has already pointed out that this view "involves so many improbabilities as to be almost unbelievable." The mode of dispersal of the Schilbeidæ as detailed above is strongly opposed to the northern origin of the Ostariophysi and appears to be entirely in accord with the recent geological work on the river and mountain systems of South-eastern Asia.

While discussing the African element in the freshwater fauna of India Annandale[2] remarked: "Doubtless the three territories (*i.e.*, Africa, S. America and India) had then a very similar freshwater fauna, but there is some evidence that Africa was its centre of distribution." Unfortunately he made no reference to this evidence, and in view of what is stated above it seems almost impossible to believe that the freshwater fauna of India was at any stage, at least during the Tertiaries, invaded by that of Africa.

Prashad[15] from his study of the recent and fossil Viviparidæ (Mollusca : Gastropoda) came to the conclusion that "Peninsular India forms the central zone whence the Viviparids of Asia and Africa are derived." At the present day, so far as freshwater fishes are concerned, Peninsular India contains many primitive forms, and thus

* Genotype: *Pseudeutropius siamensis* Sauvage, 1883.

† Genotype: *Eutropius macrophthalmus* Blyth, 1860.

superficially it may appear to be a centre of origin of the common Indo-African fauna, but the taxonomic and paleogeographical evidences adduced above show that the freshwater fish-fauna of Peninsular India was itself derived from that of South-eastern Asia.

The close relationship between certain highly peculiar genera of Indo-China and India, such as *Carpiocatla* Boulenger, and *Catla* Cuvier and Valenciennes; *Parapseudecheneis* Hora and *Pseudecheneis* Blyth, *Gyrinocheilus* Vaillant and *Psilorhynchus* McClelland; etc., etc., and the distribution of *Silurus* Linnæus and the Homalopteridæ also prove conclusively that there has been an east to west migration of the freshwater fauna in South-eastern Asia. The older genera, such as *Mastacembelus* Cuvier and Valenciennes, *Notopterus* Lacépède, *Labeo* Cuvier, *Barbus* Cuvier and Valenciennes, *Barilius* Hamilton, *Heterobranchus* Geoffery, *Clarias* Gronovius, etc., which are common to Africa and the Oriental region, probably spread from India to Africa at the time of the Cretaceous buckling which, according to Gregory[6] (p. 134), "produced a series of continental valleys trending east and west fragments of which still survive in Africa in the basins of the Zambezi, the middle Congo, and the northern section of the Niger." The physiography of India, however, underwent considerable changes during the Tertiary period.

In elucidating the geographical distribution of animals, great significance is generally attached to the occurrence of the same genus or species on two distinct land masses. According to the more or less accepted views on evolution a species or a genus can exist unchanged through millions of years only if there had been no change in its *milieu* throughout this period. Even gradual changes in the environment of an animal induce fine adjustments on the part of the organism.[8] Any small changes of organisation are utilised by taxonomists in their system of classification. As the science of taxonomy progresses, animal structure is bound to receive closer and closer scrutiny, with the result that a genus occurring over a wide area will be found to consist of several well-defined groups. Isolation and segregation are two very important factors in the production of new forms,[17] and it seems highly desirable, therefore, to pay more attention to the interrelationship of the seemingly divergent genera of different landmasses rather than to look for precisely identical animals in their fauna. The converse is also true. In the case of similar forms occurring in two widely separated places convergent evolution should not be invoked unless no other explanation seems possible. In the two sets of genera mentioned above the truth of these remarks is clearly brought out.

So far I have referred only to the Far Eastern genera that are found in the Indian waters. There is, however, one genus *Etroplus* Cuvier and Valenciennes of Peninsular India and Ceylon which has its close allies only in Madagascar. Günther[7] accounted for its occurrence in India as follows: "*Etroplus* inhabits Southern and Western India and Ceylon, and has its nearest ally in a Madagasse Freshwater fish, *Pareutroplus*. Considering that other African Chromides [Cichlidæ] have acclimatised themselves at the present day in saline water, we think it more probable that *Etroplus* should have found its way to India through the ocean than over the connecting land area; where, besides, it does not occur." I am in agreement with Günther's supposition and believe that *Etroplus* came to India *via* the sea and, after becoming a freshwater form, probably along the Malabar Coast, it remained confined only to the south-western part of the Peninsula, as the rivers of this area probably never became connected with the Indus and the Ganges systems. Further, it seems probable that *Pareutroplus* Bleeker and *Eutroplus* are derived from a common Cichlid ancestoral form that wandered across from the east coast of Africa to Madagascar and South India where they became acclimatised to freshwater conditions independently.

It is generally believed that the land connection between India and Africa disappeared somewhere about the transition period between the Cretaceous and the Tertiary. It is during the obscure interval between the Cretaceous and the Tertiary that nearly all the modern types of bony fishes originated. Regarding the freshwater Catfishes (Siluroidea), to which the Schilbeidæ belong, there is no evidence that they are of any great antiquity; their first known appearance is indicated by some fossils in the Tertiary deposits of the Siwaliks and the highlands of Pedang in Sumatra, where remains of some of the living genera have been found. I have referred above

to the continuity of distribution of the Schilbeidæ from Indo-China to Africa, and the same is true of the Catfishes of the families Clariidæ and Bagridæ. The Clariidæ live in mud in marshy areas of both countries and have thus retained their primitive habits. On account of this we find that *Heterobranchus* and *Clarias*, the two oldest members of the family, are common to the two continents. Tropical Africa with its vast stretches of ancient lakes provided a more suitable *milieu* for these fishes, some of which took to a burrowing mode of life. Consequently they became eel-shaped and their accessory respiratory organs and the associated skeletal elements became degenerate. In India, on the other hand, the conditions were very unstable during the Tertiary period, with the result that the primitive genus *Heterobranchus*, of which fossil remains have been found in the Siwalik formations of the Lower Pliocene, disappeared altogether and only one highly specialised species of *Clarias*,[9] *C. batrachus* Linn., is now found throughout India, while two other less specialised forms, *C. brachysoma* Günther and *C. dayi* Hora, are confined to Ceylon and the Wynaad Hills respectively.

The Bagridæ, like the Schilbeidæ, became established on both the continents at an early date and after the severance of the connection between the two lands evolved independently so that at the present day there is no genus common to the two regions. However, a close parallelism exists between the forms inhabiting similar situations on the two continents. *En passant* it may also be remarked that most of the other Siluroid families of India and Africa are evolved from the Bagridæ.

A remarkable feature of the Schilbeidæ is that no member of the family is found in Ceylon, which may be due to the fact that Ceylon became separated from India at a stage earlier than the disappearance of the land connection between India and Africa. The absence of the Schilbeidæ from Ceylon may also be explained on the assumption that at some period the water courses changed in such a way that in spite of the land connection between India and Ceylon no migration from the north to the south could take place. It is thus seen that unlike the distribution of the land animals, where probably the climatic considerations are of the greatest importance, the aquatic animals are bound within their watersheds and in spite of land connections and favourable climatic conditions between two adjacent lands may not spread from one to the other if their water courses had no chance to become continuous at some period or another. The distribution of fishes, therefore, though extremely important in zoogeographical studies, has thus only a limited value in elucidating the extent of the former land and sea connections.

In this east to west migration of the fauna I have assumed throughout that India was connected with the Far East, at least from the late Cretaceous onwards. This connection was of a very different nature from what it is to-day, for in the early Tertiaries a considerable part of Northern India was under the sea. The Bay of Bengal is considered to be an ancient feature of the physiography of India, so that the old connection between India and the Far East probably stretched over the Peninsula through the coal-field areas of Bengal to the Assam Hills, North Burma and beyond. At certain periods the direct land connection between Assam and Burma was cut off by an arm of the sea, but still Assam remained connected with the Far East through Tibet and Southern China. The distribution of the Indian freshwater fishes affords ample evidence in support of these routes of migration.

I may also refer here to the remarkable similarities between the faunas of the Malay Archipelago, Malabar Zone of South India and Tropical Africa. To account for these anomalies of distribution several workers have been led to establish a southern continent including South America, but of which Madagascar did not form a part. In my opinion when the primitive forms were spreading from Indo-China to Africa they sent branches to the south in all areas over which they passed, and as these southern extremities were away from the main centre of disturbance (the Himalayas) and also somewhat out of the way of the succeeding waves of migration they continued to harbour primitive animals in, what one may say, these corner seats. The islands of the Malay Archipelago, such as Java, Sumatra, Borneo, etc., the Malabar Zone of India and West and South Africa to-day form the limits of the ancient waves of migration and consequently contain many primitive forms, which, owing to the

severance of land connections, could not spread any further. Of the genera I have referred to above, *Heterobranchus* of the Clariidæ shows a discontinuous distribution as it is found in Africa on the one hand and in Banka and Borneo on the other. There is no doubt that even in the Lower Pliocene period its range of distribution must have been more or less continuous, as fossils are known from the Siwalik formations of that period.

It seems highly probable that the southward migration of the Indo-Chinese fauna in the region of the Malay Archipelago must have followed the course of the Indo-Malayan Mountains and of the Malay Arc[5] by a series of river-captures. The strong similarity between the fauna of South India and that of the Malay Archipelago[5] is probably not due to the migrations of the forms *inter se* but to their common origin from an east to west migrating, primitive stock.

In the above discussion I have not taken into consideration the route of migration that now exists between North-western India, through Baluchistan, Persia, Mesopotamia, Palestine, etc., to Africa. This route is known as Jocobi's Arabian region of dispersal and does not seem to have played any important part in the interchange of the freshwater faunas from Africa to India. Some of the Indian forms, however, such as *Glyptothorax* Blyth, *Garra* Hamilton, etc., have undoubtedly spread westwards along this route. *Scaphiodon* Heckel appears to be the only form that may have spread from Persia, Baluchistan and Sind to the Western Ghats.

To sum up it may be stated that the evidence provided by the distribution of the freshwater fishes of India indicates an eastern origin of the fauna and its subsequent dispersal to the west. The close relationship between the Indian and the African freshwater fishes can only be explained on the assumption of a land connection between the two countries. The absence of the Schilbeidæ from Ceylon and their presence in Africa suggests that Ceylon may have become separated from India at a stage earlier than the severance of the land connection between Africa and India. The distribution of freshwater fishes shows that Peninsular India had a land connection with the Far East, at least from late Cretaceous onwards, and probably at no time during this interval it became an island. The similarity in the faunas of South and West Africa, South India and the Malay Archipelago are probably due to the fact that they received branches of the primitive stock when it was migrating from the east to the west along a northern and a considerably more disturbed part of the Oriental region. The above review of the subject clearly shows that there is no African element in the freshwater fish-fauna of India. The existing connection of Africa with North-western India is comparatively of a much more recent date and does not seem to have played any important part in the dispersal of the freshwater faunas.

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