PARALLEL EVOLUTION OF THE GASTROMYZONID FISHES ON THE MAINLAND OF ASIA AND IN THE ISLAND OF BORNEO.

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(*Received January 15; read March 7, 1952.*)

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INTRODUCTION.

In his 'Zoogeography of the land and inland waters', de Beaufort (1951, p. 88) makes the following statement about the interrelationships and geographical affinities of the Gastromyzoninae of Borneo:

> 'In mountain torrents of northern Borneo certain curious fishes are found belonging to the Homalopteridae. Among fishes in this group they have gone farthest in the way of adaptation to life in fast-running water, as the whole flat underside, surrounded by the much expanded pectoral and pelvic fins, forms a large sucker by which the fish can adhere to stones or rocks. Two genera, *Gastromyzon* and *Neogastromyzon*, are known from Borneo, but closely allied forms are found in the mountain streams of southern China. They are unknown from Java, Sumatra, Malaya, or Siam; and the most probable explanation of their occurrence in Borneo is that they came by a direct route from China. This involves a connection between Borneo and China of some altitude, for it is not probable that these fishes could disperse through lowland rivers. Nor is it probable that they used the Pleistocene land bridge through the Philippines and Formosa, for in that case we should expect to find Gastromyzoninae in the mountains of these islands. As the two Bornean genera are endemic, it is also improbable that they reached Borneo so late. They seem to belong to an older invasion, and their occurrence in the upper course of the Mahakam is in favour of this view'.

In 1932, I proposed a classification of the Homalopteridae and suggested their polyphyletic origin. The two subfamilies into which they were grouped were divided into genera and it was shown that the union of pelvic fins to form a sucker had occurred independently in the two subfamilies, *Sinogastromyzon* of the Homalopterinae and *Gastromyzon*, *Neogastromyzon* and *Beaufortia* of the Gastromyzoninae. Since then, *Metahomaloptera* among the Homalopterinae has also been described with the same character. Though the adaptive nature of this character cannot be denied, no genetic significance can be attached to it, similarly as reduction of gill-openings has taken place in several diverse groups of fishes in which the ventral surface is closely applied to a hard substratum. In this paper, it will be shown that the Gastromyzonid fishes of Borneo had an independent, though parallel,

evolution from a generalized Cobitid stock and are in no way genetically related to the similar forms found in China. From a considerably wider distribution of the Homalopteridae and a somewhat restricted distribution of the Gastromyzonidae, it is abundantly clear that the former is much older than the latter, so the Gastromyzonidae could not be older than the late Pliocene when no direct connection existed between China and Borneo (*vide* de Beaufort, 1950, fig. 7, p. 86). We shall now examine the question in greater detail.

In a recent paper, I (1950, p. 46) referred to the polyphyletic origin of the family Homalopteridae and suggested its division into two families, Homalopteridae derived from the Cyprinidae and Gastromyzonidae derived from the Cobitidae. Fang (1935, p. 44) had already recognised two distinct groups of fishes among the Gastromyzonidae which he distinguished by the following characters:

> 'Crossostomoid fishes are small forms inhabiting the mountain torrents. They are well separated from the gastromyzonian fishes in having the gill openings extending to the ventral side of body and the pectoral fins set immediately behind them.'

Fang published a review of the Crossostomoid fishes of China which he derived from a 'Nemachiloid ancestral stocks'. Further, he regarded them as having been evolved independently along three lines, namely, (i) *Annamia* Hora; (ii) *Liniparhomaloptera* Fang and *Parhomaloptera* Vaillant, and (iii) *Vanmanenia* Hora, *Praeformosania* Fang, *Formosania* Oshima and *Crossostoma* Sauvage. Though one may not agree with Fang's views of the inter-relationships of the various Crossostomoid genera, it is certainly true that they form a heterogenous assemblage of independently evolved forms under the stress and strain of the very exacting environmental factors so characteristic of the torrential streams of south-east Asia.

Further support is lent to this view by the fact that the typical Gastromyzonid fishes, characterized by small gill-openings restricted to the dorsal and lateral sides and not extending to the ventral surface, also show several independent lines of evolution. The most striking fact is perhaps a uniformity of structure among the genera known from the mainland of Asia and their divergence collectively from the genera known from Borneo. In this article an attempt is made to define these two divergent groups of Gastromyzonid fishes and to indicate their independent evolution.

Distribution and Characterization of the Gastromyzonid Genera.

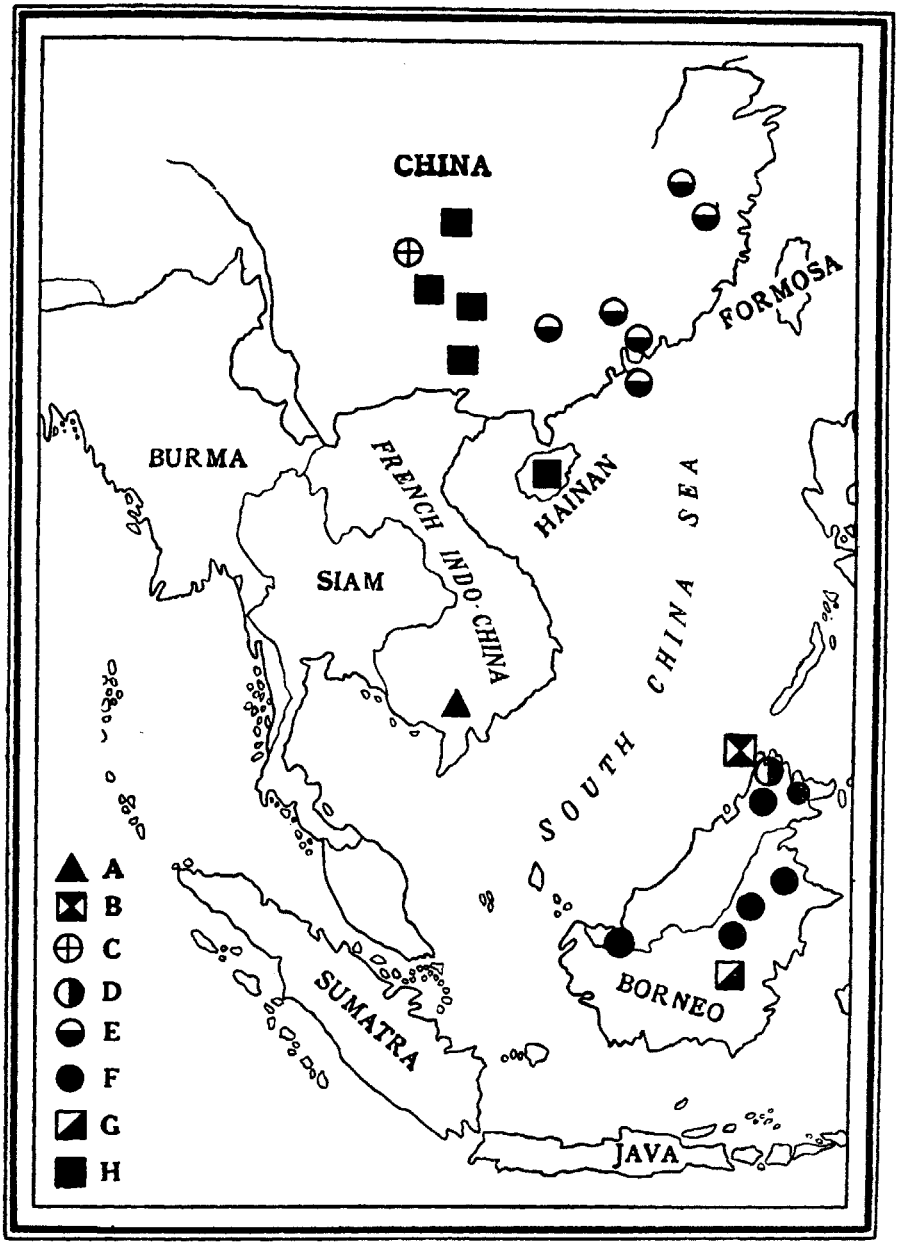
According to their distribution, the eight Gastromyzonid genera known so far can be arranged into two geographical units as given below:

Mainland of Asia.

(1) *Paraprotomyzon* Pell. & Fang	.. Szechuan, China.
(2) *Pseudogastromyzon* Nichols	.. Fukien, China.
(3) *Beaufortia* Hora ..	.. Hainan, Kwangsi & Szechuan, China.
(4) *Sewellia* Hora	.. Cochin-China.

Island of Borneo.

(1) *Protomyzon* Hora ..	.. Mt. Kina Balu, Borneo.
(2) *Neogastromyzon* Popta ..	.. Howong, Borneo.
(3) *Progastromyzon* Hora & Jayaram	.. Mt. Kina Balu, Borneo.
(4) *Gastromyzon* Günther ..	.. Torrential streams, Borneo.



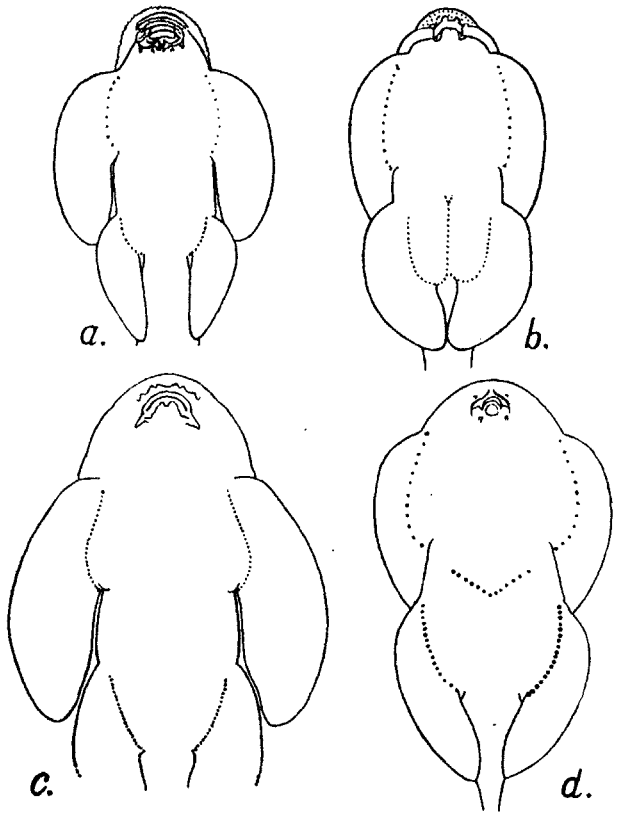
TEXT-FIG. 1. Map showing the distribution of the Gastromyzonid fishes.

A. *Sewellia* Hora; **B.** *Progastromyzon* Hora and Jayaram; **C.** *Paraprotomyzon* Pell. and Fang; **D.** *Protomyzon* Hora; **E.** *Pseudogastromyzon* Nichols; **F.** *Gastromyzon* Günther; **G.** *Neogastromyzon* Popta; **H.** *Beaufortia* Hora.

It may be noted that no genus of the mainland is found in Borneo and *vice versa*. It may also be noted that no Gastromyzonid fish has yet been recorded from Java, Sumatra, Malay Peninsula, Siam, Burma and further west. Thus the Gastromyzonid fishes are restricted to comparatively narrow geographical zones within the two regions.

Common and Contrasting Features of the Gastromyzonid Genera.

Common feature.—It has been pointed out above that all the Gastromyzonid fishes, as distinguished from the Crossostomoid fishes, are characterized by the

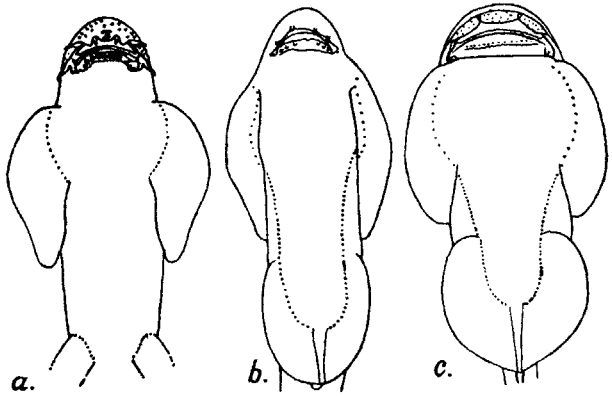


Text-fig. 2. Sketches of the ventral surfaces of the head and body of the Gastromyzonid genera of the Mainland of Asia.

(*a*) *Pseudogastromyzon* Nichols; (*b*) *Beaufortia* Hora; (c) *Paraprotomyzon* Pell. and Fang; (*d*) *Sewellia* Hora.

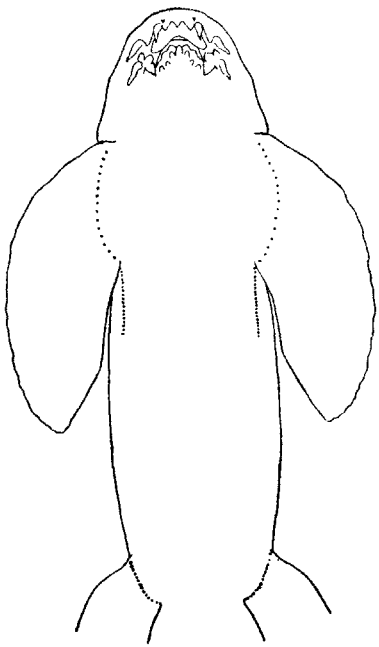
presence of restricted gill-openings. This character is shared by a number of diverse fishes that closely apply their ventral surface to rocks for adhesion. In the hill-streams of South-east Asia, I have found similar modifications among the Glyptosternoid group of Sisorid fishes (Hora & Silas, 1951) and in *Bhavania* Hora (1941) and *Metahomaloptera* Chang (1944) among the Homalopteridae. Though it is a useful taxonomic character, as explained already, it is a purely adaptive feature and, therefore, no phylogenetic significance can be attached to it.

Contrasting features.—In all the mainland genera, the pectoral fins extend beyond the bases of the pelvic fins so that the ventral surface enclosed between them can act as a sucker for adhering to rocks in swift currents. Another



TEXT-FIG. 3. Sketches of the ventral surfaces of the head and body of three Gastromyzonid genera of Borneo.

(*a*) *Progastromyzon* Hora and Jayaram; (*b*) *Neogastromyzon* Popta; (*c*) *Gastromyzon* Günther.



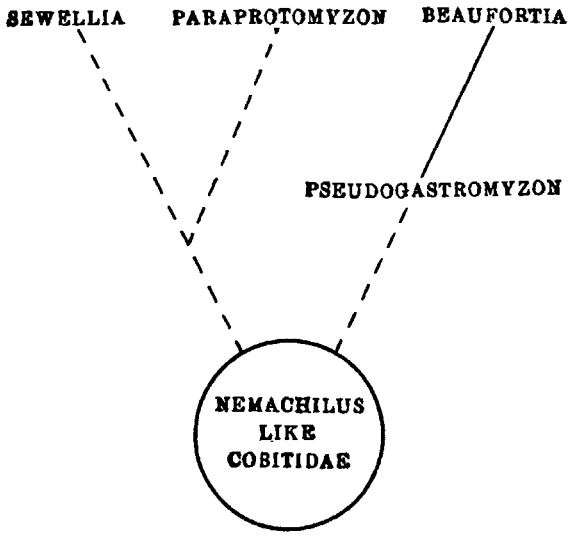
TEXT-FIG. 4. Sketch of the ventral surface of the head and body of the Bornean Gastromyzonid fish *Protomyzon* Hora.

characteristic feature of these genera is the small size of the mouth, which is less than one-third of the width of the head.

In the Bornean genera, on the other hand, the pectorals are separated from the pelvics by a considerable distance, but in highly specialized forms, such as *Gastromyzon* and *Neogastromyzon*, lateral flaps of skin are developed to bridge over the space between the paired fins so as to convert the ventral surface into a suctorial disc. Thus we have a functional convergence achieved through divergent modifications of structures. As regards the extent of the mouth, the four Bornean genera are divisible into two groups. In *Progastromyzon*, *Gastromyzon* and *Neogastromyzon*, the mouth is very extensive and is more than half of the width of the head, while in *Protomyzon* the mouth is about one-third of the width of the head. In any case, it is still of a different type than that characteristic of the mainland forms.

Relationships of the Gastromyzonid Genera.

In dealing with the common and contrasting features of the mainland and Bornean genera, it has been shown that whatever may have been their ancestral stocks, they have collectively shown independent lines of evolution in regard to

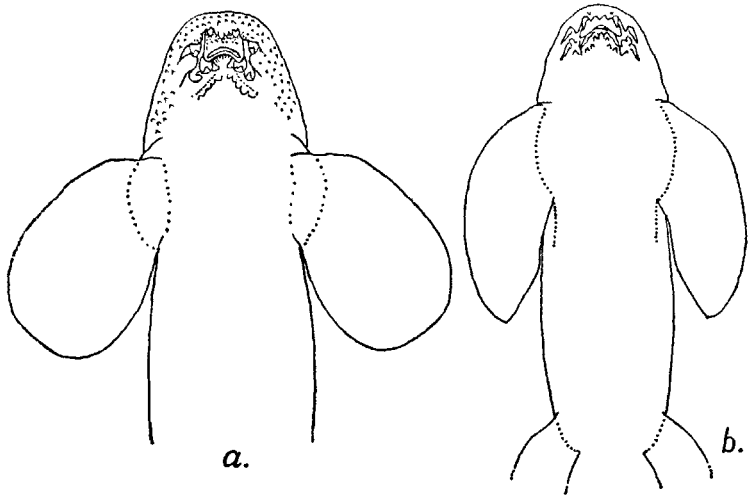


Text-fig. 5. Diagrammatic representation of the probable relationships of the mainland Gastromyzonid genera.

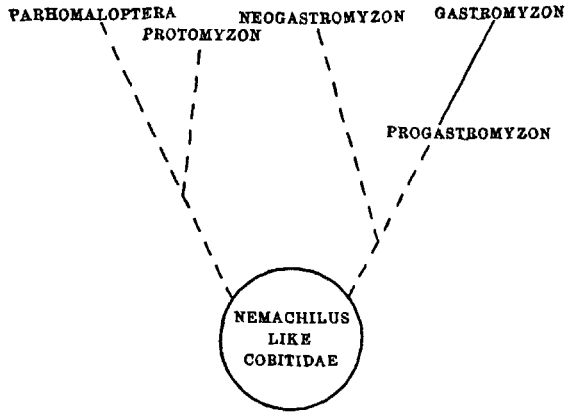
the characters of the paired fins, skin flaps and form of mouth. It is interesting to recall here that from the study of scales, Law (1950, p. 82) found a closer affinity between *Protomyzon* and *Gastromyzon* on the one hand and between *Paraprotomyzon* and *Pseudogastromyzon* on the other. The scales of *Beaufortia* were found to be quite different from either. We may now examine the inter-relationships of the genera in each geographical group.

The four genera of the mainland do not show any direct linear relationships and perhaps many forms yet remain to be discovered before we can tell the complete story of their evolution. *Sewellia* Hora (1932, p. 315), both on account of its geographical isolation in Cochin-China, as well as its peculiar respiratory mechanism and plate-like rostral barbels, seems to be quite distinct from the other three genera. Of the remaining three genera, *Paraprotomyzon* Pell. & Fang (1935) may possibly have separated off from the *Sewellia* stock at an early stage. *Pseudogastromyzon*

Nichols (Hora, 1932) seems to be somewhat more generalized and may have given rise to *Beaufortia* Hora (1932, p. 318). In the union of the pelvic fins to form a sucker, *Beaufortia* is more specialized than all the other genera of the mainland group. With our present imperfect knowledge, we may represent the evolution of these genera as shown in text-fig. 5.



TEXT-FIG. 6. Ventral surface of head and anterior part of body of *Parhomaloptera* Vaillant and *Protomyzon* Hora.
(*a*) *Parhomaloptera* Vaill.; (*b*) *Protomyzon* Hora.



TEXT-FIG. 7. Diagrammatic representation of the probable relationships of the Bornean Gastromyzonid genera.

The four Bornean genera do not show any direct linear relationships either. *Progastromyzon* and *Gastromyzon* suggest the evolution of the latter from the former, while *Neogastromyzon* may have either evolved independently or from the *Progastromyzon-Gastromyzon* stock at a very early stage. The narrow-mouthed *Protomyzon* is certainly quite different from the other three genera. From the structure of its mouth parts, it seems to have been evolved from the Crossostomoid

genus *Parhomaloptera* Vaillant. In fact, *Protomyzon* can be regarded as a *Parhomaloptera* with the gill-openings restricted to the sides and not extending to the ventral surface. We have an exact parallel to this in the two Homalopterid genera, *Bhavania* Hora and *Homaloptera* van Hass. The former is a *Homaloptera* with the gill-openings restricted to the dorso-lateral surfaces. The evolution of the Bornean Gastromyzonid fishes can be represented as shown in text-fig. 7.

It will be presumed from what is stated above that the Gastromyzonid fishes have not only evolved independently from the Cobitid stocks on the mainland of Asia and the island of Borneo, but in each geographical region they show polyphyletism in their mode of evolution. Similar adaptive modifications have occurred again and again among the fishes of the torrential streams of south-east Asia with the result that we have at present very complicated adjustments through convergences and divergences of characters. Only a careful taxonomic assessment of various characters could reveal the true systematic position of the various genera. From the remarkable anticipated discoveries made since the publication of my monograph of the 'Homalopteridae' in 1932, it seems probable that several new forms still remain to be discovered and, when this is done, they will help us to bridge the present-day gulfs in our knowledge and to elucidate correctly the evolutionary trends of these remarkable fishes.

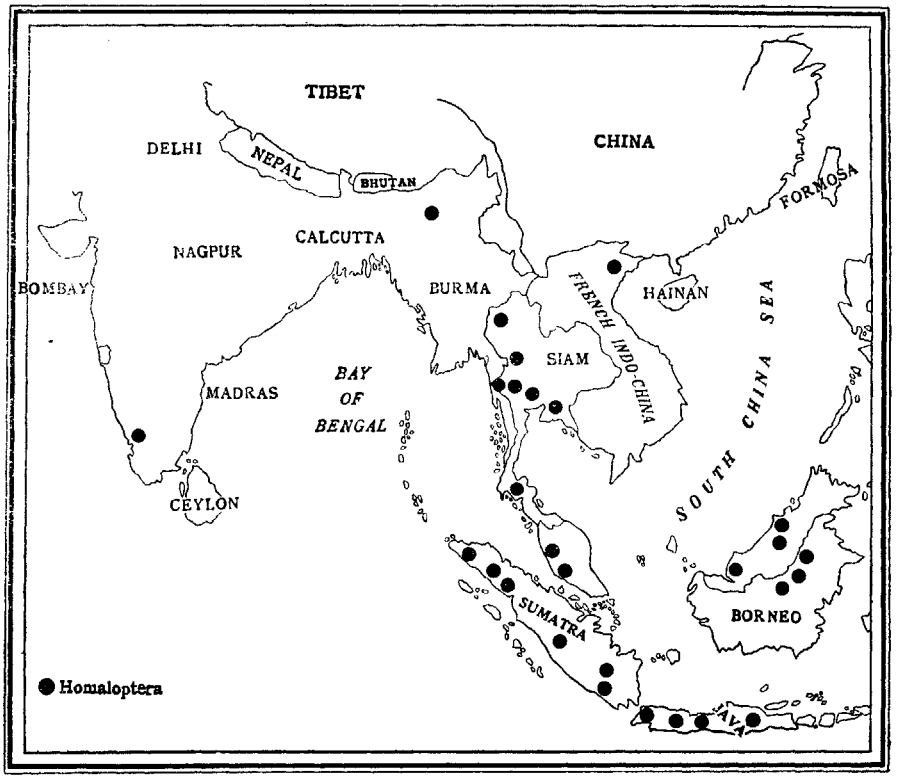
Space and Time in the Evolution of the Gastromyzonid Fishes.

Students of distribution of freshwater fishes of south-east Asia are no doubt aware that the route of dispersal of the specialized hill-stream forms from the mainland of Asia to the islands of the Indo-Australian Archipelago lay along the Malayan Arc of mountains. This is beautifully illustrated by the distribution of the fishes of the genus *Homaloptera* (*sensu lato*). To Borneo, the path from the mainland lay across the Malay Peninsula, Sumatra and Java. Borneo, with the Malay Peninsula, eastern Sumatra, part of the north coast of Java and the sea basin between them constituted the stable block known as Sundaland. Lowlands, however, presented a barrier to the dispersal of mountain species, so mere land connections could be of little use in their distribution. Text-figure 1 will show that the mainland Gastromyzonid fishes are found to the east of the Malayan Arc movements and were, therefore, not affected by this route of migration in their dispersal. This geographical fact supports the view, advanced above on morphological grounds, that the Gastromyzonid fishes evolved independently on the mainland of Asia and in Borneo, and have had no geographical continuity with each other during their evolutionary history. It has to be borne in mind that the Cobitidae, which formed the ancestral stock for the evolution of the Gastromyzonid fishes of Borneo, must have migrated along the Malayan Arc to Borneo much earlier than the period of evolution of the Gastromyzonid fishes.

As to the period taken for the evolution of the *Gastromyzonid* fishes, we have a yardstick in the evolution of the Homalopteridae in Peninsular India. The dispersal of the Cobitidae took place when India and Ceylon, and India and north-east Africa had more or less continuous hilly connections. Between Ceylon and India such a connection existed during the Pliocene (Jacob, 1949) and probably between India and Africa up to the Pleistocene (Menon, 1951). It can reasonably be presumed that Borneo also received its Cobitid fauna in the Pliocene or early Pleistocene. The genus *Homaloptera* is found in the Western Ghats just below the Palghat Gap and two other genera evolved from it, *Bhavania* and *Travancoria*, are found further south, but no Homalopterid fish has yet been recorded from Ceylon. It is presumed that the Homalopterid genera characteristic of Southern India probably came into existence when tilting of the Peninsula elevated the zone of the Western Ghats during the Pleistocene. This tilting of the Peninsular block

rejuvenated the streams in the Western Ghats and produced torrential streams characteristic of the younger mountains, like the Himalayas.

As in the case of the Homalopteridae, in the Gastromyzonidae also the taxonomic differences involved are of generic value, but this must be considered against the factors which might have influenced the evolution of the Gastromyzonidae in two distinct regions. In the author's opinion, the tempestuous environment of torrential streams having been repeatedly disturbed and intestified by the Pleistocene orogenic movements in South-east Asia provided factors of sufficient importance for inducing rapid evolutionary divergences among hill-stream fishes. I am, therefore, led to conclude that the great majority of forms dealt with in this paper are most probably not older than the early Pleistocene.



TEXT-FIG. 8. Map showing the distribution of the genus *Homaloptera* (*sensu lato*).

SUMMARY.

Morphological, palaeogeographical and geological evidences all point to the conclusion that the Gastromyzonid fishes of Borneo evolved independently of those now found on the mainland of Asia. Whereas there is a general plan of similarity of structures in the four genera of mainland, the four genera of Borneo show two independent lines of evolution even with regard to the main characters. There is sufficient evidence to indicate that even the four genera of the mainland had diverged from one another at a very early stage of their evolutionary history. In studying the characters of these genera in relation to the needs of the environment, the conclusion cannot be resisted that the Gastromyzonidae form a convergent group of forms derived from divergent Cobitid species. Though the convergent characters are no doubt due to the similarity in environment, the generic and specific differences are the results of the initial structures possessed by each evolving species.

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