EVOLUTION AND DISTRIBUTION OF GLYPTOSTERNOID FISHES OF THE FAMILY SISORIDAE (ORDER: SILUROIDEA).

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(*Received December 4, 1951; read January 1, 1952.*)

CONTENTS.

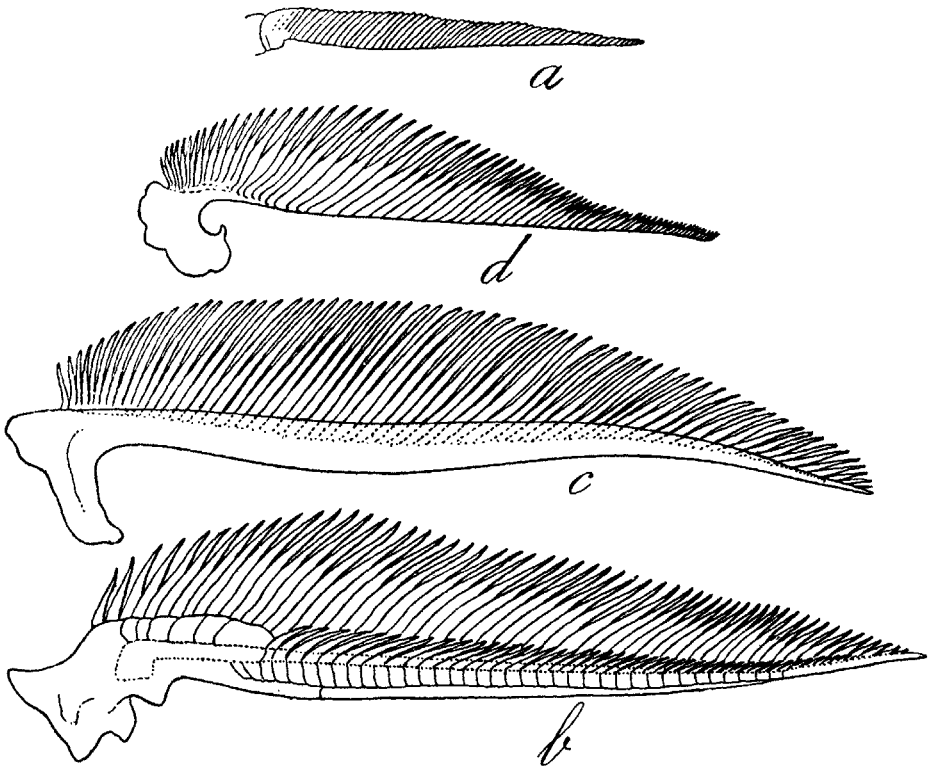
INTRODUCTION.

One of us (Hora, 1922, 1923) discussed the systematics of the Glyptosternoid fishes of the family Sisoridae nearly a generation ago and a great controversy has raged since then regarding the views expressed by him. Examination of the abundant material in the collection of the Indian Museum and the views of many eminent ichthyologists on the nomenclature and taxonomy of these fishes have enabled us (1951) to attempt a detailed revision of this remarkable association of fishes. We have now been able to recognise as many as 7 genera and 19 species pertaining to the *Glyptosternum*-group of fishes. The main diagnostic characters on which they have been separated are: (i) dentition (structure and arrangement of teeth); (ii) nature of gill-openings (whether restricted to the sides or extending to ventral surface); (iii) extent of pectorals in relation to the position of the pelvics; (iv) nature of labial groove (continuous or discontinuous); and (v) the number of rays in the pectoral and pelvic fins. Habituated as these fishes are to torrential waters and rocky streams, the adaptive significance of the above characters cannot be doubted. It is the purpose of this article to evaluate the significance of these characters in the evolution and adaptation of these genera, and to show how ecological conditions or geographical isolation have brought about a great diversity of form and structure among them.

GLYPTOSTERNOID GROUP: STRUCTURE OF THE FIRST RAY OF PECTORAL AND PELVIC FINS.

The name Glyptosternoid fishes is restricted to *Glyptosternum* McClelland and its closely allied forms, and does not include *Glyptothorax* Blyth, *Pseudecheneis* Blyth and similar other allied Sisorid genera. The fishes of the Glyptosternoid group can be readily distinguished from the other Sisorid fishes, which also live in rapid waters, by the absence of an adhesive apparatus in the thoracic region and by the complete segmentation or pinnate condition of the first ray of the pelvic and pectoral fins. In *Glyptosternum* McClelland (*sensu stricto*), 'the first ray of the pectoral and ventral fins soft and pinnate, giving off soft pointed cartilagenous

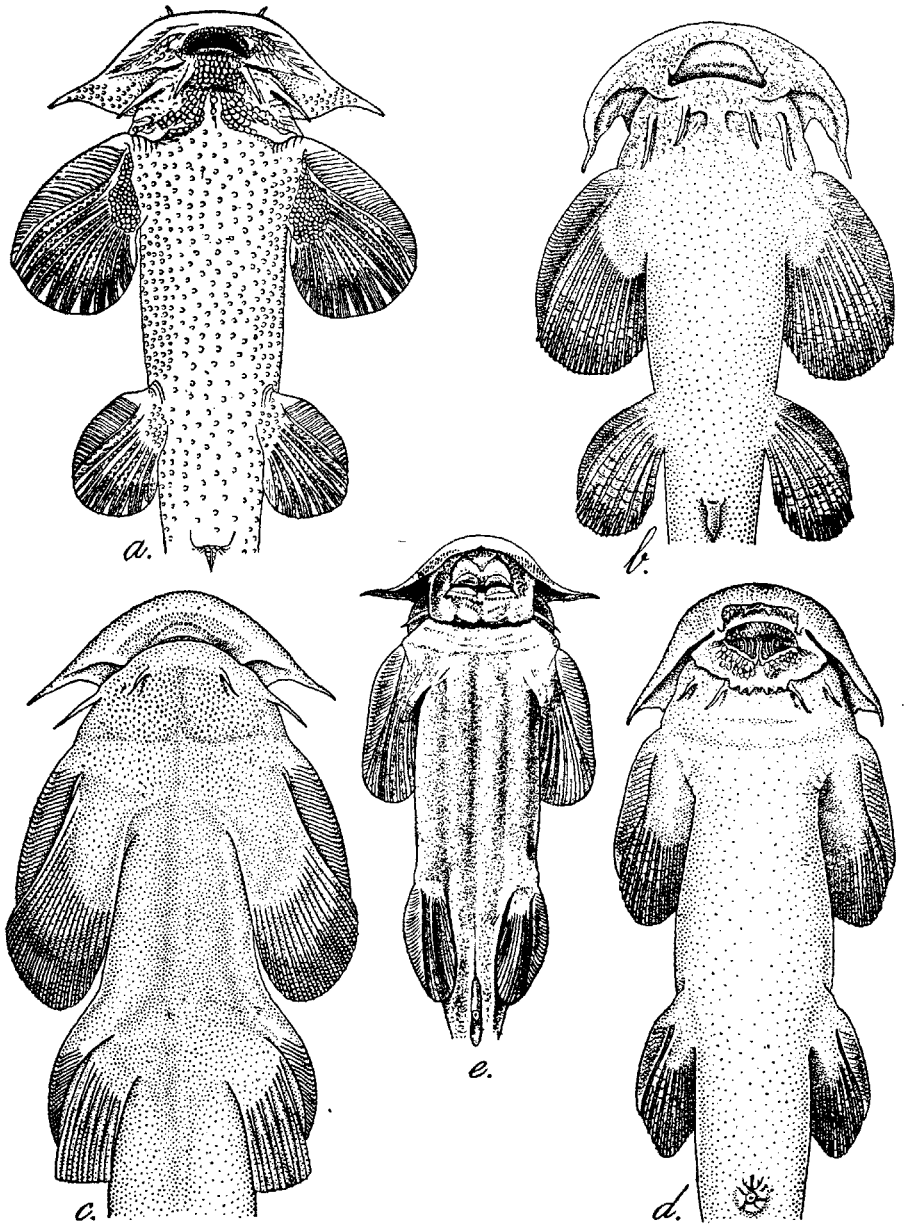
rays along the anterior margin; which are enveloped in the membrane of the fin' (McClelland 1842). In *Coraglanis* Hora & Silas,[1] *Glaridoglanis* Norman, *Euchiloglanis* Regan and *Myersglanis* Hora & Silas,[1] soft, pointed, cartilagenous rays are present, but the rays themselves are distinguishable, though segmented in part or wholly. In *Exostoma* Blyth, the rays are not pinnate but are completely segmented. In regard to the modifications of these rays, we have thus an evolutionary series from *Exostoma*-type of structure to the *Glyptosternum*-type, and there is little doubt that these modifications have an adaptive significance. The pinnae or the cartilagenous rays correspond externally to the ridges and



TEXT FIG. 1. Internal structure of the outer ray of the pectoral spine in:
(*a*) *Exostoma labiatum*. (*b*) *Euchiloglanis hodgarti*. (*c*) *Coraglanis kishinouyei*. (*d*) *Glyptosternum reticulatum*.

grooves of the skin on the ventral surfaces of these rays to which the function of adhesion has been transferred from the thoracic region. In this character, *Exostoma* is least specialised. In fact, Blyth (1860) in erecting this genus stated 'otherwise generally similar to *Glyptothorax*, but with no pectoral disk'. We also consider that the group of Glyptosternoid fishes, as defined above, originated from *Glyptothorax*-like ancestors under the stress of stronger currents and necessity for more efficient mechanism of adhesion. The segmentation of the spine makes it pliable to stresses in swift currents and its pinnate nature affords a greater adhesive area to be applied to the substratum along with flexibility.

[1] The descriptions of the new genera and species are under publication in the *Records of the Indian Museum*.



TEXT-FIG. 2. Ventral view of the Glyptosternoid fishes showing the nature of the labial-fold: (*a*) *Glyptosternum reticulatum*. (*b*) *Coraglanis kishinouyei*. (*c*) *Euchiloglanis hodgarti*. (*d*) *Oreoglanis siamensis*. (*e*) *Exostoma labiatum*.

LIPS AS ORGANS OF ADHESION: LABIAL FOLD CONTINUOUS OR INTERRUPTED.

Another character by which Blyth distinguished his *Exostoma* from *Glyptothorax* was the nature of the lips. He stated that in *Exostoma* 'Lips reflected and spread continuously round the mouth, so as to form a broad flat sucker'. In

species of *Glyptothorax*, the lips are papillated and serve as organs of adhesion (Bhatia, 1950). In species like *G. horai* Shaw and Shebbeare, the thoracic adhesive apparatus extends as far forwards as the lips. In the species of *Glyptothorax*, in which striated adhesive pads are developed on the under surface of the pelvic and pectoral spines, the adhesive organ on the chest is reduced. Thus to combat the effect of torrential currents, the lips as well as the pectoral and pelvic fin rays are both pressed into service for purposes of adhesion. Whereas in forms like *Exostoma*, *Oreoglanis* and *Myersglanis*, both the lips and the fin rays are equally useful for adhesive purposes, in *Glyptosternum*, *Coraglanis*, *Euchiloglanis* and *Glaridoglanis* the function of adhesion is more or less relegated to the fins and in consequence the labial fold is interrupted and the lips are not reflected and spread continuously round the mouth. They live in deeper waters of the main rivers of Central Asia where the swiftness of current does not affect them to the same extent as in small, shallow, torrential streams. As, owing to the position of the tooth-bands, the mouth cannot be completely closed in *Exostoma*, *Oreoglanis* and *Myersglanis*, the suctorial lips may have arisen as a respiratory adaptation so as to prevent the outflow of water through the mouth during the expiratory phase of respiration. Normally, during exhalation, most fishes keep their mouths shut but owing to the position of the tooth-bands, this is not possible in these fishes. The broad, reflected lips round the mouth now serve both at the time of exhalation and also when the fish wants to secure a firm hold to the substratum during floods. In both cases, the function of the expanded lips remains the same—adhesion.

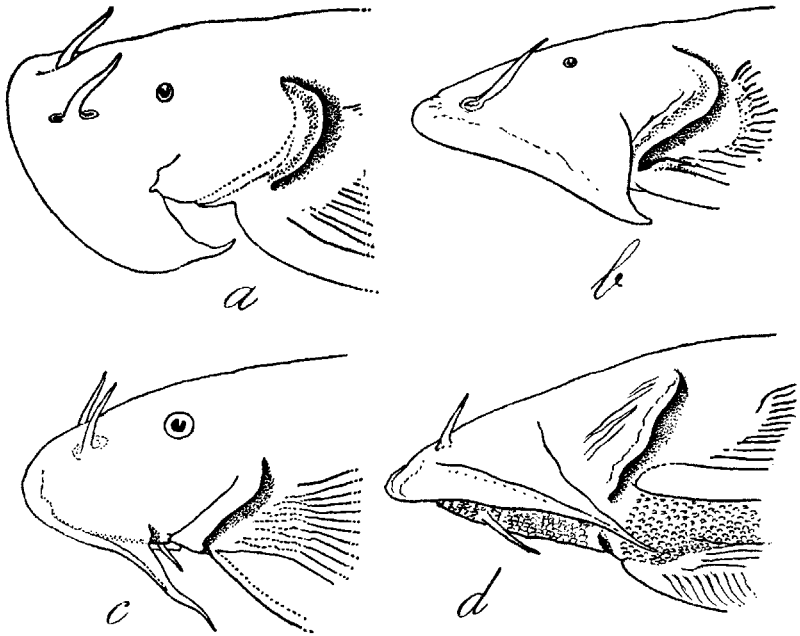
Inner rays of paired fins: Pressure-reducing device.

In specialised hill-stream fishes, it has been pointed out by one of us (Hora, 1930, p. 218), that the inner rays of the paired fins are used for pumping out leakage water from the ventral surface of the fish so as to reduce pressure on the ventral surface for ensuring perfect adhesion to the substratum. In forms, in which the first rays of the pectoral and pelvic fins have formed an efficient organ of adhesion or the currents are not so tempestuous, the need for pumping function is probably less and therefore the number of such rays remains small as in *Glyptosternum* (P. 1/11); *Coraglanis* (P. 1/13) and *Glaridoglanis* (P. 1/10). Pectorals do not overlap the pelvics in these genera and are separated from each other by a considerable distance. In *Exostoma*, where the function of adhesion is shared by the lips and the first rays of the paired fins, the number of branched rays in the pectoral fins is also less (P. 1/10–12) and the pectorals do not overlap the pelvics (exception, *E. yunnanensis* where the pectorals have 17 rays). Judging from the standpoint of functional morphology of the characters of forms like *Oreoglanis* and *Myersglanis*, they would appear to be better adapted, for a torrent life, for besides possessing adhesive fin rays and lips, they possess as many as 16–19 branched rays in the pectoral fins. The pectorals do not, however, overlap the pelvics. In ? *Oreoglanis macropterus* the pectorals overlap the pelvics thus converting the entire ventral surface into a sucker. In *Euchiloglanis hodgarti* (Hora), the pectorals just overlap the pelvics and the number of branched rays in the pectorals is 17. The increase in the number of branched rays in the paired fins and the extent of the pectorals in relation to the pelvics are highly adaptive modifications in hill-stream fishes.

Extent of Gill-openings: Restricted to above or Extending below base of pectoral.

With the exception of *Glyptosternum*, which is a Trans-Himalayan genus of deep, swift, rocky rivers, the gill-openings in all other genera are restricted to the dorso-lateral sides and do not extend to the ventral surface of the fish. In all fishes

that apply their ventral surface to some substratum, irrespective of the habitat they may live in, the lower portion of the gill-opening becomes non-functional and gets gradually closed up. The reduction of gill-openings in these fishes is further facilitated by the fact that the torrents are well-oxygenated and the fishes have



TEXT-FIG. 3. Nature of the Gill-openings in the Glyptosternoid fishes:
(*a*) *Coraglanis kishinouyei*. (*b*) *Euchiloglanis sinensis*. (*c*) *Exostoma vinciguerrae*. (*d*) *Glyptosternum reticulatum*.

developed gill-pouches to retain a certain quantity of water in the gill-chambers for respiration, like air in most air-breathing fishes. In species of the same genus, one finds that the extent of the gill-openings may vary when it is restricted to the dorso-lateral surface. This is, however, an evolutionary phase in the reduction of gill-openings to small openings well above the bases of the pectoral fins.

GEOGRAPHICAL DISTRIBUTION.

Before considering the above characters collectively as constituting genera and species, it is necessary to give the geographical distribution of the various forms. The following table and the accompanying map give the distribution pattern of the various species.

It will be seen that *Glyptosternum* is a trans-Himalayan genus with two well-defined species, one in the west (*G. reticulatum*) and the other in the east (*G. maculatum*). These two species may have had a common ancestral form when the trans-Himalayan portions of the Indus and the Brahmaputra had more connections. Now the two forms are isolated and have diverged from each other. *G. akhtari* is closely allied to *G. reticulatum*, a widely distributed and variable species, but has developed specific characters just as the Bamian Trout (*Salmo trutta orientalis*) became a distinct race in this river. There can hardly be any doubt that the ancestral form of *Glyptosternum* must have had been a *Glyptothorax*-like ancestor. The dentition, the mouth parts, etc., are of a less specialized nature.

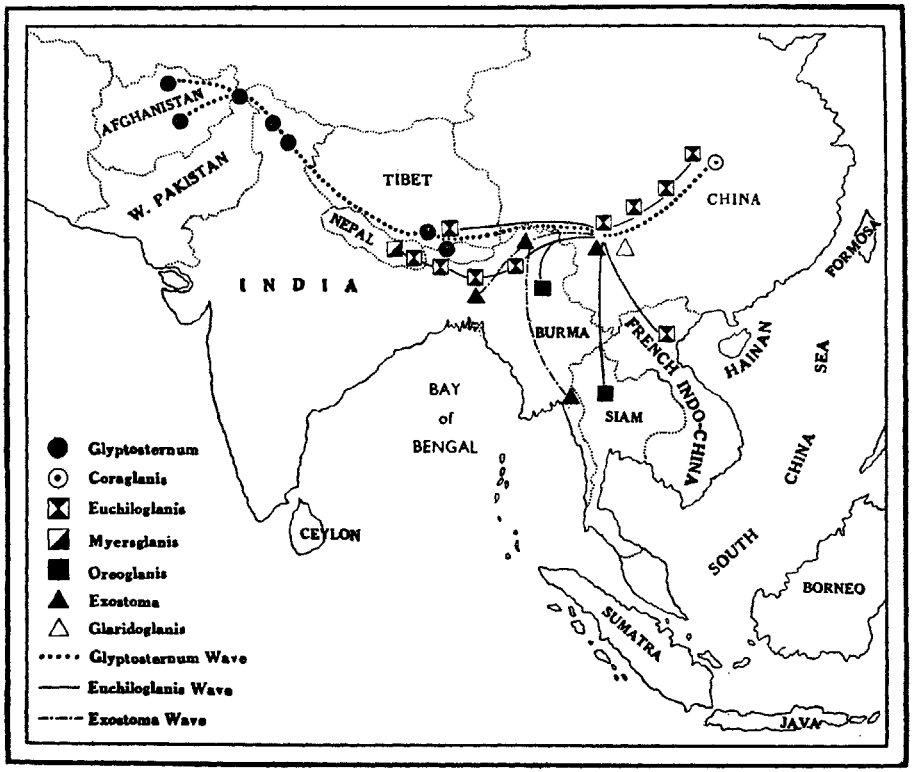
Scientific Name of Species.	Distribution of the Species.
Glyptosternum reticulatum McClelland	Harwan, Kolatse, Ladak, Sneema, Basgo, Leh, Pallagra in Kashmir; Chitral; Paghman and Surchab rivers in Afghanistan.
Glyptosternum maculatum (Regan) ..	Gangtse in Tibet; Sikkim.
Glyptosternum akhtari Silas ..	Bamian river, Oxus Water-shed, Afghanistan.
Coraglanis kishinouyei (Kimura) ..	Chengtu and Kiating (Min River Drainage) Szechuen, China.
Euchiloglanis hodgarti (Hora) ..	Pharping, Nepal; Kurseong, Riyang and Rangbi rivers, Teesta Valley, Darjeeling; Rotung and Rening, Abor Country, Assam.
Euchiloglanis davidi (Sauvage) ..	Eastern Tibet.
Euchiloglanis myzostoma Norman ..	Lo-ma-Ho, tributary of river Mekong at Lamping, Yunnan, China.
Euchiloglanis feae Vinciguerra ..	Upper Burma (Tao' and Nga Kyankka Kyonkgue).
Euchiloglanis sinensis Hora & Silas ..	Locality undetermined, (most probably Yunnan, China).
Euchiloglanis macrotrema Norman ..	Ngoi-Tio, Col-des Nuages, Tonkin, Indo-China.
Myersglanis blythi (Day) ..	Pharping in Nepal.
Glaridoglanis andersonii (Day) ..	Hotha, Yunnan; Ponsee, China.
? *Oreoglanis macropterus* (Vinciguerra)	Upper Burma, Kakhyan Hills, and Pazi, Mekong, Hispi State.
Oreoglanis siamensis Smith ..	River Kang near Doi-Anga, Siam.
Exostoma berdmoeri Blyth ..	Tenasserim, Burma.
Exostoma vinciguerra Regan ..	Putao Plains, N.E. Burma, 'Catcin' Burma, Pazi Monghong, Hsipi State, N. Shan-States.
Exostoma stuarti (Hora) ..	Nam Yak River, Putao Plains, N.E. Burma.
Exostoma labiatum McClelland ..	Egar stream between Rening and Rotung, Abor Country, Assam; Lizo river (Tiza river) Naga Hills, Assam.
Exostoma yunnanensis (Tchang) ..	Yunnan, China.

Coraglanis from Szechuen, in its dentition and mouth parts, is similar to *Glyptosternum* but in the possession of more rays in the pectorals, it shows better adaptation for life in torrential streams. A further proof of this assumption is afforded by the fact that, whereas the gill-openings extend to the ventral surface in *Glyptosternum*, they are restricted to above the base of the pectoral spine in *Coraglanis*. There can be no doubt of the general affinities of the two genera while their divergences can be attributed to the ecological conditions under which they live at present, *Glyptosternum* in somewhat deeper rivers and *Coraglanis* probably in streams more liable to flooding. From the distribution pattern of the two genera, Yunnan would appear to be the centre of their origin and subsequent distribution to the west, and east during the Pleistocene.

Euchiloglanis, with six species, is distributed from eastern Tibet, Tista drainage in Eastern Himalayas, through Burma and Yunnan to Tonkin in Indo-China and to Szechuen in China. The tooth-bands, though somewhat restricted, are not very different from those of *Glyptosternum* and *Coraglanis* and the mouth parts are also similar. The Eastern Himalayan species, *E. hodgarti* (Hora), is perhaps the most highly specialized member of the genus. In this species, the pectorals overlap the pelvics and possess 17 branched rays. The gill-openings are greatly restricted. In *E. davidi* from Eastern Tibet, Yunnan and Szechuen the pectorals just reach the pelvics and the number of branched rays in the pectorals varies from 13 to 15. The gill-openings are greatly restricted. In other species from Yunnan, *E. myzostoma* and *E. sinensis*, the pectorals are separated from the pelvics by a considerable distance and the number of branched pectoral rays is 14 to 15 in *E. myzostoma* and 13 in *E. sinensis*. The gill-openings are greatly restricted in *E. myzostoma* and extend to the base of the pectorals in *E. sinensis*. In Upper Burma,

we have *E. feae* in which the pectorals do not overlap the pelvics, but possess 15 branched rays and gill-openings are very much restricted. In the Indo-Chinese species, *E. macrotrema*, the pectorals do not overlap the pelvics but possess 16 branched rays and the gill-openings extend to the base of the pectorals.

Of the six species of *Euchiloglanis*, two are known from South China (Yunnan), one from Eastern Tibet, Yunnan and Szechuen, one from Upper Burma, one from Eastern-Himalayas and one from Indo-China. Judging from the number of branched fin rays in the pectorals, the Eastern Himalayan and the Indo-Chinese species are better specialized for life in torrential streams whereas species in the intermediate regions with Yunnan as the centre show various gradations and combinations of characters. Like *Glyptosternum* and *Coraglanis*, in *Euchiloglanis*



TEXT-FIG. 4. Map showing the present day distribution of the Glyptosternoid Fishes and the probable routes of migration.

all the teeth in both the jaws are conical and pointed but the teeth in the upper jaw form a slightly bilobed band which is not produced at the sides. From a zoogeographical point of view, it would seem probable that *Euchiloglanis* was evolved from the supposed ancestral stock of the *Glyptosternoid* fishes later than *Glyptosternum* and *Coraglanis* because of their very much more extensive distribution and became distributed within a narrow belt comprising Eastern Tibet, Upper Burma and Eastern Himalayas towards the west and to Szechuen and Indo-China in the north-east and south-east respectively.

In Nepal, we have the genus *Myersglanis*, which combines the teeth characters of *Euchiloglanis*, but shows an advance in its adaptive modifications. Though the pectorals do not overlap the pelvics, the number of branched rays in the

pectorals is 16–17. The gill-openings extend to the base of the pectorals which is a somewhat less specialized character. The greatest advance is in the fact that the lips are continuous and reflected round the mouth to form an adhesive disk. Thus in the Eastern Himalayas and Nepal, where tectonic movements are known to have been very severe during the Pleistocene, we witness the evolution of *Euchiloglanis hodgarti* and *Myersglanis blythi* from a common ancestral form of the less-specialized *Euchiloglanis*-type.

In the remaining three genera of Glyptosternoid-group, all teeth in both jaws are not conical and pointed. The Yunnanese genus *Glaridoglanis* shows a very high specialization of teeth, combined with a large number of primitive characters. Though the teeth in the upper jaw form a band which is not produced backwards at the sides, they are greatly compressed, with broad emarginate or notched apices. The less specialized characters are:

(1) Pectorals and pelvics separated by a considerable distance.
(2) Pectorals with only 11 branched rays.
(3) Lips not continuously reflected round the mouth.

In the characters of gill-openings, however, it is highly specialized, for they are restricted above the bases of the pectoral fins. This is a monotypic genus restricted to Yunnan. It would seem probable that it originated as an independent unit from the earliest ancestors of the Glyptosternoid stock.

Oreoglanis of Siam is not different from *Myersglanis* of Nepal, except that in the former all teeth in the lower jaw are not conical and pointed, the anterior being much larger with slender bases and free end expanded into a truncate-spatulate shape with inner surface slightly hollow. Like *Myersglanis*, the pectorals do not overlap the pelvics but possess 17 to 18 branched rays. The gill-openings are greatly restricted and the lips are continuously reflected round the mouth to form a suctorial disk. *Oreoglanis* would thus seem to us to be a specialization of *Euchiloglanis* in the same way as *Myersglanis*.

Special attention must be invited here to *Exostoma macropterus* Vinciguerra from Upper Burma. In this species, the pectorals overlap the pelvics and possess 19 branched rays. The gill-openings extend to the base of the pectorals but the lips are continuously reflected round the mouth to form a suctorial disk. One of us (Hora, 1923) had noted on a previous occasion that all the teeth are not pointed and conical, but that material is now lost. Until the type material in the Genova Museum is examined and the exact systematic position of this species determined, we have provisionally retained it in the genus *Oreoglanis*. In any case, it appears to be a specialized *Euchiloglanis* in the direction of *Myersglanis* and *Oreoglanis*.

The last group of five species referred to the genus *Exostoma* Blyth has a number of primitive characters and a number of highly specialized features. The less specialized characters are:

(1) The outer rays of the pectoral and pelvic fins are segmented but not pinnate.
(2) The pectorals do not overlap the pelvics and possess 10 to 12 branched rays. (In one exception 17.)

The specialized characters are:

(1) Teeth in upper and lower jaws arranged in two well separated patches.
(2) Teeth in both jaws oar-shaped: flattened distally.
(3) Lips continuously reflected round the mouth to form a sucker.
(4) Gill-openings restricted to the dorso-lateral surface.

Three species of *Exostoma* are known from Upper Burma; one from Assam hills and Eastern Himalayas, and one from Yunnan. This is a compact group which seems to have independently evolved at a much later stage and got dispersed from Yunnan only to Burma and North-East India.

As a result of the above discussion, there seems little doubt that the original home of the Glyptosternoid fishes was Yunnan and that the various genera and species originated in a series of waves at such intervals as the tectonic movements in this region occurred. We can, however, account for three likely waves.

Glyptosternum-wave.—Trans-Himalayan, spreading from Yunnan to the Brahmaputra, Indus and Oxus river-systems (*Glyptosternum*) and Szechuen (*Coraglanis*). As the dentition and the mouth parts of these two genera are least specialized we regard them as the earliest Glyptosternoid fishes though both are specialized in the structure of the outermost fin ray of the paired fin and *Coraglanis* is further specialized in regard to the gill-openings, which are restricted above the bases of the pectorals, and in having larger number of pectoral rays. From the point of view of their function to secure better hold on rocks in swift currents, both these characters are adaptive.

Euchiloglanis-wave.—This wave also originated in Yunnan and spread both towards the west as far as Eastern Himalayas and the east to Szechuen and Indo-China. The six species of *Euchiloglanis* show great diversity of structure among themselves. As a consequence of the same wave, but probably after some time lag, we got the genus *Oreoglanis* (*O. siamensis*) in Siam and (? *O. macropterus*) in Burma and *Myersglanis* in Nepal. The inter-relationships of these forms from the evolutionary point of view have been referred to above already.

Exostoma-wave.—This wave is at present restricted to Yunnan, Upper Burma and the Assam Hills and would thus appear to be of a later origin than the earlier waves. It would seem to have started also from Yunnan.

Glaridoglanis is endemic in Yunnan and would appear to have developed from the original Glyptosternoid stock last of all. Tendency towards differentiation of teeth had already started with the origin of the *Exostoma*-wave.

Time of evolution of the Glyptosternoid Group.

In the following table the main diagnostic features of the genera and species of the Glyptosternoid group are given in order to show at a glance that no one character can give us an idea of any straight line of evolution of these forms. Repeated divergences and convergences have, as a rule, formed the basis of great diversity of form and structure that we notice today.

In considering the time taken for the evolution of this group, two main considerations must be borne in mind—firstly, the ecological conditions under which these fishes live demand immediate adaptive features for survival in torrential streams; secondly, during the late Tertiaries and particularly the Pleistocene, tectonic movements were very frequent and of a high magnitude. With the frequent uplift of the Himalayas and associated ranges of mountains, the streams were being constantly rejuvenated thus subjecting the animals living in them to constant strains and stresses with the result that there was a rapid evolution of new forms within a comparatively short interval. This is what seems to have happened in the case of the Glyptosternoid group of fishes. It seems probable that the entire group evolved during the Pleistocene period and our reasons for this supposition are the following:—

(1) Though *Glyptothorax* Blyth, the likely ancestral form of the *Glyptosternum*-group, is widely distributed in the Indian and the Indo-Malayan regions and beyond, the Glyptosternoid fishes have a comparatively much restricted distribution.

(2) Homalopteridae, for which one of us (Hora, 1949) has opined Pliocene as the probable age, has spread to the extreme part of Peninsular India on the one hand and to the Malayan Archipelago on the other. There are several species in Peninsular India which correspond to the species found in the Malayan region and their dispersal probably

TABLE I.

Salient Characters of the Glyptosternoid fishes.

No.	Name of species.	Pectorals overlapping pelvics.	Gill-openings extend to			Teeth conical and pointed.	Labial groove continuous.	No. of branched rays in the pectorals.
			(1) Above base of pectoral.	(2) Opposite base of pectoral.	(3) Ventral surface.			
1	*Glyptosternum reticulatum* McClelland ..	..	..	..	X	X	..	11
2	*Glyptosternum maculatum* (Regan)	..	..	..	X	X	..	11
3	*Glyptosternum akhtari* Silas ..	..	..	..	X	X	..	11
4	*Coraglanis kishinouyei* (Kimura)	..	X	..	..	X	..	13
5	*Euchiloglanis hodgarti* (Hora) ..	X	X	..	..	X	..	17
6	*Euchiloglanis davidi* (Sauvage) ..	..	X	..	..	X	..	13–15
7	*Euchiloglanis myzostoma* Norman	..	X	..	..	X	..	13–15
8	*Euchiloglanis feae* (Vinciguerra) ..	..	X	..	..	X	..	15
9	*Euchiloglanis sinensis* Hora and Silas ..	..	..	X	..	X	..	13
10	*Euchiloglanis macrotrema* Norman	..	..	X	..	X	..	16
11	*Myersglanis blythi* (Day) ..	..	..	X	..	X	X	16–19
12	*Glaridoglanis andersonii* (Day) ..	..	X	..	..	..	..	10
13	? *Oreoglanis macropterus* (Vinciguerra) ..	X	..	X	..	..	X	19
14	*Oreoglanis siamensis* Smith ..	..	X	..	..	..	X	13
15	*Exostoma berdmorei* Blyth ..	..	X	..	..	..	X	10
16	*Exostoma vinciguerrae* Regan ..	..	..	X	..	..	X	10–12
	Exostoma stuarti (Hora) ..	..	..	X	..	..	X	10–12
17	*Exostoma labiatum* (McClell.) ..	..	..	X	..	..	X	12
18	*Exostoma yunnanensis* (Tichang)	..	X	..	..	..	X	17

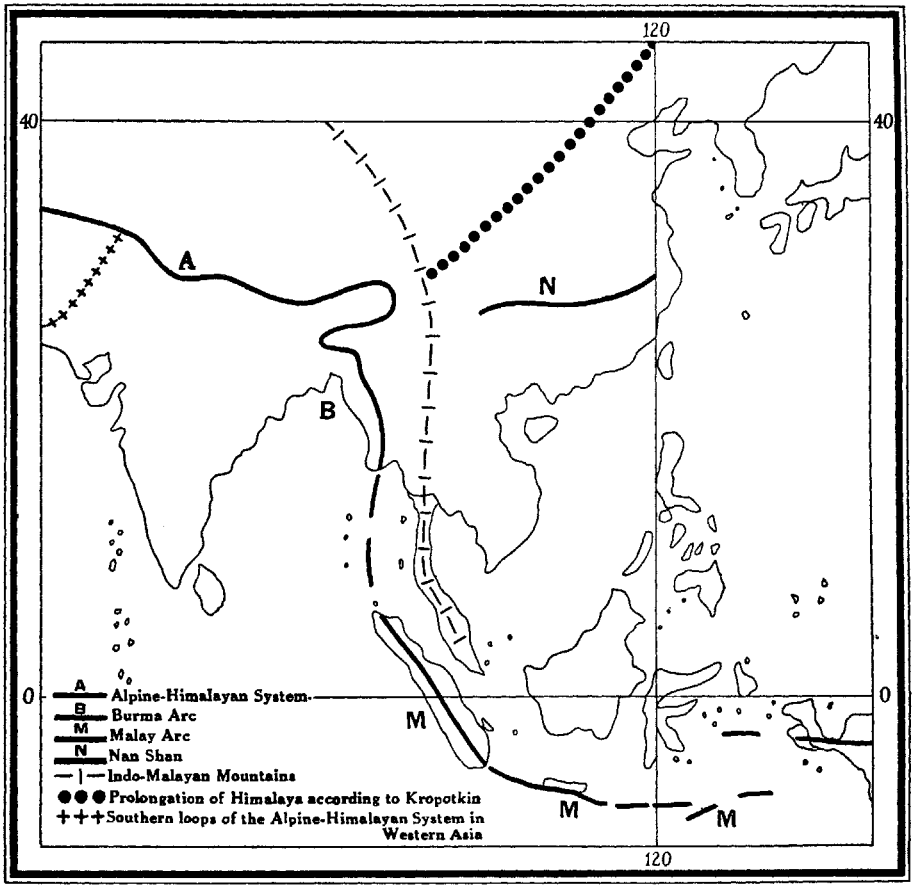
took place during the very late Pliocene or Pleistocene. The Glyptosternoid group, on its distributional records, seems to be younger than the Homalopteridae.

(3) Taking into consideration quick rate of evolution of species (Zeuner, 1948), it is possible to account for the evolution of the entire group within about a million years. Forms living in torrents, undergoing rejuvenation with every successive orogenic movement, probably had a faster rate of speciation than even terrestrial forms.

To understand the causes of quick evolution and dispersal, it is necessary to consider some geological facts about the Pleistocene geography of Yunnan and of the adjacent countries.

Pleistocene Geology of Yunnan and the neighbouring countries.

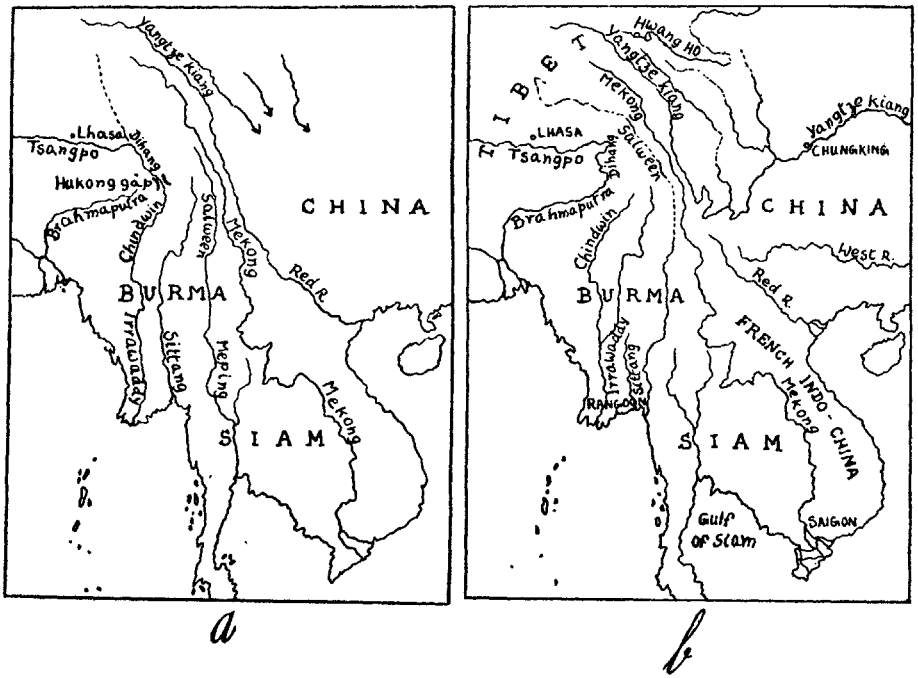
Gregory and Gregory (1923), and Gregory (1925) have given a very lucid account of some of the recent geological changes in South Eastern Asia, with a view to make clear the geographical relations and the evolution of the mountains and river systems in this part of the continent.



Text-fig. 5. The Alpine-Himalayan System and their Hypothetical Eastern connections. (Modified from Gregory, J. W., and Gregory, C. J., 1923.)

The direct Himalayan uplift and the later crustal upfolds have adversely affected the Chinese Tibet and South-Western China, *viz.*, Yunnan. Different views have been expressed regarding the eastern continuity of the Alpine-Himalayan uplift. The altaids which are of a much earlier time and date with the Hercynian systems of Europe, are represented at present by the Indo-Malayan mountain trend cross the Chinese Tibet on lines approximately north and south and continue southward as the Indo-Malayan mountains. This older system is

supposed to have stemmed the eastward extension of the direct Himalayan uplift. In the region of the Chinese Tibet where the Himalayas and the Altaid Systems meet, crustal movements have produced very complex topographical features. As a result of the resistance offered by the Altaid mountains, the Himalayan movements became resolved into two factors, one resulting in a chain of intense folding across Southern China known as the Nan Shan and the other in the uplift of the Burmese-Malay Arc, which pass through Western Burma to Malay and thence to the islands of the Archipelago, such as, Sumatra, Java, New Guinea and to Papua. The dissected plateaus of Western Yunnan are parts of the eastern uplift of the direct Himalayan movements. In Yunnan these movements have occurred in the foot hills and have been planed down by the rivers. Post-Himalayan movements have been particularly felt in Yunnan and its immediate vicinity. These movements and the resulting habitudinal variations are supposed to have been



TEXT-FIG. 6. Map showing (*a*) The Post-Himalayan River System of South-East Asia. (*b*) Existing River System of South-East Asia. (After Gregory, J. W., 1925.)

responsible for the differentiation of the Glyptosternoid-group of fishes from the ancestral stock. The Pleistocene orogenic movements, which affected the drainage systems in South-Eastern Asia, also helped in the dispersal of their aquatic fauna. It would seem that to the Glyptosternoid fishes, which radiated having Yunnan as the centre, the main Himalayan trend in the west, the Burmese Arc in the south and the Nan Shan trend in the east acted as the principal migratory highways.

In order to understand how this distribution was effected, it is essential to know the changes that took place in the main river systems in South-Eastern Asia during this period. A vivid account of the various changes in the river systems are thus given by Gregory and Gregory (1922, pp. 172–173).

"The southern drainage after the close of the Himalayan movements was discharged by five (four) main rivers: (1) the Dihang, which carried the drainage from the Tsangpo and much

of the western Tibet southward as the Lower Irrawaddy; (2) the Upper Irrawaddy in north-eastern Burma which was probably not then connected to the Lower Irrawaddy but discharged to the sea as the Sittang River, near Pegu, through the broad valley between the Shan Plateau and Lower Irrawaddy; (3) the Salween which then probably continued through the Meping and Menam rivers to the Gulf of Siam at Bangkok; (4) the Mekong, which doubtless discharged as at present, across Tonking, though along its present course; and (5) the Yangtze, which was probably continued from its great bend at the Shikhu through the valley of Kienchwan (Chien-chuan Chou) past Tali and through the Red River to the Gulf of Tonking near Hanoi. This simple river system was broken up by subsidences probably consequent of the reaction from the Himalayan compression. One subsidence made the valley of Assam which diverted the Dihang through the Lower Brahmaputra to the Ganges; this change beheaded the Chindwin, which till then had been the main stream of the Irrawaddy. That river, however, was compensated for the loss of its Tibetan head-stream by capturing the drainage of north-eastern Burma, by beheading the Sittang River, through the reach around the end of the Sagaing range. The Salween was diverted by the formation of a series of young gorges westward to the Gulf of Martaban. The development of the Yangtze gorges enlarged that river by the capture of the former Tibetan tributaries of the Red River." Gregory and Gregory (1922, pp. 172–173).

The agency which enabled the rivers of Yunnan to cut their canyons has been regarded generally as a regional uplift, but Gregory and Gregory have shown that the same results can be obtained by regional subsidence of the areas under consideration. Whatever may be the correct explanation of the deep valleys of south-western Chinese rivers, from the point of view of distribution of fishes, it is noteworthy of remark that the original Salween which is supposed to have discharged through the Meping and Menam rivers to the Gulf of Siam had its eastern branch diverted towards the west which now discharges into the Gulf of Martaban and is known as the Salween, while its eastern branch joined the Mekong River and its waters were thus diverted towards the east. All the rivers of the west of Salween had their head waters beheaded by more eastern rivers. These facts indicate the probable directions of subsidence from south-western China, and enable us to understand the distribution of the torrential fishes.

Conclusion.

Thus it seems that the Glyptosternoid fishes, like the Homalopteridae, got dispersed along certain routes aided by the exigences of nature. As explained above, their distribution has been effected in a series of waves, which probably synchronized with the glaciation periods of the Pleistocene when precipitation was higher and rate of evaporation low thus giving rise to more perennial torrential streams in the hilly regions. It is also evident that wherever and whenever changes in the environment occurred, specific differentiations set in the group, thus giving rise to adaptive variations discussed above.

Since the distribution of the Glyptosternoid fishes is at present restricted to within eastern Nepal and Assam Hills in the west, to Siam and Tenasserim in the south, to Szechuan and Yunnan in the north-east and the Indus and Oxus Systems in the north-west it is reasonable to surmise that the evolution and distribution of the Glyptosternoid fishes took place during the Pleistocene and that the great taxonomic variation observed among them is the result of the late Himalayan orogenic movements playing upon the older Altaid mountains and getting resolved along the lines of distribution of the Glyptosternoid fishes.

Summary.

Fluctuations in ecological conditions and geographical isolation have brought about a great diversity of form and structure in the Glyptosternoid-group of Catfishes of the family Sisoridae, which live in the torrential streams of certain parts of south-eastern Asia. The adaptive significance of the modifications of characters, such as (*a*) the structure of the first ray of the pectoral and pelvic fins; (*b*) the lips as organs of adhesion; (*c*) inner rays of paired fins as a pumping mechanism; (*d*) the relative extent of the gill-openings; (*e*) the nature of the

dentition; and (*f*) the extent of the pectorals in relation to the pelvics, is discussed and the directiveness of evolutionary trends in these fishes indicated. An account of the geographical distribution of the various genera and species is given and discussed. Evidence for the evolution and distribution of the Glyptosternoid fishes during the Pleistocene is adduced. Geological data, as well as the present day distribution of the group, indicate that the Glyptosternoid fishes originated somewhere in the region of Yunnan in south-western China. Later orogenic movements, such as the Himalayan uplift and the consequential river-capture in south-eastern Asia, facilitated the dispersal of these fishes along certain mountainous highways to far off places. As a result of subsequent long isolation and continued orogenic disturbances, speciation took place with the formation of new genera and species within comparatively restricted geographical areas. Thus the great variation observed among the Glyptosternoid fishes seems to be the result of the late Himalayan orogenic movements playing upon the older Altaid mountains and getting resolved along the lines of the present-day distribution of these fishes.

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