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ZOOGEOGRAPHY OF LOACHES OF THE SUPERFAMILY COBITOIDEA (COBITIDAE AND HOMALOPTERIDAE)

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INTRODUCTION

Hora (1932) divided his Homalopteridae into two subfamilies, Gastromyzoninae and Homalopterinae and considered the former as a derivative of the family Cobitidae and the latter the Cyprinidae. Subsequently in 1950 he raised the subfamilies to the rank of families. Sawada (1982) on the basis of comparative osteological studies of the Homalopteridae, Gastromyzonidae and Cobitidae combined the families Homalopteridae and Gastromyzonidae relegating them to the rank of a subfamily : Homalopterinae. He further considered the Noemacheiline loaches phylogenetically closer to Homalopteridae than to Cobitidae and accordingly transferred the Noemacheilinae to the family Homalopteridae. The Cobitidae traditionally considered as an independent family of the suborder Cyprinoidei has been placed along with the Homalopteridae under the superfamily Cobitoidea bringing about the following major changes in the phylogenetic classification of the Suborder Cyprinoidei.

Superfamily COBITOIDEA
Family COBITIDAE
  Subfamily BOTIINAE
  Subfamily COBITINAE
Family HOMALOPTERIDAE
  Subfamily NOEMACHEILINAE
  Subfamily HOMALOPTERINAE

The important findings of Sawada (*Op. cit.*) based on osteological studies on the interfamilial and intrafamilial relationship of the Cobitidae, Homalopteridae and Gastromyzonidae have raised certain points of great zoogeographical interest. To elucidate these points the distribution of the Cobitoid fishes, both in time and space, has been carefully investigated which led me to certain important considerations which form the subject matter of this short communication.

DISTRIBUTION IN TIME

The first fossil record of the Cobitoid fish is by Laube (1901) who described *Noemacheilus tener* from the Bohemian Oligocene. However it has not been established with certainty that the species belongs to the genus *Noemacheilus* (Nalbant, 1963). Laube (*Op. cit.*) in the same work recorded four species belonging to the Cobitidae from the Upper Miocene of Ohningen, near lake Konstanz, West Germany. However, it is hard to decide whether they belong to *Noemacheilus* or *Cobitis* (Nalbant, *Op. cit.*). The next record of a *Cobitis*, *C. senogalliensis* Erasmo, is from the Neogene of Senogallia, Italy (Nalbant, *Op. cit.*). Next is that of Lebedev (1959) who described numerous specimens of a *Cobitis*, closely related to *C. taenia* from the Mid-Miocene beds of Saisson Nor Lake, near the source of the Irtysh river, W. Siberia. The latest record is that of Gau-

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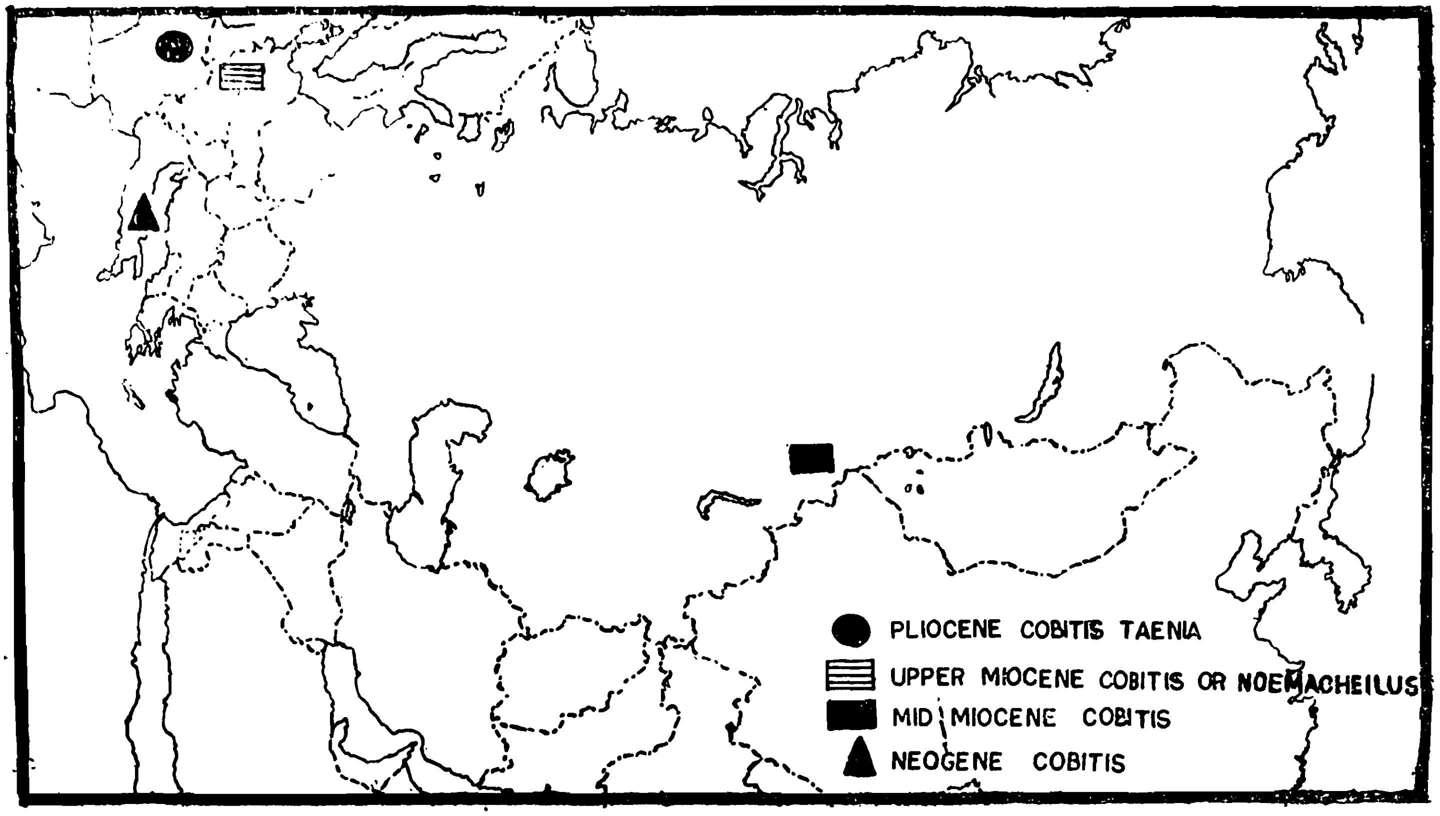

Fig. 1. Map of Eurasia showing the distribution of fossil Cobitoidea

dant (1976) who reported a single incomplete fossil *Cobitis* related to the recent species *Cobitis taenia* from the lignitic shales of Pliocene of Puy-de-Dome, France.

The above mentioned fossil records lead one to the following conclusions :

1. The Cobitidae (*Cobitis*) and the Homalopteridae (*Noemacheilus*) had differentiated from their Cyprinoid ancestors at almost the same time, probably in the early Miocene.

2. Their dispersal to Europe took place through Siberia during the Mid-Miocene—Pliocene period when favourable climatological conditions prevailed in Northern Europe and Siberia.

The above conclusions can however, be assessed only after a careful consideration of the present-day distribution and the phylogenetical routes of dispersal of the superfamily.

Present-Day Distribution

Distribution of the Cobitidae : The family Cobitidae comprising of two subfamilies Botiinae and Cobitinae is found to-day in Eurasia and the adjacent islands and the northern part of Africa.

Distribution of the Botiinae : The subfamily comprises of two genera *Leptobotia* Bleeker and *Botia* Gray (Sawada, *loc. cit.*, p. 184). The *Leptobotia* is confined to the Amur drainage from Blagoveschensk to Liman, Ussuri, Sungari and Liao drainages in North-East Asia, Central Japan and Fukien in S. E. China. The genus *Botia* is found today from South China to Sumatra and Borneo on the one hand and through Mekong and Menam drainages to Burma and on the other to Ganges-Brahmaputra and the Indus drainages.

Distribution of the Cobitinae : The Cobitinae is the largest of all the four subfamilies of the superfamily and has 13 genera : (1) ***Misgurnus*** Lacépède (2) *Cobitis* Linnaeus, (3) ***Sabanejewa*** Vladykov (4) *Niwaella* Nalbant (5) *Somileptes* Swainson, (6) *Enobarichthys* Whitley (7) *Acanthopsis* Van Hasselt (8) *Acanthopsoides* Fowler (9) *Lepidocephalus* Bleeker (*Lepidocephalichthys* Bleeker) (10) *Paralepidocephalus* Tchang (11) *Acanthophthalmus* Van Hasselt (=*Cobitops* Myers), (12) *Neoeucirrhichthys* Banarescu and Nalbant and (13) *Eucirrichthys* Perugia. The distribution of the subfamily covers more or less the same area as that of the family Cobitidae.

Distribution of the Homalopteridae : The family consisting of two subfamilies is distributed in Eurasia and its adjacent islands and the north-eastern part of Africa.

Distribution of the Noemacheilinae : The subfamily is composed of Five genera : *Noemacheilus* Van Hasselt, *Oreonectes* (=*Lefua*) Gunther, *Aborichthys* Chaudhuri, *Turcinoemacheilus* Banarescu and Nalbant and *Vaillantella* Fowler. The genus *Noemacheilus* comprising of over 100 nominal species has the widest distribution of all Cobitoid genera. It is known from Eurasia to Sakhalin Islands, Hokkaido, Hainan, Borneo, Sumatra, Java, Sri Lanka and the Blue Nile of East Africa. *Turcinoemacheilus* is restricted to Turkey, *Lefua* to N. E. Asia and *Vaillantella* to Malay Archipelago while the distribution of *Oreonectes* is discontinuous having found in Japan, Amur drainage, Korea and North China on the one hand and South China and Indonesia on the other (Banarescu and Nalbant, 1968).

Distribution of the Homalopterinae : The subfamily is restricted to South and South-East Asia.

CENTRE OF ORIGIN AND DISPERSAL

It is a well-known fact that the centre of origin and dispersal of the Cyprinoid fishes is in South-East Asia, most probably in South China (Hora, 1949). The Cobitoid fishes were most probably differentiated from a Cyprinid ancestor (Greenwood *et al*, 1966) in the South-West Chinese region during the early Miocene period and had spread to Europe and thence to Northern Africa during Mid-Miocene or early Pliocene through a Siberian route when the climatological conditions there were favourable (Banarescu, 1973). Their dispersal westwards to Central Asiatic Highlands seems to have been along an eastern Tibetan route during the late Miocene or early Pliocene period (*Vide*, Hora, 1937) and to India and thence to West Asia along the southern face of the Himalayas during the late Pliocene or early Pleistocene. The migration southwestwards to the Indian Peninsula and southwards to the Malay Archipelago had most probably taken place only during the Pluvial periods of the Pleistocene.

THE GEOLOGICAL HISTORY OF THE HIMALAYAN AND THE SOUTH-WEST CHINESE MOUNTAIN SYSTEMS

In considering the time of origin and evolution of any group of animals of which the fossil evidences are meagre, two main facts are taken into consideration—firstly, the present-day ecological requirements of the animal and secondly, the geological history of the countries it inhabits. In the case of Cobitoid fishes the evolution of adaptive characters for torrential life seems to be closely related to the evolution of mountain systems in South-East Asia. In order to understand therefore the causes of evolution and dispersal, it is necessary to consider the

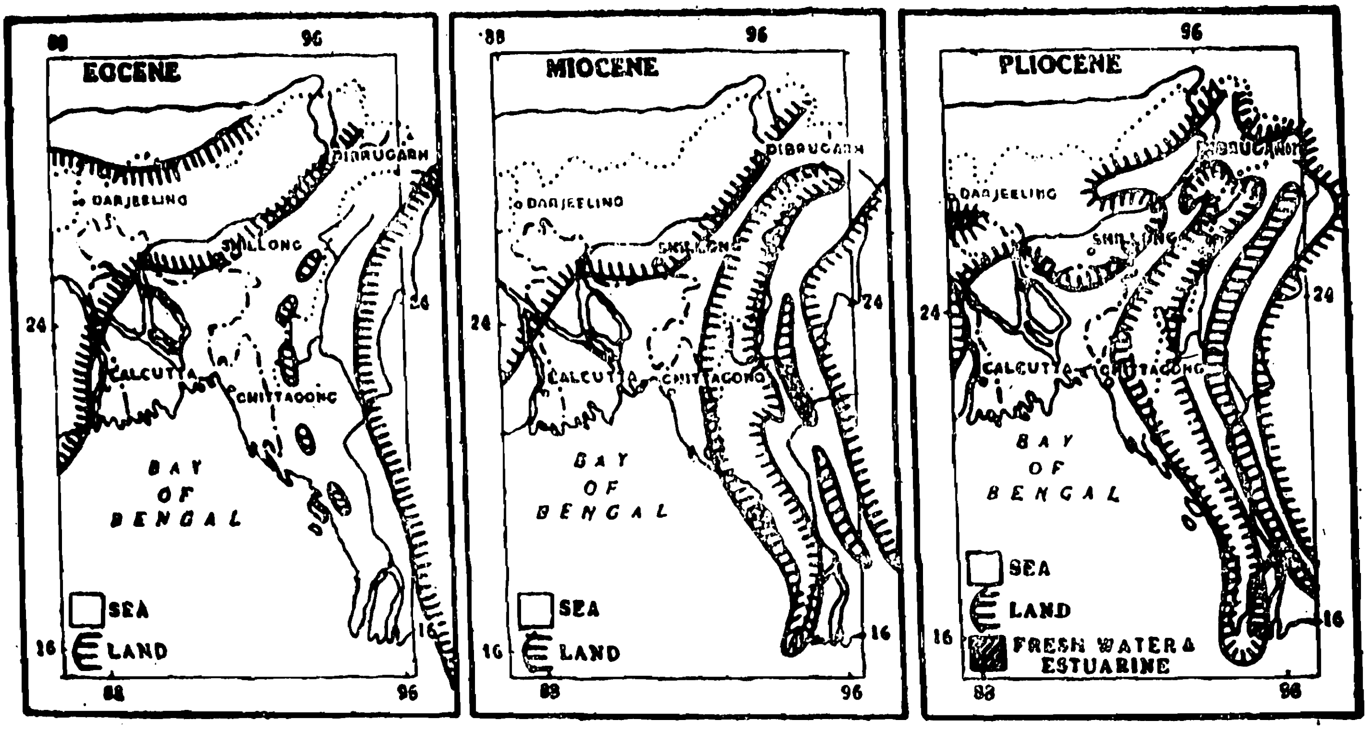

Fig. 2. Map of north-eastern India showing the northward transgression of the Bay of Bengal during the Eocene, Miocene and Pliocene periods. After Krishnan (*Bull. nat. Inst. Sci. India*, 1, 26-28, 1952.)

geological facts regarding the evolutionary history of the mountain systems of the South-East Asia.

THE HIMALAYAS

There is no evidence to show that the Himalayas as a great mountain range are older than the latter part of the Eocene period (Burrad and Hayden, 1933). Before that the Himalayan area formed the northern coast of Gondwanaland and a number of rivers flowed northward into the Tethys Sea of that time. The orogenic movement which was strongly pronounced during the Oligocene, probably began in late Cretaceous times and continued through the Eocene and Middle Tertiary periods. There is considerable evidence to show that it was still active during the Pliocene and later periods. The ossiferous beds of Ngari Khorsum and of the Karewas of Kashmir, however, indicate that during the Pleistocene period the Himalayas had already acquired the general features of their present day form. The nature of the Siwalik deposits shows that the main drainage lines of the south face of the Himalayas date as far back as the Pliocene epoch and that the rivers which brought down sands and boulders from the mountains to build up the Siwaliks of the Duns and Hundes were the direct ancestors of the modern Sutlej and Ganges.

THE MOUNTAIN SYSTEMS OF CHINA AND THE MALAY ARCHIPELAGO

The eastwards extension of the Alpine-Himalayan systems has long been a subject of great controversy. According to one view it passed north-eastward across China to Bering straits; according to another it was bent round against the mass of Chinese Tibet and passed through western Burma to Sumatra and thence along the southern Islands to the eastern Archipelago. The interpretation of the mountain structure of Chinese Tibet is however, complicated by being due to movements at two different periods. The Himalayan movements as has been pointed out are not older than the latter part of the eocene period while the other group is much older, this movement being culminated in South-East Asia in the middle Permian. The older system is represented in Europe by the Hercyian mountains, and in Asia by the Altaids, the members of which cross China Tibet on lines approximately north and south, and continue southwards as the Indo-Malayan mountains. This older system is supposed to have stemmed the eastward extension of the direct Himalayan uplift. In this region of the Chinese Tibet where the Himalayan and the Altaid mountains meet, crustal movements have produced 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 Nan Shan and the other in the uplift of the Burmese-Malayan arc.

MIOCENE—PLIOCENE GEOLOGY AND DISTRIBUTION OF COBITOID FISHES

The spread of Cobitoid fishes westwards to Central Asiatic Highlands was facilitated along Chinese Tibet during the late Miocene or early Pliocene period. The drainage of Central and south-eastern Asia before the major Pliocene upheaval of the Himalayas was probably mainly through broad east to west trending valleys due to the gentle buckling of the earths crust. The Himalayan movements confirmed this system, but during the subsequent settling down of the country the eastward outlet of the Tibetan rivers was reduced and Tibet became a land of lakes (Gregory 1925).

Geologists have shown that a transgression of the Bay of Bengal during the Mid-Eocene cut off the land route between India and Burma and it lasted the whole of the Miocene. During this period no freshwater fish seems to have migrated into India from South China (Hora and Menon, 1953). It is known (Menon, 1951) that during the Pliocene wet tropical conditions prevailed along the southern face of the Himalayans extending to China in the east and beyond Baluchistan towards the west facilitating the spread of marsh-loving fishes from south-west China to as far as Africa. The clear water hill-stream fishes like *Noemacheilus* had most probably dispersed along the southern face of Himalayan during the early Pleistocene period. During the end of Pliocene or early Pleistocene, the major final upheaval of the Himalayas had occurred which raised the Siwalik sediments into dry land and the Siwalik fore-deep (Krishnan, 1943) gradually disappeared leaving a shallowed depression—the Pleistocene fore-deep—which with the formation of the Assam Plateau by then began draining northern India from Assam to the Arabia Sea (Hora, 1953). The Pleistocene river was probably not pouring into the sea exactly at the place where the Indus to-day joins the Arabian Sea for the floor of the north Western part of the Indian Ocean as we know it to-day assumed its present form as a result of compression in Tertiary times, probably contemporaneously with upheaval of Alpine-Himalayan Mountain

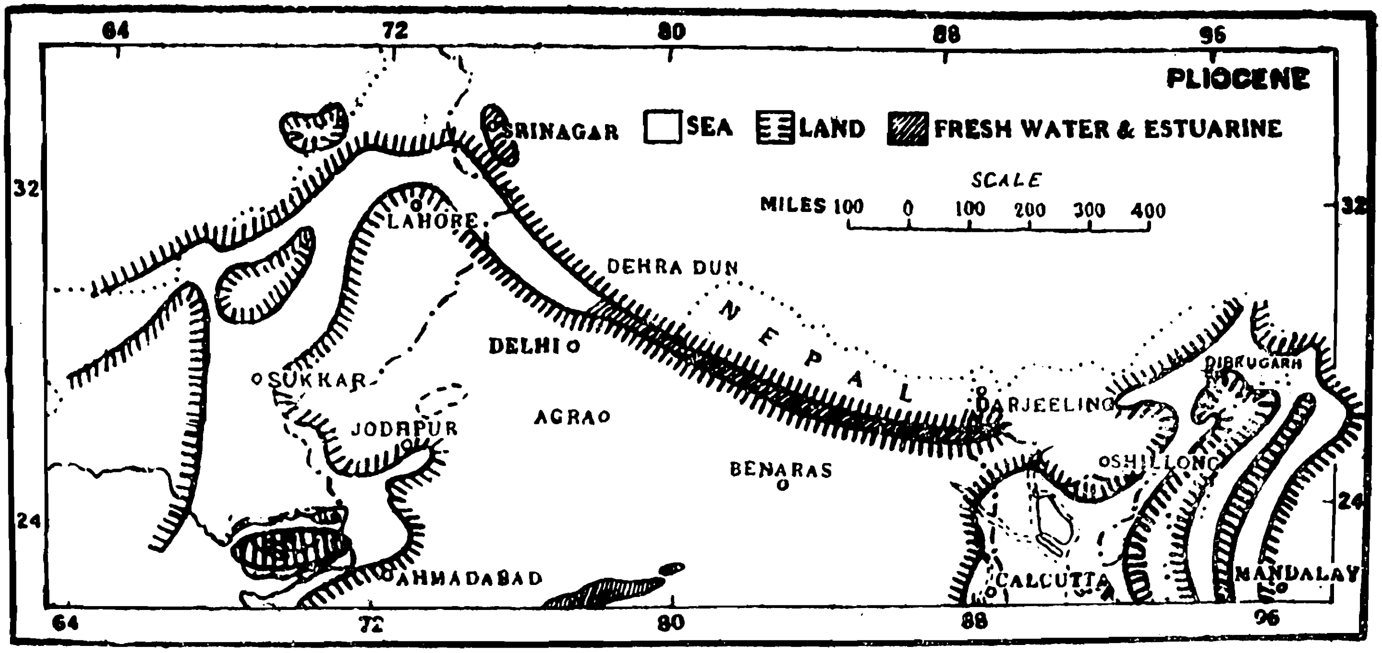

Fig. 3. The Siwalik fore-deep of the Pliocene period. After Krishnan (*Ibid.*, p. 28).

system and the Arcs of the Malay Archipelago and the formation of the rift valley. Consequently, in Pliocene or Post-Pliocene times the area of land that once filled the triangle now bounded by the northern part of the East African coast and its continuation, the south-east coast of Arabia, the Baluchistan coast and the west-coast of India, became separated off by a series of faults and was submerged to its present depth (Wiseman and Sewell, 1937).

From the present-day distribution of *Noemacheilus* (*N. abyssinicus*) it would appear that the land mass between East African coast and the west-coast of India had submerged only quite recently, probably simultaneously with the birth of Ganges and the Indus. Till then the present-day Persian Gulf must have probably been a river valley in continuation with Euphrates-Tigris basin and the Pleistocene fore-deep of the Himalayas may have had connections with it during the Pluvial periods of the Glacial epochs. Thus from the Yunnan Plateau in the east up to the head-waters of Euphrates-Tigris rivers there must have been a continuous route along which the *Noemacheilus* seems to have been got distributed as far west as Anatolia (*Vide*, Cosswig, 1955).

The Garo Rajmahal gap was under the sea during the whole of the Pliocene period and therefore practically no migration of Cobitoid fishes from the north to the Indian Peninsula was possible. During the Pleistocene, however, the Garo-Rajmahal gap became a dry land facilitating the migration of hill stream fishes (Hora 1951). During the Glacial periods of this epoch, aeustatic drop in the sea level of 600 feet had actually bridged up the Garo-Rajmahal gap topographically and climatically enabling the Cobitid fishes like *Lepidocephalus* and Homalopterids like *Noemacheilus*, *Balitora* and *Homaloptera* to cross over from the north to the Peninsula. There was also greater runoff of water in the streams and rivers especially in the big rivers like the Narbada-Tapti along the Satpura-Vindhyas during the Ice-ages of the Pleistocene enabling the quick spread of

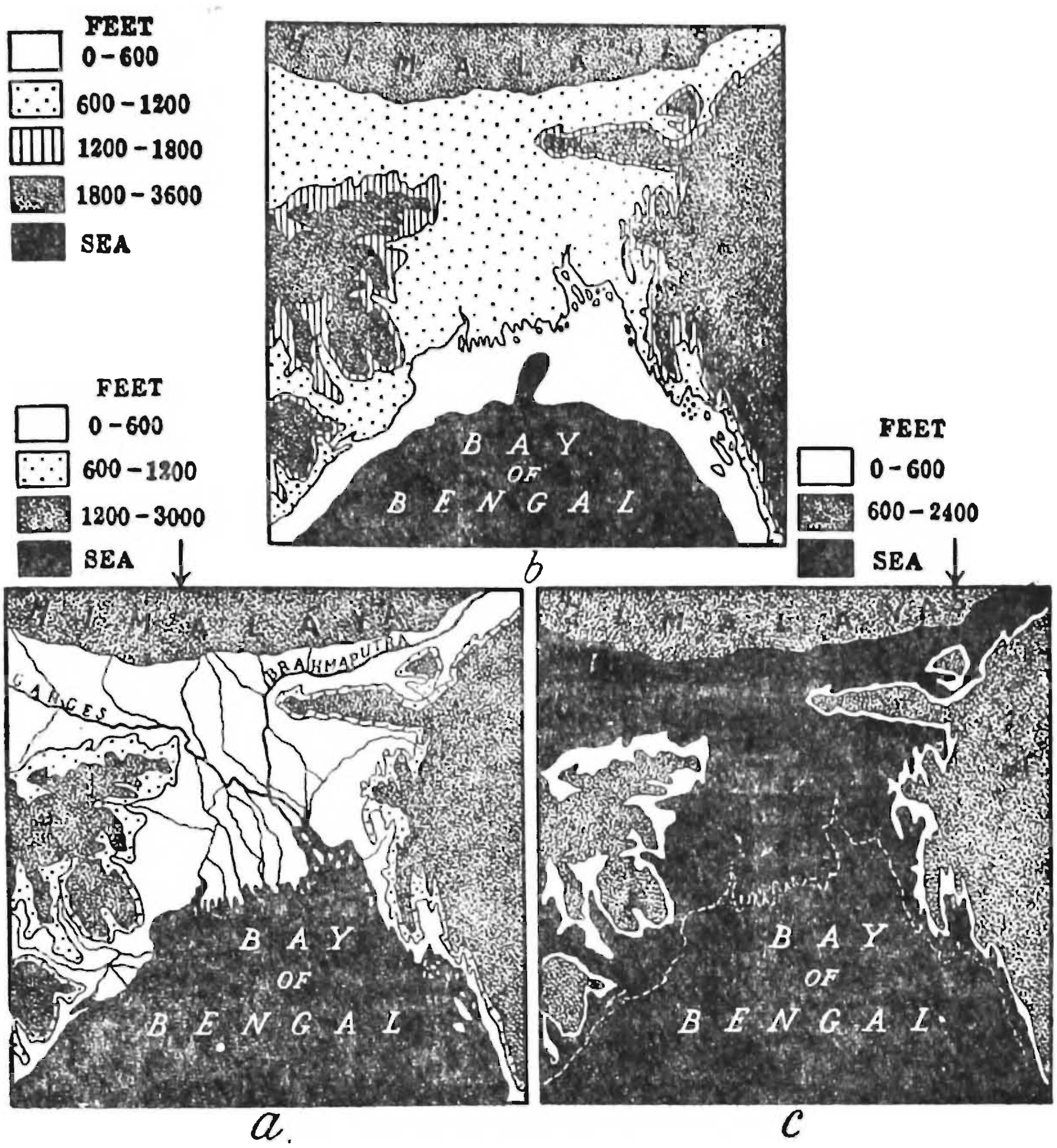

Fig. 4. Orographic features of Garo-Rajmahal gap. a. Present-day conditions, b. Conditions during a glacial period, c. Conditions during an interglacial period. After Hora (*Proc. nat. Inst. Sci.*, **17**, p. 439, 1951).

these fishes to the Peninsula, and *Noemacheilus* and *Leptocephalus* even to Sri Lanka, the final separation of Sri Lanka from the Peninsula being about 10,000 years ago (Jacob, 1949).

The spread of the Homalopterinae and the Noemacheilinae from South-China to the Malay Archipelago occurred during the Pluvial periods of the Pleistocene (Silas, 1952).

CONCLUSION

The superfamily seems to have evolved from a Cyprinoid ancestor which had adapted to a bottom-living habitat. Bottom-living Cyprinid fishes are known to have developed the pipette-like system of suction feeding method with the ability to protrude the mouth (Alexander, 1966). The Cyprinid feeding method with such a protrusion mechanism is useful in taking food from the bottom with the long axis of the body remaining as nearly horizontal as possible in fast flowing hill-streams where to maintain an oblique position of the body against the force of current is impossible. From such a Cyprinid ancestor the ancestors of the Cobitidae and the Homalopteridae were differentiated. The ancestors of the Cobitidae gave rise to two subfamilies, the Botiinae and the Cobitinae. The Botiinae retained the original Cobitoid habitat while the Cobitinae through reduction of fins and elongation of the body adapted to a complete bottom habitat and movement at the bottom by undulation. The gradual reduction of pelvic fin and the elongation of the body of *Misgurnus*, *Niwaella*, *Acanthopsoides* and *Acanthopthalmus* are closely associated with the adaptation to moving at the bottom by undulation (Sawada, *loc. cit.*, p. 155).

The ancestors of the Homalopteridae gave rise to the Noemacheilinae and the Homalopterinae, the former with the gradual modification of the body to a subcylindrical shape and with considerably reduced and compact paired fins having adapted for life in shallow, fast-flowing waters amongst pebbles and boulders at the foot-hills and the latter for torrential habitats through the development of a perfect suctorial disc (Hora, *op. cit.*).

Evolutionary changes in Cobitoid fishes had thus taken place towards achieving definite objectives and to fit them to the needs of different environments. In the case of the hill stream fishes of south-east Asia the production of new families, subfamilies, genera and species can be correlated with the orogenic movements due to the birth of the Himalayas which had produced complex topographical features in the south-west Chinese region. So long as the environment remains static, the organisms do not change much. Plaeogeographical changes have often converted a static environment into a dynamic one and it is during such periods of the earth's history that vast evolutionary changes have occurred.

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