Title	PHYLOGENY AND ZOOGEOGRAPHY OF THE SUPERFAMILY COBITOIDEA (CYPRINOIDEI, CYPRINIFORMES)
Author(s)	SAWADA, Yukio
Citation	MEMOIRS OF THE FACULTY OF FISHERIES HOKKAIDO UNIVERSITY, 28(2), 65-223
Issue Date	1982-03
Doc URL	http://hdl.handle.net/2115/21871
Type	bulletin (article)
File Information	28(2)_P65-223.pdf

PHYLOGENY AND ZOOGEOGRAPHY OF THE SUPERFAMILY COBITOIDEA
(CYPRINOIDEI, CYPRINIFORMES)

By

Yukio SAWADA

Laboratory of Marine Zoology, Faculty of Fisheries,
Hokkaido University

Contents

I. Introduction

The fishes of the superfamily Cobitoidea, inhabiting various habitats in rivers, streams, lakes and ponds are distributed in Eurasia and its adjacent islands and a

part of Africa. This fish group which includes more than 200 species is the second largest group of the suborder Cyprinoidei.

The phylogeny of the cobitids in this fish group has been studied by many authors on the basis of the comparative osteology (Regan, 1911; Rendahl, 1930, 1933a; Berg, 1940; Alexander, 1964b; Mester-Bacescu, 1970; Mester, 1972, 1973). The first osteological investigator who treated these fishes as a group was Regan (1911). On the basis of the skull anatomy, he defined this group as the family Cobitidae, and then divided the family into the subfamilies Cobitinae and Noemacheilinae. Later, from the more extensive osteological anatomy, Berg (1940) divided Regan's subfamily Cobitinae into the two subfamilies Botiinae and Cobitinae, and as a result he established three subfamilies Botiinae, Cobitinae and Noemacheilinae of the family Cobitidae. After that, his classification of the family Cobitidae was accepted by many authors. After this classification, many authors have studied the osteological features of this fish group. Kobayasi (1954, 1956) observed the scale in some Japanese and Chinese species, and deduced the phylogenetic relationships among them. Alexander (1964b) studied the functional aspect of the Weberian apparatus and gasbladder capsule of the group in order to find out the interrelationships among subfamilies. Mester-Bacescu (1970) and Mester (1972, 1973) attempted to classify some species of the group on the basis of the pectoral and pelvic anatomy. However, it is difficult to understand the phylogeny within the family from these studies, because most of them have been based on too few species or subspecies and only a few osteological characters. The only extensive work of the phylogeny of the family was carried by Ramaswami (1953). Regrettably, his method of research lacks the logical consistency. Furthermore, in some cases, unfortunately his observations were not accurate. Thus, the interrelationships among cobitid fishes are still poorly known.

On the other hand, the phylogenetic relationships between Berg's family Cobitidae and other cyprinoid families have attracted some investigator's interest (Hora, 1932; Ramaswami, 1952c, 1952d, 1953; Nelson, 1969; Lundberg and Marsh, 1976; Wu et al., 1981). Their interest originated in Hora's work (1932). He divided his family Homalopteridae into the two subfamilies Gastromyzoninae and Homalopterinae, and considered the former as a derivative of Berg's family Cobitidae and the latter as a descendant of the family Cyprinidae. Later, from this hypothesis, Hora (1950) raised the subfamilies Gastromyzoninae and Homalopterinae to independent cyprinoid families. However, this hypothesis has not been always accepted (Greenwood et al., 1966; Lundberg and Marsh, 1976).

Under these circumstances, it is necessary to reexamine the interfamilial relationships among Berg's family Cobitidae and Hora's families Gastromyzonidae and Homalopteridae as well as the intrafamilial relationships of Berg's Cobitidae on the basis of as many species and osteological characters as possible. In order to estimate the phylogenetic relationships of the present fish group, Hennig's (1966) cladistic approach is adopted, because it is authorized by the logical consistency and the repeatability.

Biogeography has recently become occupied an important part of the fish phylogenetic study (e.g. Rosen, 1974; Wiley, 1976; Vari, 1978). However, concerning the cobitid fishes, there have been few discussions of biogeography except for descriptions of distributions (Rendahl, 1948; Nalbant, 1963; Banarescu

and Nalbant, 1964, 1966, 1968; Banarescu, 1970, 1972, 1973, 1976). Recently, Banarescu (1970) mentioned the center of origin and the phylogenetic dispersal route of the cobitid fishes in the discussions on the zoogeography of terrestrial and freshwater animals. However, as far as the zoogeographical history of the fishes is concerned, his conclusion lacks the logical base. In the present study, thus, the biogeographical history of the superfamily Cobitoidea is presumed according to the branching pattern cladistically reconstructed from osteological features.

II. Materials and Methods

The specimens examined for the present study are listed with their catalogue numbers, the number of specimens, sizes and localities. The abbreviations profixed to the catalogue numbers indicate the following institutions where those specimens belong:

AMNH　:　American Museum of Natural History, New York

BMNH　:　British Museum (Natural History), London

BSKU　:　Department of Biology, Faculty of Science, Kochi University, Kochi

F　　　:　Zoological Survey of India, Calcutta

HUMZ　:　Laboratory of Marine Zoology, Faculty of Fisheries, Hokkaido University, Hakodate

IBRP　:　Institute for Breeding Research, Tokyo University of Agriculture, Tokyo

NSMT-P:　Department of Zoology, National Science Museum, Tokyo

RMNH　:　Rijksmuseum van Natuurlijke Historie, Leiden

USNM　:　U. S. National Museum, Washington, D. C.

Group A
(Definitions of the groups A, B and C, see Chapter IV)

Leptobotia curta, HUMZ 50705–50709, 90389, 90392, 7 specimens, 80.9–142.2 mm SL, Yoshii River, Japan.

Botia macracantha, HUMZ 90393, 90406, 2 specimens, 43.1–50.0 mm SL, locality unknown.

B. hymenophysa, BSKU 14769, 14770, 14772, 18652, 18654, 5 specimens, 68.9–102.7 mm SL, Tonle Sap Lake, Cambodia.

B. modesta, BSKU 18943, 18644, 18646, 18648, 18649, 18753, 18764, 18765, 8 specimens, 49.0–103.6 mm SL, Tonle Sap Lake, Cambodia.

B. dayi, HUMZ 64172–64177, 6 specimens, 56.7–84.4 mm SL, Ganges River, Nepal.

Misgurnus anguillicaudatus, HUMZ 57305–57307, 3 specimens, 72.4–100.2 mm SL, Jeonbug, Korea; HUMZ 57455–57462, 8 specimens, 78.1–132.0 mm SL, Anegawa, Lake Biwa, Japan; HUMZ 90390, 1 specimen, 132.5 mm SL, Kaminokuni, Hokkaido, Japan.

M. fossilis, HUMZ 74659–74663, 5 specimens, 93.3–118.6 mm SL, Czechoslovakia.

M. mizolepis, HUMZ 57463–57483, 21 specimens, 93.3–118.6 mm SL, Seoul, Korea.

Cobitis taenia taenia, NSMT-P 13681–13685, 12 specimens, 56.4–93.2 mm SL, Roumania; HUMZ 90395, 1 specimen, 90.6 mm SL, Fukagawa River, Nagato, Japan; HUMZ 90396, 1 specimen, 87.3 mm SL, Tafuse River, Saga, Japan.

C. taenia striata, HUMZ 50694–50704, 90402, 90403, 13 specimens, 54.3–75.0 mm SL, Yumesaki River, Himeji, Japan; HUMZ 50720–50722, 3 specimens, 60.5–70.8 mm SL, Hayashida River, Hyogo Pref., Japan.

C. biwae, HUMZ 50675–50693, 90397, 90398, 21 specimens, 44.4–103.3 mm SL, Yumesaki River, Himeji, Japan.

C. takatsuensis, HUMZ 52549–52559, 90399, 12 specimens, 45.8–55.5 mm SL, Takatsu River, Shimane Pref., Japan.

C. koreensis, HUMZ 57433–57444, 12 specimens, 59.0–84.0 mm SL, North Han River, Korea.

C. paludicola, HUMZ 62245–62248, 4 specimens, 46.5–60.4 mm SL, Spain.

Niwaella delicata, HUMZ 50425–50436, 90400, 90401, 14 specimens, 43.9–74.7 mm SL, Hida River, Gifu Pref., Japan.

N. multifasciata, HUMZ 57225–57231, 57301, 57302, 9 specimens, 57.1–99.3 mm SL, Nagtong River, Korea.

Sabajenewia aurata vallachica, NSMT-P 13732–13736, 14 specimens, 39.2–60.0 mm SL, Southeastern Romania.

Somileptes gongota, F. 11113/1, 1 specimen, 85.7 mm SL, Siliguri, India. Radiographs only.

Acanthopsis choirorhynchos, BSKU 14748, 14750, 18656, 18657, 18660, 18661, 18665, 7 specimens, 83.0–133.8 mm SL, Tonle Sap Lake, Cambodia; NSMT-P 18016–18018, 3 specimens, 97.3–119.5 mm SL, Cantho, Vietnam.

Acanthopsoides graciroides, IBRP 4242, 5829, 8 specimens, 20.9–34.6 mm SL, Makong River, Laos.

Lepidocephalus guntea, HUMZ 64418–64421, 4 specimens, 32.2–39.5 mm SL, Himachal Pradesh, India.

Acanthophthalmus kuhli, HUMZ 90405, 91143–91146, 5 specimens, 59.0–63.6 mm SL, locality unknown.

A. anguillaris, IBRP 4221, 4291, 2 specimens, 47.8–58.5 mm SL, Mekong River, Laos.

Lefua echigonia, HUMZ 58470–58480, 11 specimens, 24.4–35.8 mm SL, Iruma, Saitama Pref., Japan; HUMZ 58467–58469, 3 specimens, 39.9–44.3 mm SL, Tsurumi River, Yokohama, Japan; HUMZ 90394, 1 specimen, 40.5 mm SL, Siga Pref., Japan.

L. nikkonis, HUMZ 90404, 50726–50735, 11 specimens, 57.7–79.3 mm SL, Chitose River, Hokkaido, Japan.

L. costata, HUMZ 65433–65442, 74812, 11 specimens, 28.6–40.0 mm SL, Korea.

Noemacheilus barbatulus, HUMZ 57528–57531, 4 specimens, 38.2–69.5 mm SL, France.

N. toni, HUMZ 50745–50753, 9 specimens, 87.8–137.0 mm SL, Shizunai River, Hokkaido, Japan; HUMZ 90391, 1 specimen, 123.6 mm SL, Chitose River, Hokkaido, Japan; HUMZ 57499–57504, 6 specimens, 59.6–94.8 mm SL, Han River, Korea.

N. postventralis, AMNH 10323, 25 specimens, 50.9–99.3 mm SL, Inner Mongolia.

N. stoliczkai, AMNH 10332, 25 specimens, 32.3–42.8 mm SL, Inner Mongolia; AMNH 10342, 2 specimens, 77.2–98.9 mm SL, Inner Mongolia.

N. pleurotaenia, AMNH 10351, 2 specimens, Yunnan, China, previously dissected specimens; BMNH 1904.1.26: 36–7, 2 specimens, radiograph only; BMNH 1904.11.29: 52–3, 2 specimens, radiographs only; BMNH 1921.7.26: 49, 1 specimen, radiographs only.

N. botia, HUMZ 64181, 64182, 2 specimens, 43.3–48.9 mm SL, Ganges River, Nepal.

N. pulcher, AMNH 10347, 12 specimens, 35.4–49.7 mm SL, Hainan, Kwangtung, China.

N. masyae, HUMZ 64180, 1 specimen, 42.7 mm SL, Ganges River, Nepal; IBRP 4998, 1 specimen, 34.7 mm SL, Mekong River, Laos.

N. fasciatus, HUMZ 88094, 1 specimen, 57.3 mm SL, Java, Indonesia.

N. breviceps, IBRP 3245, 20 specimens, 36.2–55.0 mm SL, Mekong River, Laos.

N. fowlerianus, IBRP 6077, 12 specimens, 36.3–60.0 mm SL, Mekong River, Laos.

N. rupecula, HUMZ 64160–64170, 11 specimens, 37.2–54.9 mm SL, Ganges River, Nepal.

N. angorae jordanicus, HUMZ 52472–52474, 3 specimens, 33.9–49.5 mm SL, N. Fara, Israel.

N. tigris, HUMZ 52469–52471, 3 specimens, 34.6–46.2 mm SL, Kinneret, Israel.

N. pantera, HUMZ 52465–52468, 4 specimens, 37.2–53.2 mm SL, Ein Facher, Israel.

N. evezardi, F. 9702/1, 2 specimens, 31.9–35.0 mm SL, Khandala, India.

N. savona, HUMZ 62552–62562, 11 specimens, 29.3–52.1 mm SL, Ganges River, Nepal.

N. fasciolata, AMNH 10296, 3 specimens, Hainan, Kwangtungi, China, previously dissected specimens.

N. potanini, AMNH 10547, 1 specimen, 73.3 mm SL, Szechwan, China, radiographs only.

N. abyssinicus, BMNH 1902.12.13: 435, 1 specimen, Tana Lake, radiographs only.

Vaillantella euepiptera, RMNH 7782, 1 specimen, 61.1 mm SL, Sintang, Borneo, radiographs only.

Homaloptera smithi, IBRP 3239, 15 specimens, 34.9–44.7 mm SL, Houei Nhang River, Laos.

Hemimyzon formosanum, HUMZ 71602–71618, 17 specimens, 27.3–38.8 mm SL, Taiwan.

Sinogastromyzon puliensis, HUMZ 67088, 1 specimen, 50.4 mm SL, locality unknown.

Annamia normani, IBRP 3241, 7 specimens, 26.6–61.5 mm SL, Houei Nhang River, Laos.

Crossostoma lacustre, HUMZ 71174–71192, 19 specimens, 33.4–87.1 mm SL, Taiwan.

Abbotina rivularis, HUMZ 50483, 1 specimen, 54.2 mm SL, Tafuse River, Saga, Japan.

Pseudogobio esocinus, HUMZ 50625, 1 specimen, 90.6 mm SL, Miyano, Yamaguchi Pref., Japan.

Saurogobio dabryi, HUMZ 51463, 1 specimen, 195.0 mm SL, locality unknown.

Squalidus biwae, HUMZ 52413, 1 specimen, 68.1 mm SL, Seta, Lake Biwa, Japan.

Biwia zezera, HUMZ 52433, 1 specimen, 59.7 mm SL, Lake Biwa, Japan.

Microphysogibio koreensis, HUMZ 57350, 1 specimen, 74.4 mm SL, Korea.

Group B

Catostomus catostomus, USNM 61501, 4 specimens, radiographs only; HUMZ 17365, 1 specimen, 160.0 mm SL, Prince George Area, British Columbia, Canada.

C. commersoni, USNM Acc 275753, 2 specimens, radiographs only.

C. insignis, USNM 36855, 5 specimens, radiographs only.

C. macrocheilus, USNM 104798, 5 specimens, radiographs only.

C. microps, USNM 104421, 5 specimens, radiographs only.

C. occidentalis, USNM 73671, 4 specimens, radiographs only.

C. tahoensis, USNM 75277, 5 specimens, radiographs only.

Carpiodes carpio, USNM 212123, 4 specimens, radiographs only; HUMZ 62274, 62275, 2 specimens, radiographs only.

Erimyzon succetta, USNM 129386, 5 specimens, radiographs only.

Hypenthelium nigricans, USNM 210597, 3 specimens, radiographs only; HUMZ 62272, 1 specimen, 103.2 mm SL, Bayfield, Ontario, Canada.

Ictiobus bubalus, USNM 42967, 5 specimens, radiographs only.

Minytrema melanops, USNM Acc 279361, 3 specimens, radiographs only.

Moxostoma erythrurym, USNM 70506, 4 specimens, radiographs only.

M. robustum, USNM 39529, 3 specimens, radiographs only.

Myxocyprinus asiaticus, NSMT-P uncatalogued, 1 specimen, radiographs only.

Pantosteus lahontan, USNM 61190, 2 specimens, radiographs only.

Thoburnia rhothoeca, USNM 39529, 3 specimens, radiographs only.

Group C

Acheilognathus lanceolata, HUMZ 50486, 1 specimen, 58.7 mm SL, Tafuse River, Saga, Japan.

A. rhombea, HUMZ 90409, 1 specimen, 66.8 mm SL, Tafuse River, Saga, Japan.

Acanthorhodeus atremius, HUMZ 50515, 1 specimen, 23.4 mm SL, Tafuse River, Saga, Japan.

Coreoleuciscus splendidus, HUMZ 57312, 1 specimen, 48.9 mm SL, Jeonju, Korea.

Cultriculus eigenmani, HUMZ 57517, 1 specimen, 113.4 mm SL, Korea.

Garra rufus, HUMZ 52479, 1 specimen, 50.6 mm SL, Ein Moda, Israel.

Gobiobotia brevibarba, HUMZ 57492, 1 specimen, 74.9 mm SL, Geum River, Korea.

G. macrocephalus, HUMZ 57496, 1 specimen, 76.3 mm SL, Geum River, Korea.

Gyrinocheilus aymoneri, BSKU 14744, 1 specimen, 81.1 mm SL, Cambodia.
Hemibarbus barbus, HUMZ 57635, 1 specimen, 306.7 mm SL, Jusanko Lake, Aomori Pref., Japan.
Hypephthalmichthys molitrix, HUMZ 90408, 1 specimen, 168 mm SL, locality unknown.
Leucaspius delineatus, HUMZ74649, 1 specimen, 55.9 mm SL, Czechoslovakia.
Moroco steindachneri, HUMZ 52029, 1 specimen, 72.9 mm SL, Yoneshiro River, Akita Pref., Japan.
Opsariichthys uncirostris, HUMZ 52432, 1 specimen, 199 mm SL, Lake Biwa, Japan.
Phoxinus phoxinus, HUMZ 74651, 1 specimen, 45.6 mm SL, Czechoslovakia.
Rasbora argyrotaenia, HUMZ 90404, 1 specimen, 50.3 mm SL, Indonesia.
Sarcocheilichthys variegatus, HUMZ 43379, 1 specimen, 78.6 mm SL, locality unknown.
Tribolodon ezoe, HUMZ 87777, 1 specimen, 87.3 mm SL, Hokkaido, Japan.

In the present study, the bones with the intraspecific variation were excluded from "characters" for reconstucting the phylogeny. For the osteological observations, the specimens were cleared and stained with Alizarin Red "S". Meristic characters were mainly counted on the basis of radiographs. In the observations of the developmental sequence of the osteological characters, the larval and juvenile specimens were cleared and stained according to Dingerkus and Uhler (1977), and were preserved in 100% glycerin. The drawings of the bones were made with the Wild M–8.

The terminology of the bones follows Harrington (1955), Nelson (1973) and Howes (1978).

III. Acknowledgements

VI. Methodology

1. SYSTEMATIC METHODOLOGY

Prerequisite validating a systematic methodology is that the methodology is objective and repeatable (see Sneath and Sokal, 1973).

There are currently three theories of systematic methodology (Mayr, 1976). Among them, evolutionary systematics may not satisfy the prerequisite because of the absence of logical consistency of actual analysis, although it has contributed to the development of the evolutionary theory. Thus, it is not used in the present study. On the other hand, the prerequisite seems to be satisfied in two alternative theories, phenetics (Sneath and Sokal, 1973) and cladistics (Hennig, 1966). In the present study, however, the former is not adopted on account of my criticism to the phenetic similarity. A component of the phenetic similarity, the patristic similarity, is criticized here. Sneath and Sokal (1973: 37–38) states that the patristic similarity should be conceptually subdivided into the primitive and derived similarities, which result from the primitive and derived character states respectively. In a character, the primitive character state always appears preceding the derived character state at the time dimension (Maslin, 1952), although both character states are relative concepts (Hennig, 1966: 89). It is thought, therefore, that the temporal relationship between both states is heterochronic. Nevertheless, in their actual analysis, Sneath and Sokal (1973) have proceeded as if the temporal relationship between both states is contemporaneous, and dealt with all the components of patristic similarity as homogeneous. This is a self-contradiction of their logic which leads to an apparent defect of the phenetic methodology.

Thus, the basic methodology used for reconstructing the branching pattern in the present study is that of Hennig (1966). The most fundamental in this cladistic methodology is the principle of synapomorphy which states that the common possession of apomorphous (derived) character states among species or species groups provides a basis of assuming that the species or species groups form a monophyletic* group. As criticized by pheneticists and evolutionary systematists

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* The term "monophyletic" used here should be regarded to be synonymous with "paraphyletic" in Ashlock's sense (1971).

(Sneath and Sokal, 1973; Mayr, 1969, 1976), however, this principle involves some difficulties. The principle of synapomorphy is considered to be applicable only if two basic questions are answered: 1) the determination of polarity in the morphocline, and 2) the elimination of the convergence and parallelism from the phylogeny.

1) THE DETERMINATION OF POLARITY IN THE MORPHOCLINE

The determination of the direction of change, namely polarity (Maslin, 1952), in a morphocline is one of the most important problems in the cladistic approach (Mayr, 1969; Schaeffer et al., 1972; Hecht and Edwards, 1977). In every morphocline, there is always a single most primitive state, while there may be one or more derived states (Hecht and Edwards, 1977). Therefore, it is reasonable to consider that the most important problem in the determination of polarity is to develop criteria to determine the most primitive state.

To determine the most primitive state in the morphocline, the following three criteria have been commonly used.

a) A character state of a group regarded to be ancestral to the group under consideration is primitive.

b) A character state associated with states of other correlated characters known from other evidences to be primitive is primitive.

c) A character state that has the widest distribution among closely related taxa is primitive.

Fig. 1. Ancestor-descendant relationships.

The first criterion has been used by many Japanese ichthyologists. However, a question arises as to how the ancestor is recognized. The ancestor is not self-evident (Englemann and Wiley, 1977). Therefore, as shown in Fig. 1, to recognize the ancestor (B) of a given group (A), its ancestoral group (C) has to be employed. Also, to recognize the ancestor of the group (C), its ancestral group (D) has to be employed. Thus, the first criterion must lead either to an infinite regress or to the doctorine of apriorism. Therefore, this criterion cannot be used.

The second criterion includes the principle of paradromism of Maslin (1952), the criterion of the correlation of series of transformations of Hennig (1966) and the third category of Kluge and Farris (1969). In this criterion, however, there is no accessary criterion for the determination of the correlation among morphoclines. Thus, it may be also rejected here.

The third criterion, which is proposed by Kluge and Farris (1969), is the most commonly used one (for example, Barbour and Miller, 1978). Hecht and Edwards (1977) called this criterion the commonality principle of character distribution. The third criterion is considered to be clearly rejected on the basis of two criticisms. The first criticism is that a character state having the widest distribution among taxa is not necessarily the most primitive. Assume that the phylogenetic relationships among three taxa A, B and C is as Fig. 2, and that
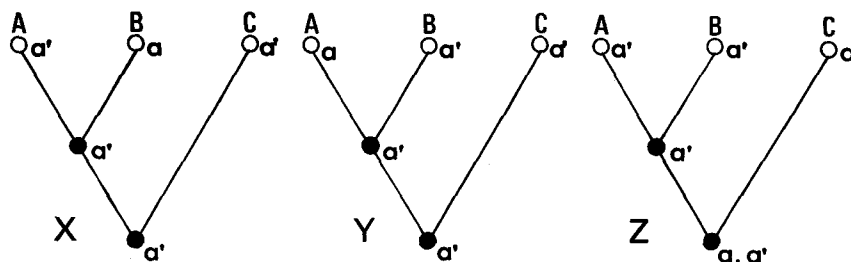
Fig. 2. Commonality principle of character state distribution. a, a', different character states of a character.

among three taxa the character state **a'** is always more than the character state **a** in number (Fig. 2).   If the third criterion is right, the character state **a'** should be always the most primitive.   In one of three cases (Fig. 2Z), however, it is impossible to determine whether the most primitive state is **a** or **a'**. This fact suggests that the third criterion is not always effective for the determination of polarity. The second criticism is pointed at the method for selecting "closely related group". Kluge and Farris (1969) noted that closely related groups could be selected through estimates of overall similarity that make no assumption about the primitive state. This statement leads them to the abandonment of their cladistic standpoint because of the adoption of overall=phenetic similarity, and therefore loosen the basis of the logical consistency from their methodology.

In the present study, the polarity in the morphocline is determined by the following procedure.

[1]   the basic criterion for the determination of polarity and its accessary criteria

If two character states of two morphoclines found in a given group and its closest related group are identical, the identical character states are the most primitive (Fig. 3).   This basic criterion, however, is applicable only if the closest related group is recognized.   In order to recognize the closest related group, a criterion is proposed: if a group shares the same unique unreversed character states with a given group, the group is the closest related group of the given group. The definition and identification of the unique unreversed character states are

Fig. 3.   Basic criterion for the determination of polarity in the morphocline. a, b, c, character conditions of the character A. a, the most primitive condition.
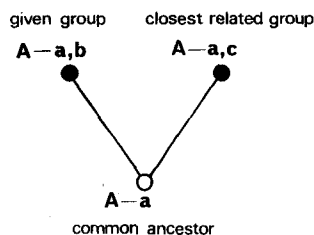
problematical.   The definition of the unique unreversed character state used here agrees with that of Wilson (1965): "character state, which now exists in one or more species, appeared in the past only once and in one species, and has never reverted to a prior state in any of the species giving rise to the contemporaneous taxon".   Thus, the unique unreversed character state may have the same function as the autapomorphous character of Hennig (1966).   On the other hand, the difficulty lies in the identification of the unique unreversed character state.   In the present study, the unique unreversed character states are tentatively selected according to the two following criteria: a) character state restricted in a small particular group, and b) character state unknown from fossils of any other group except for the particular group.   In addition, in order to determine whether the character states selected are unique and unreversed or not, they are tested by Wilson's (1965) consistency test.   If a set of taxa defined by the selected character states are wholly overlapped each other, it is suggested that the character states are unique and unreversed. Therefore, the group sharing them with the given group is considered to be the closest related group.   Therefore, it is reasonable to consider that the basic criterion for the determination of polarity becomes applicable.

1. LOWER PHARYNGEAL WITH 1 TO 3 ROWS OF TEETH

2. PRESENCE OF KINETHMOID

3. PRESENCE OF SUBLINGUALS

4. LOWER PHARYNGEAL WITH NUMEROUS COMB-LIKE TEETH
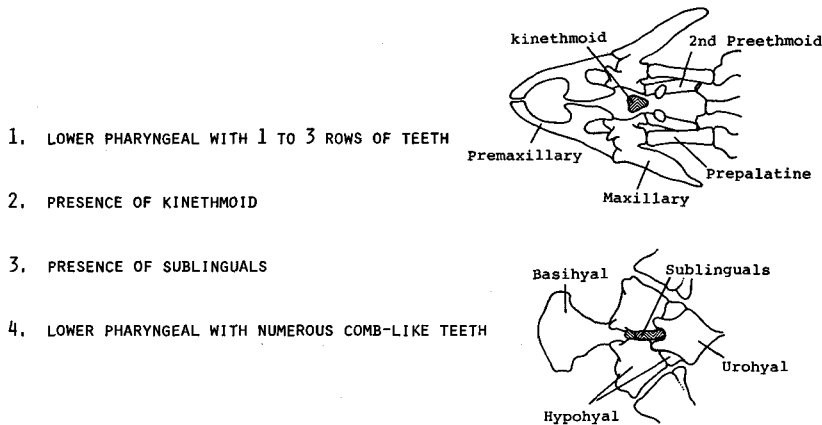
Fig. 4.   Four unique unreversed character states used in the recognition of the closest related group.

[2]   the application of the basic criterion to morphoclines found in cobitoid fishes

As the first step to apply the basic criterion, the closest related group of the group under consideration has to be recognized.   In the present study, the recognition of the closest related group is made on the basis of four unique unreversed character states which have passed the consistency test: (1) lower pharyngeal with 1 to 3 rows of teeth, (2) the presence of kinethmoid, (3) the presence of sublinguals, and (4) lower pharyngeal with numerous comb-like teeth (Fig. 4).   Based on these character states, all cyprinoid fishes are classified into three groups (Fig. 5a).   The first group (A) having the character states (1), (2) and (3) includes fishes of the families Cobitidae of Berg (1940) and Homalopteridae

(including Gastromyzonidae) in Ramaswami's (1952c, 1952d, 1953) sense and most members of the subfamily Gobioninae of the family Cyprinidae (see chapter II, Materials and Methods).   The second group (B) having all four character states

a

Fig. 5. a.   Three cyprinoid groups based on the four unique unreversed character states. Character 1, the lower pharyngeal with 1 to 3 rows of teeth; 2, the presence of kinethmoid; 3, the presence of sublinguals; 4, the lower pharyngeal with numerous comb-like teeth.
b.   Relationship model drawn from Fig. 5a.

b A   B   C

common
ancestor
of
A and **B**
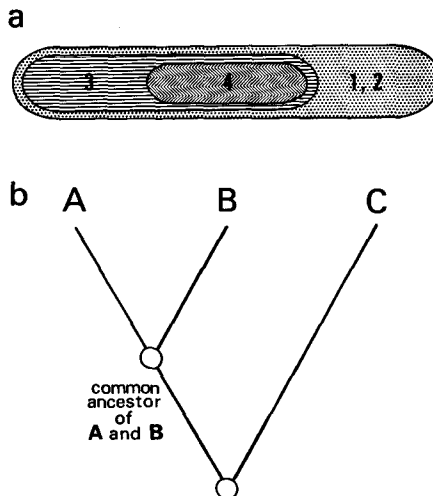
includes the fishes of the family Catostomidae.   The third group (C) having the character states (1) and (2) includes all other cyprinoids.   According to Wilson (1965), the relationship model among these three groups will be constructed as Fig. 5b on the basis of the unique unreversed character states.   Thus, it is shown that the group (A) is the most closely related to the group (B), and next closely to the group (C) (Fig. 5b).

The polarities of all morphoclines found in the group (A) are able to be determined according to the relationship model among the three groups (Fig. 5b). This method is practically followed by the following three fundamental operations (Fig. 6).

(a) If a character state of a morphocline found in the group (A) is identical with that of the group (B), the identical character state is determined to be the most primitive (Fig. 6, character 1).

	A	B	C
character 1	a – a'	a – b	a – c
character 2	d – d'	e – e'	d – f
character 3	g – g'	g – g'	g – g'

character states of
common ancestor of A and B
{ character 1   a
  character 2   d
  character 3   ?

Fig. 6.   The application of the basic criterion to morphoclines of three different characters 1, 2 and 3.   For explanations, see text.

(b) If the most primitive character state of a morphocline cannot be determined by the correlation between two morphoclines in the groups (A) and (B), the character state identical with that of the group (C) is the most primitive (Fig. 6, character 2).

(c) If all character states of morphoclines found in the groups (A), (B) and (C) are identical, the most primitive character state of the morphocline is undeterminable (Fig. 6, character 3).

Thus, the most primitive states of all morphoclines found in the group (A) are able to be determined.
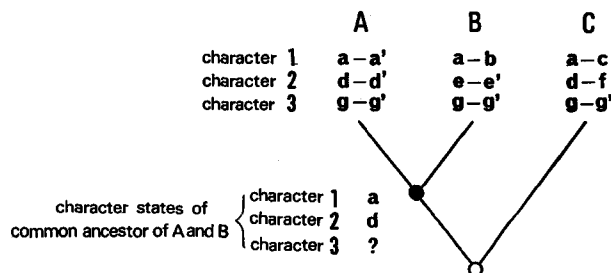
2) THE ELIMINATION OF CONVERGENCE AND PARALLELISM FROM PHYLOGENY

The determination of the polarity is not the last step in the reconstruction of the branching pattern because of the occurrence of the convergence and parallelism. Thus, it is necessary to analyze apomorphous character states held in common, and to distinguish between synapomorphous character states resulting from the immediate common ancestor and analogous features due to the convergence and parallelism. The recognitions of the convergence and parallelism are obviously related to that of the homology (Hennig, 1966; Wiley, 1976). Therefore, the distinction between homologue and nonhomologue may be useful to eliminate analogous features. However, the recognition of homologue is problematical, because it is impossible to determine directly the essential criterion for the recognition of homologue (Hennig, 1966). Thus, several accessary criteria based on the similarity in position and in form have been proposed (Remane, 1952; Hennig, 1966; Bock, 1969). The ontogenetic evidences have been considered to be useful as the basis for these criteria (Bock, 1969). Thus, differences in the ontogenetic origin of a character observed in the present study may contribute toward eliminating analogous features. Nevertheless, many analogous features may still be included in apomorphous character states held in common. Consequently the final recognition of the convergence and parallelism can be done only after the establishment of the branching pattern. However, the purpose of the present study is the reconstruction of the branching pattern. Therefore, the principle of parsimony, which is never an evolutionary process (Inger, 1967; Hecht and Edwards, 1977), is adopted as a method of analysis to get a few possible conclusions. The principle of parsimony used in the present study agrees with that of Nelson (1970): (a) minimum parallel evolution, and (b) minimum reversal of evolutionary trends. Thus, the branching pattern is able to be reconstructed on the basis of Hennig's methodology (1966).

Finally, the reconstructed branching pattern may provide for a basis of the ranking. In the present study, the ranking is made as follows: (a) species or species groups are ranked according to their time of origin represented by the branching sequence of the branching pattern, and (b) such sister groups are given equal rank (Hennig, 1966).

2. ZOOGEOGRAPHICAL METHODOLOGY

The purpose of the present zoogeographical study is the elucidation of the center of origin and phylogenetic dispersal route. Therefore, the vicariance model,

which rejects the concepts of center of origin and dispersal of species as a conceptual model of general applicability in the biogeographical study (Croizat et al., 1974), is not applied to the present study. On the other hand, there are currently two alternative approaches looking upon the biogeographical study in terms of the center of origin and the dispersal from it: classical evolutionary approach derived from the evolutionary systematics (e.g. Darlington, 1957; Banarescu, 1970; Briggs, 1979) and cladistic approach derived from cladistics (e.g. Hennig, 1966; Brundin, 1966). There is one characteristic common to both approaches. It is that the biogeographical hypothesis is never free from the hypothetical phylogenetic relationships among given taxa. The consideration that the knowledge of phylogeny is a prerequisite for understanding the past and present geographical distributions of the taxa has been emphasized by many authors (Banarescu, 1970; Ashlock, 1974; Cracraft, 1975; Keast, 1977; Andersen, 1978; Breure, 1979). Therefore, the validity of biogeographical history of a group depends upon that of the phylogenetic relationships of the taxa in question from which the history is reconstructed. As the validity of the latter is closely related to the logical consistency of the methodology, this suggests that the systematic methodology necessarily requires objectivity and repeatability. Concerning this point, as pointed out in the previous section, the classical evolutionary approach is disqualified from deducing the center of origin and dispersal route because this approach does not provide any reaseonable method for reconstructing the phylogenetic relationships. To the contrary, the cladistic approach is a more powerful tool because the systematic methodology proposed by Hennig (1960, 1966) and Brundin (1966) has a logical consistency. Thus, it is used in the present study.

The present analytical method of determining the center of origin and the dispersal route consists in associating geographic differences of the taxa with successive branching points in the reconstructed branching pattern. It will be made according to two steps: (1) application of the distribution of each non-hypothetical taxon to the branching pattern reconstructed based on the principle of synapomorphy, and (2) inference of the distribution of each hypothetical ancestor, beginning with the most recent common ancestor and working backward in sequence, according to the principle of parsimony. Assume that the phylogenetic relationships among three taxa **a**, **b** and **c** is as Fig. 7A. When the distribution
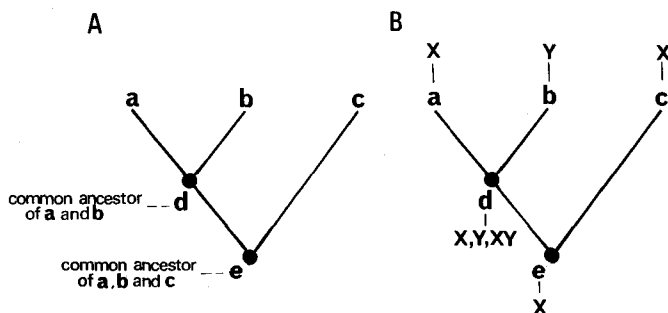

Fig. 7.   The method determining the center of origin and dispersal route of the group from the distributional ranges of living forms. **a**, **b** and **c**, non-hypothetical taxa. **d** and **e**, hypothetical ancestors. X and Y, distributional ranges. For explanations, see text.

of each taxon (area X or Y) is applied to this cladogram (Fig. 7B), the assumed distributions of the common ancestor **d** of taxa **a** and **b,** and the common ancestor **e** of taxa **a, b** and c will be easily inferred as to be X and/or Y and X respectively. Concerning the assumed distribution of the common ancestor **d,** there are three possibilities: Area X, Area Y, or Areas X and Y. If any sound evidence on the geographical history is available, it may be possible to select only one possibility among three cases (see, Morse and White, 1979). However, the detailed knowledge of the geology of the earth is still too meager to select it. Even if the assumed distribution of the common ancestor **d** cannot be limited, it is logically considered that the older common ancestor **e** was probably distributed in Area X from the distribution of taxon c. Thus, the distribution of the oldest common ancestor **e** in the given branching pattern (Fig. 7B) indicates the center of origin of the group consisting of taxa **a, b** and c. Furthermore, the distributional changes from the ancestor **e** to taxa **a** or **b** through the ancestor **d** show the direction of dispersal (X→ Y or X→Y→X), although it is considered that taxon c has been remained in the ancestral distributional range. Thus, the possible succesive changes of the distribution of each common ancestor mean the direction of the phylogenetic dispersal.

V. Comparative Osteology and Discussion

1. CRANIUM (Figs. 8–26; Tables 1–5)

Cranium consists of the following elements: the preethmoid, the supraethmoid-ethmoid complex, the lateral ethmoid, the prevomer, the supraorbital, the frontal, the orbitosphenoid, the pterosphenoid, the parasphenoid, the prootic, the pterotic, the basioccipital, the supraoccipital, the parietal, the sphenotic, the epiotic, the exoccipital and the fronto-parietal fontanelle. The opisthotic is absent. The deep subtemporal fossa formed by the prootic, the exoccipital and the pterotic is present in *Homaloptera smithi* and *Sinogastromyzon puliensis*, members of the subfamily Homalopterinae (Figs. 19A and 20), while in other cobitoid fishes examined, it is absent.

Preethmoids (pe) are a pair of small egg-shaped bones situated lateral to the anterolateral part of the supraethmoid-ethmoid complex. In some members of the subfamily Noemacheilinae such as *Lefua echigonia, L. nikkonis, L. costata, Noemacheilus toni, N. postventralis, N. barbatulus, N. stoliczkai, N. pleurotaenia, N. fasciolata* and *N. pulcher,* and fishes of the subfamily Homalopterinae, the bone is present (Figs. 15, 16, 17B, 19–21), while in other members examined of the superfamily, it is absent (Figs. 8–14, 17A, 18). Anteriorly, if present, the bone has a movable articulation with the posterior facet of the second preethmoid (Fig. 29).

Supraethmoid-ethmoid complex (sec) is a I-shaped or inverted T-shaped bone in section forming the anteriormost part of the median dorsal surface of the skull. Anteroventrally, the bone is connected to the ventral end of the kinethmoid by a strong ligament, and laterally to the anteromedial part of the palatine by ligaments. In fishes of the subfamilies Noemacheilinae and Homalopterinae, the bone is posteriorly firmly joined to the anterior part of the frontals (Figs. 15–21), while in fishes of the subfamilies Botiinae and Cobitinae, it is articulated with a

socket formed by the anteromedial part of the frontals (Figs. 8–14).   In fishes of the subfamily Noemacheilinae such as *Lefua echigonia*, *L. nikkonis*, *L. costata*, *Noemacheilus toni*, *N. postventralis*, *N. barbatulus*, *N. stoliczkai*, *N. pleurotaenia* and *N. fasciolata*, and the subfamily Homalopterinae, the bone is ventrally firmly attached to the dorsal surface of the prevomer (Figs. 15, 16, 19–21), while in fishes of the

Fig. 8. Cranium of a botiine *Leptobotia curta*. bo, basioccipital; eo, exoccipital; ep, epiotic; fon, fronto-parietal fontanelle; fr, frontal; le, lateral ethmoid; os, orbitosphenoid; pa, parietal; pro, prootic; ps, parasphenoid; pt, pterotic; pts, pterosphenoid; pv, prevomer; sec, supraethmoid-ethmoid complex; so, supraoccipital; sp, sphenotic. Top, dorsal view; middle, lateral view; bottom, ventral view. Scale indicates 1 mm.
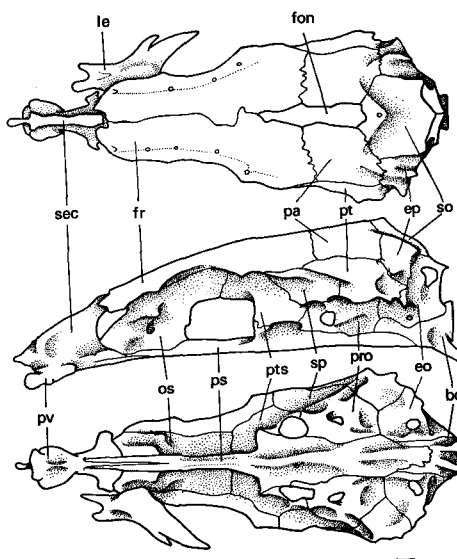
subfamily Botiinae, Cobitinae and Noemacheilinae except fishes of the genus *Lefua* and above six species belonging to the genus *Noemacheilus*, it is fused with the prevomer (Figs. 8–14, 17, 18).

Lateral ethmoids (le) are a pair of moderate bones lying lateral to the anterior upper part of the orbitosphenoid.   Medially, in fishes of the subfamilies Noemacheilinae and Homalopterinae, the bone is firmly attached to the anterolateral part of the orbitosphenoid, and laterally extends forward to form a projection (Figs. 15–21). In fishes of the subfamilies Botiinae and Cobitinae except the genus *Misgurnus*, the bone is produced into a bifid erectile spine movably articulating with the orbitosphenoid (Figs. 8–14), which is sometimes projected from skin.   In fishes of the cobitine genus *Misgurnus*, the bifid erectile spine is less developed (Fig. 11A).

Prevomer (pv) is a single small, flat paddle-shaped median bone forming the anterior part of the roof of the mouth. The bone is posteriorly tapered to form an acute process overlapping the parasphenoid.   In fishes of the subfamilies Botiinae, Cobitinae and Noemacheilinae such as *Noemacheilus botia*, *N. pulcher*, *N. masyae*, *N. savona*, *N. rupecula*, *N. angorae jordanicus*, *N. tigris*, *N. pantera* and *N. evezardi* (Figs. 8–14, 16–18), the bone is fused with the supraethmoid-ethmoid complex, while in other cobitoid fishes, it is attached to the ventral surface of the complex (Figs. 15, 19–21).   In fishes of the subfamilies Homalopterinae and Noemacheilinae such as *Lefua echigonia*, *L. nikkonis*, *L. costata*, *Noemacheilus toni*,
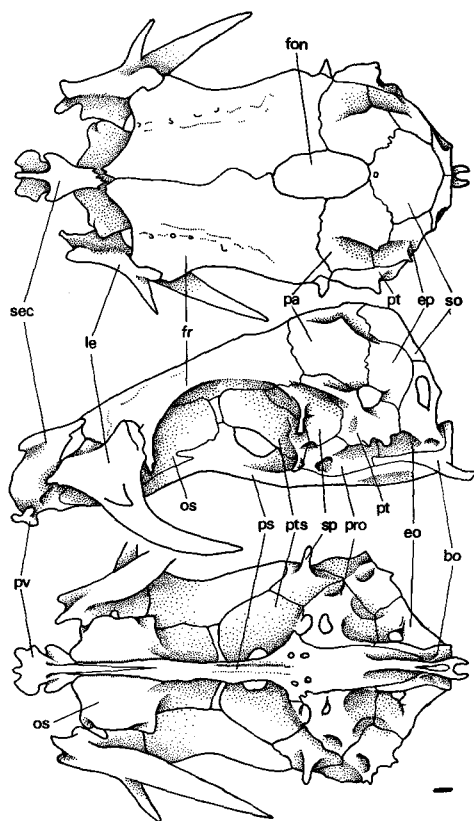
Fig. 9. Cranium of a botiine *Botia macra-cantha*. For abbreviations, see Fig. 8. Top, dorsal view; middle, lateral view; bottom, ventral view. Scale indicates 1 mm.

Fig. 10. Cranium of a botiine *Botia dayi*. For abbreviations, see Fig. 8. Top, dorsal view; middle, lateral view; bottom, ventral view. Scale indicates 1 mm.

N. postventralis, N. barbatulus, N. pleurotaenia, N. stoliczkai, N. fasciolata and *N. pulcher*, the anterolateral part of the bone is attached to the preethmoid (Figs. 15, 16, 19–21).

Supraorbitals (sor) are a pair of flat bones lying lateral to the frontals. In fishes of the subfamilies Botiinae, Cobitinae such as *Acanthophthalmus kuhli* and *A. anguillaris*, Noemacheilinae and Homalopterinae such as *Hemimyzon formosanum* and *Crossostoma lacustre*, the bone is absent (Figs. 8–10, 14–18, 19B, 21B), while in other members of the superfamily, it is present (Figs. 11–13, 19, 20, 21A).

Frontals (fr) are a pair of the largest bones of the skull roof, meeting tightly in the midlongitudinal line. The bone is anteriorly articulated with the posterior portion of the supraethmoid-ethmoid complex, posteriorly overlied with the parietal. In most members of the superfamily, the bone ventrally meets the orbitosphenoid, the pterosphenoid and the sphenotic (Figs. 11B, 12, 13, 15–21), while in fishes of the subfamily Botiinae, it borders the pterotic in addition to above three bones
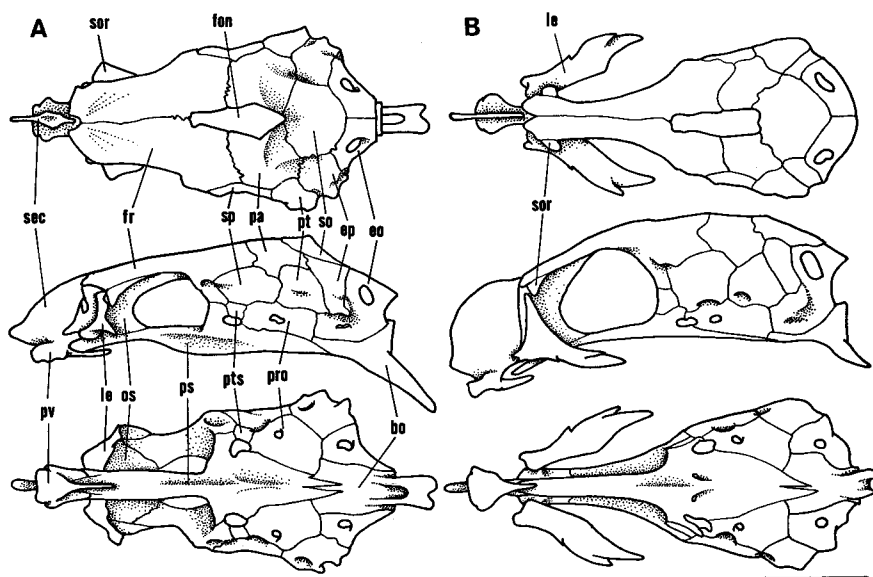
Fig. 11. Crania of two cobitine fishes. A, *Misgurnus fossilis*; B, *Cobitis paludicola*. sor,
    supraorbital. For other abbreviations, see Fig. 8. Top, dorsal view; middle, lateral
    view; bottom, ventral view. Scales indicate 1 mm.
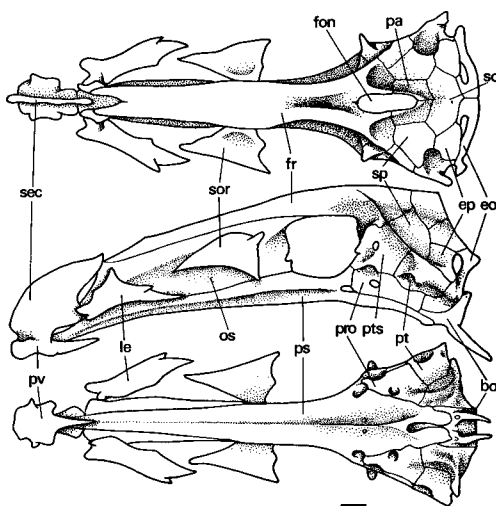
Fig. 12. Cranium of a cobitine
    Acanthopsis choirorhynchos. For
    abbreviations, see Figs. 8 and
    11. Top, dorsal view; middle,
    lateral view; bottom, ventral
    view. Scale indicates 1 mm.

(Figs. 8–10), and in some members of the subfamily Cobitinae such as *Misgurnus
anguillicaudatus*, *M. fossilis*, *M. mizolepis*, *Acanthophthalmus kuhli* and *A.
anguillaris*, it meets the parasphenoid to remove the pterosphenoid backward (Figs.
11A and 14). In *Acanthopsis choirorhynchos*, a member of the subfamily Cobitinae,
the bone is fused with its fellow to form a single element on the midlongitudinal
line (Fig. 12).

Orbitosphenoids (os) are a pair of bones forming the anterolateral wall of the skull. The bone is dorsally sutured with the frontal, and ventrally with the parasphenoid, and laterally meets the lateral ethmoid, and anteriorly the supraethmoid-ethmoid complex. In many members of the superfamily, the bone is fused with its fellow, while in some members of the subfamily Noemacheilinae such as *Lefua echigonia*, *L. nikkonis*, *L. costata*, *Noemacheilus toni*, *N. postventralis*, *N. barbatulus* and *N. stoliczkai*, and fishes of the subfamily Homalopterinae, it is separated from its fellow. In fishes of the subfamilies Botiinae, Noemacheilinae and Homalopterinae, the bone is posterodorsally sutured with the pterosphenoid, and posteroventrally forms the anterior boundary of the orbital foramen (Figs. 8–10, 15–21). On the other hand, in fishes of the subfamily Cobitinae, the bone posteriorly forms the anterior boundary of the foramen, but lacks its connection to the pterosphenoid by the insertion of the frontal (Figs. 11–14).

Pterosphenoids (pts) are a pair of bones forming the major portion of the posterior wall of the orbit. In fishes of the subfamilies Botiinae, Noemacheilinae and Homalopterinae, the bone anteriorly meets the orbitosphenoid, dorsally the frontal, posteriorly the sphenotic and the prootic, and ventrally the parasphenoid (Figs. 8–10, 15–21). On the other hand, in fishes of the subfamily Cobitinae, the positional relationships of the pterosphenoid to adjacent elements are varied. Posterodorsally and posteroventrally, in fishes of the genera *Cobitis*, *Niwaella*, *Sabajenewia*, *Lepidocephalus* and *Acanthopsoides*, the bone meets only the sphenotic (Figs. 11B and 13), while in fishes of the genera *Misgurnus*, *Acanthopsis* and *Acanthophthalmus*, it meets the prootic in addition to the sphenotic (Figs. 11A,
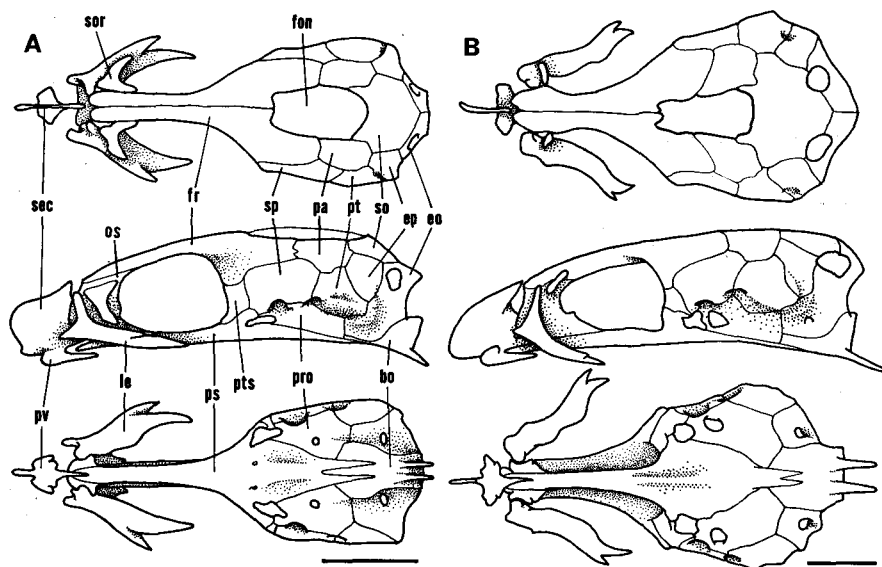
Fig. 13. Crania of two cobitine fishes. A, *Acanthopsoides graciroides*; B, *Lepidocephalus guntea*. For abbreviations, see Figs. 8 and 11. Top, dorsal view; middle, lateral view; bottom, ventral view. Scales indicate 1 mm.
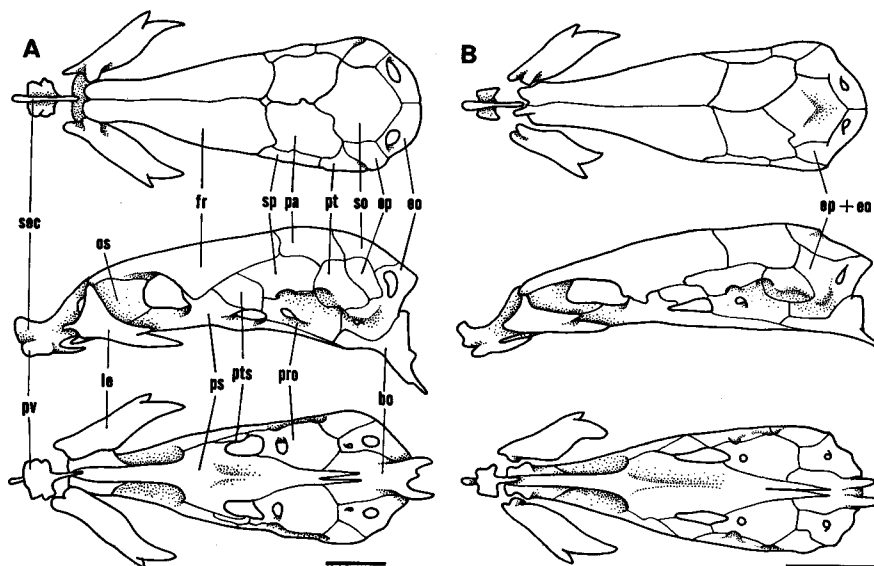
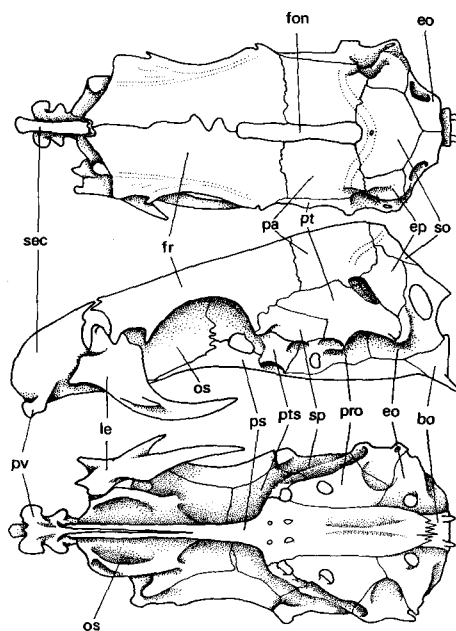Fig. 14. Crania of two cobitine fishes. A, *Acanthophthalmus kuhli*; B, *A. anguillaris*.
Top, dorsal view; middle, lateral view; bottom, ventral view. For abbreviations,
see Figs. 8 and 11. Scales indicate 1 mm.

12, 14). In addition, in *Acanthopsis choirorhynchos*, the bone posteriorly meets the
pterotic (Fig. 12).

Parasphenoid (ps) is an elongate median bone forming much of the ventral
contour of the cranium. The bone is anteriorly inserted between the supraethmoid-
ethmoid complex and the prevomer or into the supraethmoid-ethmoid-prevomer
complex, and anterodorsally borders the orbitosp henoid. The bone posterolaterally
forms two lateral wings meeting the pterosph enoid and the prootic, and posteriorly
sutured with the basioccipital. In most members of the superfamily, the bone
meets the pterosphenoid and the prootic, while in some members of the subfamily
Cobitinae such as *Misgurnus anguillicaudatus*, *M. fossilis*, *M. mizolepis*, *Acantho-
phthalmus kuhli* and *A. anguillaris*, the bone dorsally meets the frontal in addition
to the pterosphenoid and the prootic (Figs. 11A and 14).

Prootics (pro) are a pair of moderately large bones forming the ventrolateral
wall of the cranium. The bone ventrally meets the parasphenoid, posteriorly the
basioccipital and the exoccipital, and dorsally the sphenotic and the pterotic.
Anteriorly, in most members of the superfamily, there is a contact between the bone
and the pterosphenoid, while in fishes of the cobitine genera *Cobitis*, *Niwaella*,
Sabajenewia, *Acanthopsoides* and *Lepidocephalus*, there is not (Figs. 11B and 13).
The bone posterolaterally forms a part of the anterior wall of the subtemporal fossa.
In the ventromedial part of the bone, there are two foramens to penetrate nerves.

Pterotics (pt) are a pair of bones forming the posterolateral corner of the
skull roof. The bone is posteroventrally sutured with the exoccipital, and
anteroventrally, with the prootic. Anteroventrally, the bone provides a posterior

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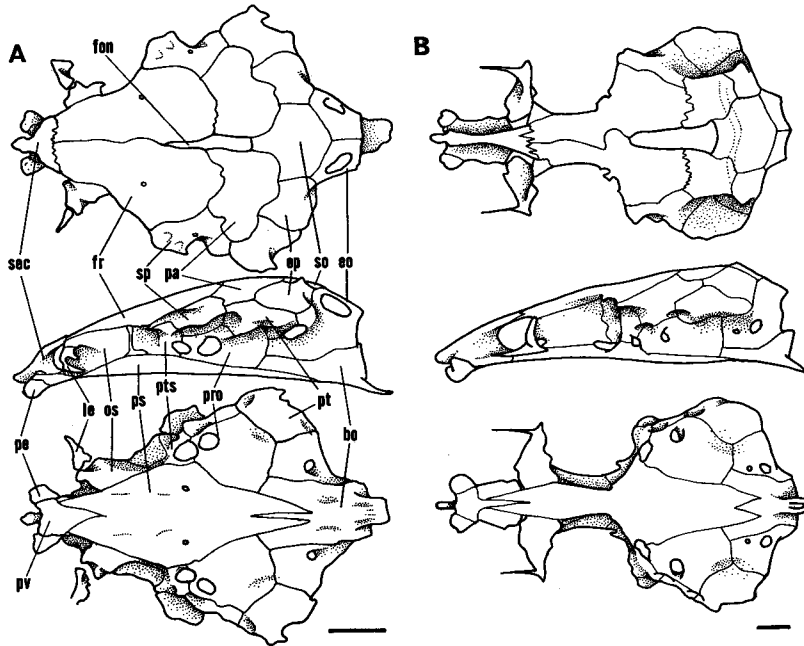
Fig. 15. Crania of two noemacheiline fishes. A, *Lefua echigonia*; B, *Noemacheilus barbatulus*.
pe, preethmoid. For other abbreviations, see Fig. 8. Top, dorsal view; middle, lateral
view; bottom, ventral view. Scales indicate 1 mm.
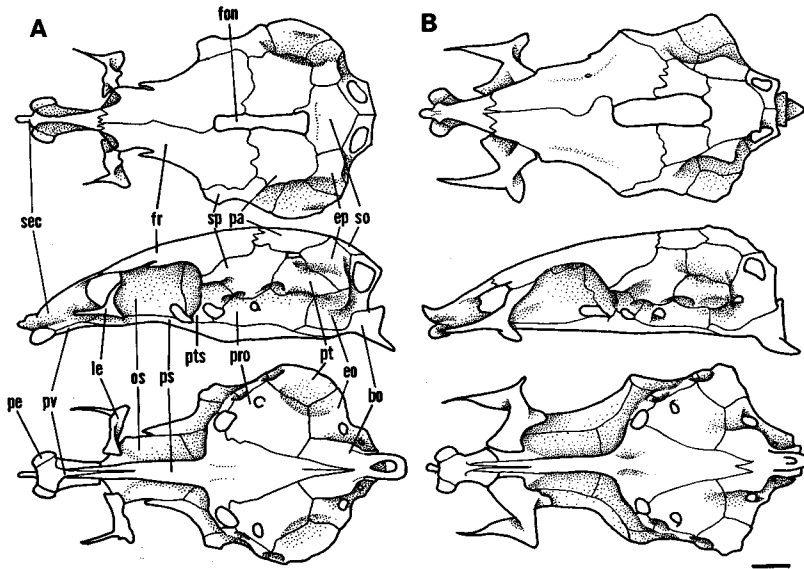
Fig. 16. Crania of two noemacheiline fishes. A, *Noemacheilus stoliczkai*; B, *Noemacheilus
pleurotaenia*. For abbreviations, see Figs. 8 and 15. Top, dorsal view; middle, lateral
view; bottom, ventral view. Scales indicate 1 mm.

fossa for a movable articulation with the hyomandibular.   In most members of the superfamily, the bone anteriorly meets the sphenotic, while in a cobitine *Acanthopsis choirorhynchos*, it meets the pterosphenoid (Fig. 12).   Anterodorsally, in fishes of the subfamily Botiinae, the bone borders the frontal (Figs. 8–10), while in other members of the superfamily, it does not.   In most members of the superfamily, the bone meets the parietal, while in a cobitine *Acanthopsis choirorhynchos*, and members of the subfamily Noemacheilinae except the genus *Lefua*, the bone is separated from the parietal by the insertion of the anterior extension of the epiotic (Figs. 12, 15B–18). In some members of the subfamily Noemacheilinae such as *Noemacheilus botia*, *N. savona*, *N. fasciatus*, *N. fasciolata*, *N. breviceps*, *N. fowlerianus* and *N. rupecula*, the bone laterally extends to form the parietal-pterotic bridge (Fig. 17A).   Posterodorsally, in fishes of the subfamilies Cobitinae except *Acanthophthalmus anguillaris* and *Acanthopsis choirorhynchos*, Botiinae and Homalopterinae, the bone meets the parietal and the epiotic, while in *A. anguillaris*, it is attached to the exoccipital-epiotic complex and the parietal (Fig. 14B) and in *A. choirorhynchos*, to the sphenotic and the epiotic (Fig. 12).

Basioccipital (bo) is a single median bone forming the posterior portion of the cranial floor.   The bone is anteriorly sutured with the parasphenoid and the prootic, dorsally with the exoccipital, and posteriorly articulated with the first centrum. From the ventral surface of the bone, two processes which are sometimes distally fused with each other extend backward to form the pharyngeal process.
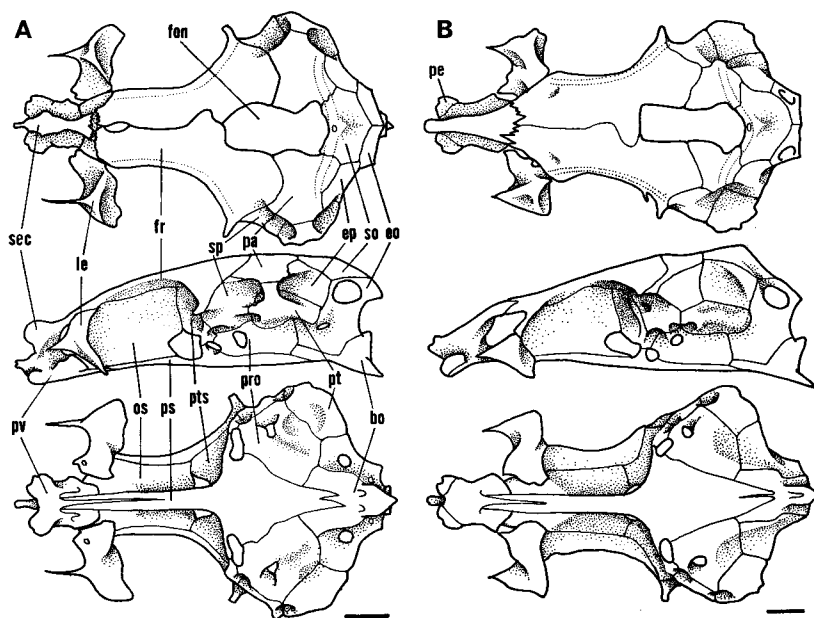
Fig. 17. Crania of two noemacheiline fishes. A, *Noemacheilus botia*; B, *Noemacheilus pulcher*. For abbreviations, see Figs. 8 and 15. Top, dorsal view; middle, lateral view; bottom, ventral view. Scales indicate 1 mm.
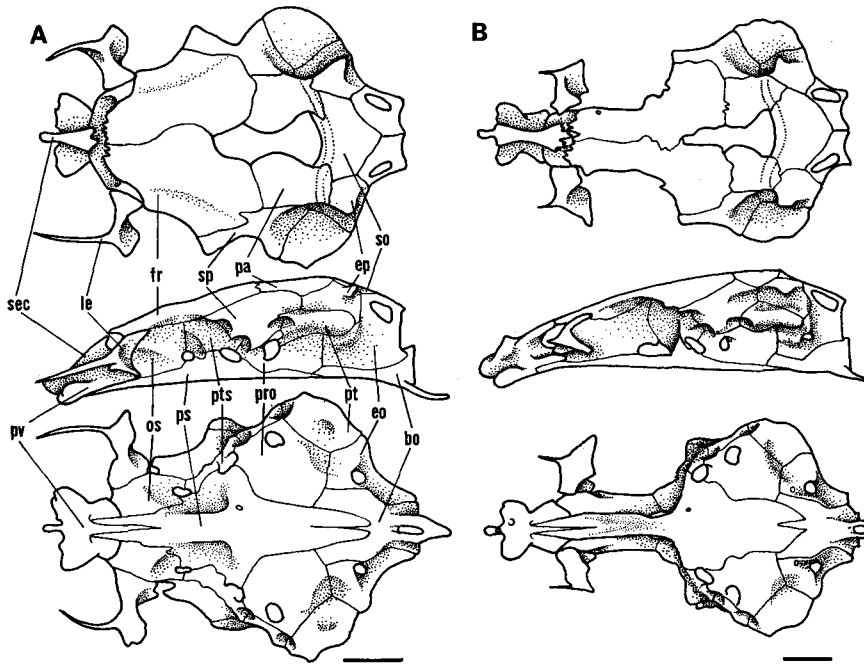
Fig. 18. Crania of two noemacheiline fishes. A, *Noemacheilus evezardi*; B, *Noemacheilus tigris*. For abbreviations, see Fig. 8. Top, dorsal view; middle, lateral view; bottom, ventral view. Scales indicate 1 mm.

Supraoccipital (so) bearing a canal or groove to penetrate the posttemporal commissure is a single hexagonal bone occupying much of the posterior dorsal skull roof. In most cobitoid fishes, the bone posteriorly borders the exoccipitals, anteriorly the parietals and the fronto-parietal fontanelle, and laterally the epiotic. On the other hand, in *Acanthopsis choirorhynchos*, *Acanthophthalmus kuhli* and *A. anguillaris*, members of the subfamily Cobitinae, and *Sinogastromyzon puliensis*, a member of the subfamily Homalopterinae, the bone anteriorly meets only the parietal because of the lack or the forward shift of the fronto-parietal fontanelle (Figs. 12, 14, 20). In addition, in *A. choirorhynchos*, it anterolaterally meets the sphenotic, and in *A. anguillaris*, it laterally meets the exoccipital-epiotic complex (Figs. 12 and 14B).

Parietals (pa) are almost square paired bones forming the middle part of the skull roof. The bone is anteriorly overlapped with the frontal, and posteriorly with the supraoccipital. Laterally, in fishes of the subfamily Botiinae, the bone is overlapped with the pterotic and the epiotic (Figs. 8–10). In members of the subfamily Cobitinae except *Acanthopsis choirorhynchos*, some members of the subfamily Noemacheilinae such as fishes of the genus *Lefua*, and fishes of the subfamily Homalopterinae, the bone is overlapped with the sphenotic in addition to the epiotic and the pterotic (Figs. 11, 13, 14, 15A, 19–21), while in *A. choirorhynchos*, it is laterally attached to only the sphenotic (Fig. 12), and in most

members of the subfamily Noemacheilinae except the genus *Lefua*, it loses laterally its connection to the pterotic by the insertion of the epiotic (Figs. 15B–18). Medially, in most members of the superfamily, each parietal is separated by the fronto-parietal fontanelle, while in *Acanthopsis choirorhynchos*, a member of the subfamily Cobitinae, each parietal is anteriorly separated by the fontanelle and then posteriorly meets its fellow on the dorsomedian line (Fig. 12), and in *Acanthoph-thalmus kuhli* and *A. anguillaris*, members of the subfamily Cobitinae, and *Sino-gastromyzon puliensis*, a member of the subfamily Homalopterinae, each parietal is wholly overlapped on the dorsomedian line (Figs. 14 and 20). In some members of the subfamily Noemacheilinae such as *Noemacheilus botia*, *N. savona*, *N. fasciolata*, *N. rupecula*, *N. fasciatus*, *N. breviceps* and *N. fowlerianus*, the lateral extension of the bone is attached to the upward projection of the pterotic to form the parietal-pterotic bridge (Fig. 17A).

Sphenotics (sp) are somewhat square paired bones forming the lateral portion of the skull. The bone ventrally meets the prootic, anterodorsally the frontal, and anteroventrally the pterosphenoid. Ventrally, the bone provides an anterior fossa for a movable articulation with the hyomandibular. In fishes of the subfamily Botiinae, the bone is posteriorly sutured with only the pterotic (Figs. 8–10). In
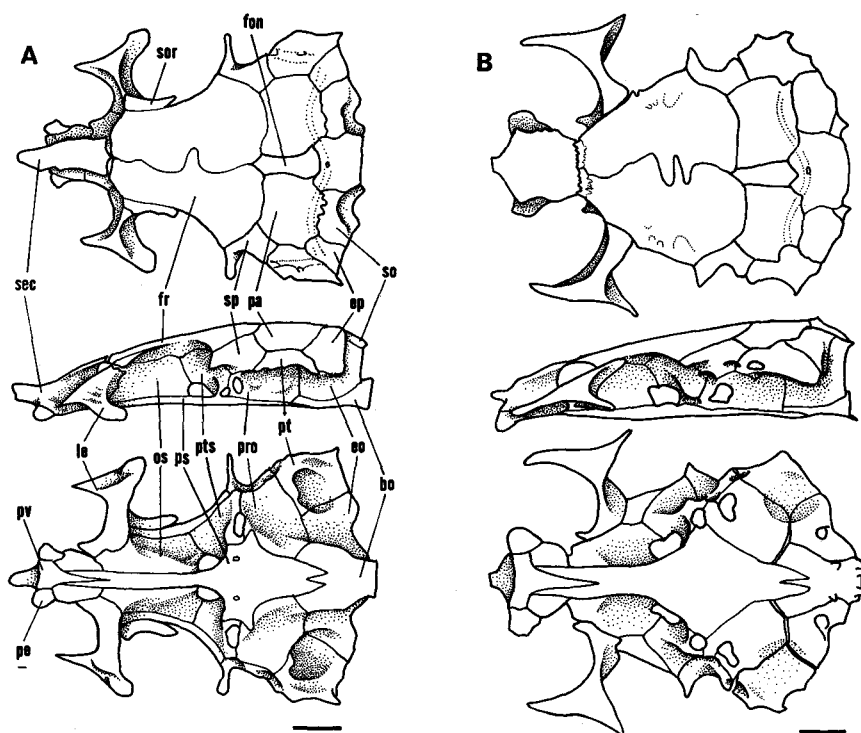
Fig. 19. Crania of two homalopterine fishes. A, *Homaloptera smithi*; B, *Hemimyzon formosanum*. For abbreviations, see Figs. 8, 11 and 15. Top, dorsal view; middle, lateral view; bottom, ventral view. Scales indicate 1 mm.

members of the subfamily Cobitinae except *Acanthopsis choirorhynchos*, some members of the subfamily Noemacheilinae such as fishes of the genus *Lefua* and *Noemacheilus stoliczkai*, and fishes of the subfamily Homalopterinae, posteriorly the bone is sutured with the pterotic and the parietal (Figs. 11, 13–15A, 16A, 19–21), while in most members of the subfamily Noemacheilinae except the genus *Lefua* and *N. stoliczkai*, it is sutured with the epiotic in addition to the pterotic and the parietal (Figs. 15B, 16B, 17, 18). In *A. choirorhynchos*, it is sutured with the supraoccipital in addition to the parietal and the epiotic (Fig. 12).

Epiotic (ep) are a pair of bones forming the posterolateral portion of the skull. The bone is anteriorly sutured with the parietal, medially with the supraoccipital, anterolaterally with the pterotic, and posteriorly with the exoccipital. In *Acanthophthalmus anguillaris*, a member of the subfamily Cobitinae, the bone is fused with the exoccipital to form a single large element* (Fig. 14B). In many members of the superfamily, the bone anteriorly meets the pterotic, while in *Acanthopsis choirorhynchos*, a member of the subfamily Cobitinae, and in most members of the subfamily Noemacheilinae except fishes of the genus *Lefua* and

Fig. 20. Cranium of a homalopterine *Sinogastromyzon puliensis*. For abbreviations, see Figs. 8, 11 and 15. Top, dorsal view; middle, lateral view; bottom, ventral view. Scale indicates 1 mm.

*Noemacheilus stoliczkai*, it meets the sphenotic in addition to the pterotic (Figs. 12, 15B, 16B, 17, 18). In fishes of the subfamilies Botiinae, Noemacheilinae and Homalopterinae, the bone has a loose articulation with the uppermost element of the pectoral girdle (in fishes of the subfamilies Botiinae and Noemacheilinae, with the posttemporal; in fishes of the subfamily Homalopterinae, with the supracleithrum). In most members of the subfamily Cobitinae except *Misgurnus anguillicaudatus*, the bone anterolaterally provides a groove to which the

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* In *Lepidocephalus, Acanthopsis, Acanthospoides* and *Acanthophthalmus*, Nalbant (1963) and Ramaswami (1953) described the lack of epiotic. However, in the present examination, the bone is observed in all genera except *Acanthophthalmus anguillaris*.
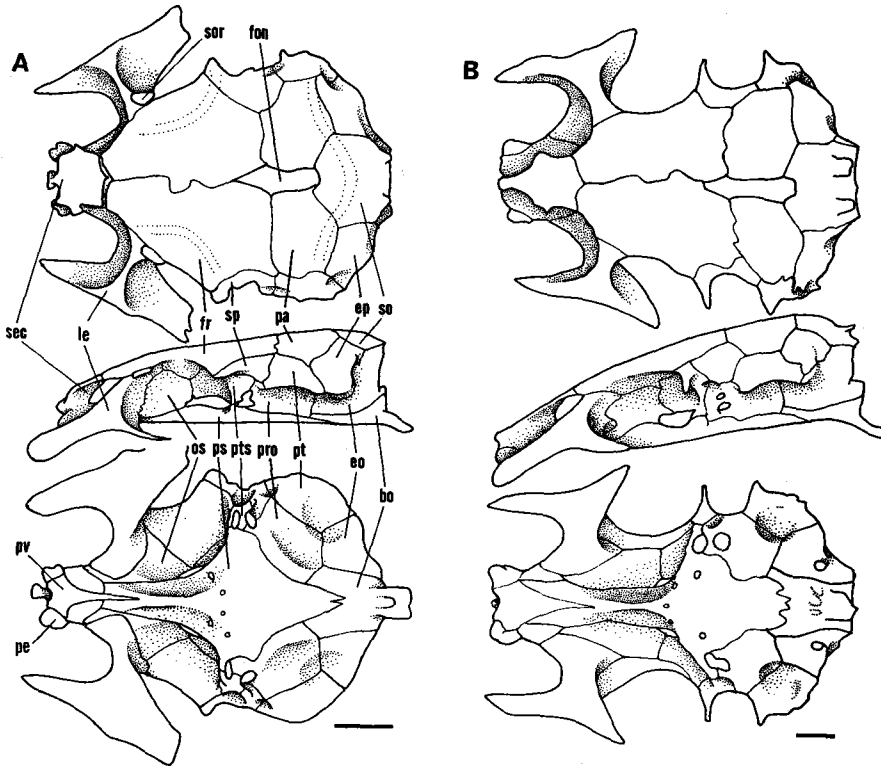
Fig. 21.   Crania of two homalopterine fishes. A, *Annamia normani*; B, *Crossostoma lacustre*.
For abbreviations, see Figs. 8, 11 and 15.   Top, dorsal view; middle, lateral view;
bottom, ventral view.   Scales indicate 1 mm.

posttemporal is firmly attached, while in *M. anguillicaudatus*, it is laterally fused
with the posttemporal.

Exoccipitals (eo) are a pair of bones forming the posteriormost part of the
cranium.   The bone is attached to its fellow above the foramen magnum, and
dorsally and anteriorly articulated with the epiotic and the supraoccipital
respectively, ventrally with the basioccipital, anterodorsally with the pterotic
and anteroventrally with the prootic.   In *Acanthophthalmus anguillaris*, a
member of the subfamily Cobitinae, the bone is fused with the epiotic to form a
single large element (Fig. 14B).   In fishes of the subfamily Homalopterinae, each
exoccipital is separated by the supraoccipital (Figs. 19–21).

Fronto-parietal fontanelle (fon) is an unossified area bordering by the frontals,
the parietals and the supraoccipital.   In some members of the subfamily Cobitinae
such as *Acanthophthalmus kuhli* and *A. anguillaris*, and *Sinogastromyzon puliensis*,
a member of the subfamily Homalopterinae, the fontanelle is absent (Figs. 14 and
20).

DISCUSSION

The cranium of the superfamily Cobitoidea has been considered as one of the most important parts in elucidating the intra- and inter-superfamilial relationships of the superfamily (Sagemehl, 1891; Regan, 1911; Hora, 1932, 1950; Gregory, 1933; Berg, 1940; Ramaswami, 1948, 1952c, 1952d, 1953; Filek, 1962; Wu et al., 1981). Thus, three features have been proposed as the peculiarities of the cobitid cranium: 1) the supraethmoid-ethmoid complex fused with the prevomer (Remaswami, 1953), 2) the orbitosphenoid fused with its fellow to form a single bony element (Ramaswami, 1953), and 3) the orbitosphenoid attached to the supraethmoid-ethmoid complex (Berg, 1940). However, the first two of them are invalid, because in the present study opposite conditions of these characters are observed in some members of the subfamily Noemacheilinae of the family Homalopteridae (Table 3). To the contrary, the third feature is still valid. However, it is not clear whether the feaeture is a definite evidence showing the monophyly of the superfamily Cobitoidea or not, because it has not been determined whether it is derived or primitive, and thus it will be analyzed here. On the other hand, several cranial characters have been used for the division of the subfamilial level of the superfamily (Regan, 1911; Hora, 1932; Berg, 1940; Ramaswami, 1952c, 1952d, 1953). On the basis of the present character analysis, these characters will be also reexamined.

Among cobitoid fishes examined here, differences are found in the presence or absence of the preethmoid, the presence or absence of the supraorbital, the presence or absence of the epiotic, the presence or absence of the fronto-parietal fontanelle and the presence of absence of the parietal-pterotic bridge, the movability of the lateral ethmoid, the relations between the supraethmoid-ethmoid complex and the frontals, between both frontals, between both orbitosphenoids, between the prevomer and the supraethmoid-ethmoid complex, between both exoccipitals, between the frontal and the parasphenoid, between the pterosphenoid and the prootic, between the parietal and the sphenotic, between the parietal and the pterotic, between the sphenotic and the epiotic, between the orbitosphenoid and the pterosphenoid, between the sphenotic and the supraoccipital, and between the pterotic and the ptero-

Table 1. Comparison of several cranial characters in four subfamilies of the Cobitoidea. eo, exoccipital; fr, frontal; le, lateral ethmoid; opis, opisthotic; os, orbitosphenoid; pa, parietal; pts, pterosphenoid; sec, supraethmoid-ethmoid complex; sp, sphenotic.

Morpho-type	Character								Subfamily
	Movability of le	Articulation between sec and fr	Contact between os and pts	Contact between pa and sp	Contact between both eo	opis	Contact between os and sec		
A	present	movable	present	absent	present	absent	present		Botiinae
B			absent						Cobitinae
C	absent	firm	present	present					Noemacheilinae
D					absent				Homalopterinae

sphenoid, and the presence or absence of the deep subtemporal fossa (Tables 1–4). However, the absence of the opisthotic and the presence of the contact between the orbitosphenoid and the supraethmoid-ethmoid complex show shared conditions of characters in all members of the superfamily examined (Table 1).

On the basis of the combinations among conditions of the above 20 characters excluding the latter two features, the cobitoid cranium is divided into four morpho-types (Table 1).

The first type, Type A, including fishes of the subfamily Botiinae, is characterized in that the lateral ethmoid is movable, the supraethmoid-ethmoid complex is movably articulated with the frontals, the orbitosphenoid borders the pterosphenoid, the parietal meets the sphenotic, the exoccipital is attached to its fellow on the middorsal line, the opisthotic is absent, and the orbitosphenoid borders the supraethmoid-ethmoid complex (Table 1; Figs. 8–10).

Type B, consisting of fishes of the subfamily Cobitinae, is different from Type A in the absence of the contact between the orbitosphenoid and the pterosphenoid, and the presence of the contact between the parietal and the sphenotic (Table 1; Figs. 11–14). This type is further classified into five subtypes based on 10 characters (Table 2). The first subtype, Subtype a, which includes fishes of the genus *Misgurnus*, is characterized by the frontal separated from its fellow, the presence of the epiotic, the presence of the fronto-parietal fontanelle, the frontal bordered by the parasphenoid, the pterosphenoid bordered by the prootic, the parietal overlapped by the pterotic, the presence of the supraorbital, the sphenotic separated from the epiotic, the sphenotic free from the supraoccipital, and the pterotic separated from the pterosphenoid (Table 2; Fig. 11A). The second sub-type, Subtype b, includes members of the genera *Cobitis*, *Niwaella*, *Sabajenewia*, *Acanthopsoides* and *Lepidocephalus* (Figs. 11B and 13). This subtype is different from Subtype a in having the frontal separated from the parasphenoid, and the pterosphenoid separated from the prootic. Subtypes c and d closely resemble Subtype a except the absences of the fronto-parietal fontanelle and the supraorbital. However, Subtype c including *Acanthophthalmus kuhli* (Fig. 14A) is distinguished from Subtype d consisting of *Acanthophthalmus anguillaris* (Fig. 14B) in having the epiotic. The last subtype, Subtype e, including only *Acanthopsis choirorhynchos*, is very peculiar (Fig. 12). In this subtype, the frontal is fused with its fellow, the pterosphenoid is attached to the prootic, the parietal is separated from the pterotic, the sphenotic borders the epiotic, the sphenotic meets the supraoccipital, and the pterotic meets the pterosphenoid.

The third type, Type C, is represented by fishes of the subfamily Noemachei-linae. This type is different from Types A and B in having the supraethmoid-ethmoid complex firmly joined to the frontals and the immovable lateral ethmoid, and from Type D in that the exoccipital meets its fellow on the dorsomedian line (Table 1; Figs. 15–18). This type is subdivided into eight subtypes on the basis of six characters (Table 3). The first subtype, Subtype f, is characterized in having the preethmoid, the parietal bordered by the pterotic, the sphenotic free from the epiotic, the prevomer separated from the supraethmoid-ethmoid complex, and the orbitosphenoids separated from each other, and in lacking the parietal-pterotic bridge. This is composed of fishes of the genus *Lefua* (Fig. 15A). The second subtype, Subtype g, consisting of only *Noemacheilus stoliczkai*, is similar to Subtype

Table 2. Comparison of ten cranial characters in the subfamily Cobitinae (Type
sphenoid; pa, parietal; pt, pterotic; pts, pterosphenoid; so, supraoccipi-

Subtype				Character		
	fr	ep	fon	Contact between fr and ps	Contact between pts and pro	Contact between pa and pt
a	separate	present	present	present	present	present
b				absent	absent	
c			absent	present	present	
d		absent				
e	fused	present	present	absent		absent

f, but in the absence of the contact between the parietal and the pterotic,
it differs from the latter subtype (Fig. 16A). The third subtype, Subtype h,
includes *Noemacheilus toni*, *N. postventralis* and *N. barbatulus*, and is different
from Subtype g in having the sphenotic bordered by the epiotic (Fig. 15B). The
fourth subtype, Subtype i, is identical with Subtype h except that the orbito-
sphenoid is fused with its fellow to form a single element. In this subtype, only
Noemacheilus pleurotaenia is included (Fig. 16B). Four other subtypes are
defined on the basis of three characters: the presence or absence of the preethmoid,
the presence or absence of the parietal-pterotic bridge, and the relationship
between the supraethmoid-ethmoid complex and the prevomer. Subtypes j and k
are composed of only one species respectively, *Noemacheilus fasciolata* and *N.
pulcher* (Fig. 17B). Both subtypes have the preethmoid in common. However,
Subtype j is different from Subtype k in the presence of the parietal-pterotic bridge
and the fusion between the supraethmoid-ethmoid complex and the prevomer.
The seventh subtype, Subtype 1, is identical with Subtype m in that the preethmoid
is absent and the supraethmoid-ethmoid complex is fused with the prevomer, but
the former is distinguishable from the latter by the absence of the parietal-
pterotic bridge. In Subtype 1, *Noemacheilus masyae*, *N. angorae jordanicus*, *N.
tigris*, *N. pantera* and *N. evezardi* are included (Fig. 18), while in the last subtype,
Subtype m, *Noemacheilus botia*, *N. savona*, *N. rupecula*, *N. breviceps*, *N. fowlerianus*
and *N. fasciatus* are included (Fig. 17A).

The last type, Type D, differs from other types in that the exoccipitals are
separated from each other because of the presence of the supraoccipital, and

B). ep, epiotic; fon, fronto-parietal fontanelle; fr, frontal; pro, prootic; ps, para-
tal; sor, supraorbital; sp, sphenotic.

Contact between sp and ep	Contact between sp and so	Contact between pt and pts	sor	Species
absent	absent	absent	present	*Misgurnus fossilis* *M. anguillicaudatus* *M. mizolepis*
				Cobitis taenia taenia *C. taenia striata* *C. takatsuensis* *C. biwae* *C. koreensis* *C. paludicola* *Niwaella delicata* *N. multifasciata* *Sabajenewia aurata vallachica* *Acanthopsoides graciroides* *Lepidocephalus guntea*
			absent	*Acanthophthalmus kuhli*
				A. anguillaris
present	present	present	present	*Acanthopsis choirorhynchos*

comprises fishes of the subfamily Homalopterinae (Table 1). This type is subdi-
vided into four subtypes on the basis of three characters: the presence or absence
of the fronto-parietal fontanelle, the presence or absence of the deep subtemporal
fossa and the presence or absence of the supraorbital (Table 4). The first
subtype, Subtype n, consisting of *Homaloptera smithi* is characterized by having
the fronto-parietal fontanelle, the deep subtemporal fossa and the supraorbital (Fig.
19A). The second subtype, Subtype o, differs from Subtype n only by the absence
of the fronto-parietal fontanelle, and includes only *Sinogastromyzon puliensis* (Fig.
20). The last two subtypes, Subtypes p and q, are identical in the absence of
the deep subtemporal fossa and the presence of the fronto-parietal fontanelle.
However, Subtype p consisting of *Hemimyzon formosanum* and *Crossostoma lacustre*
(Figs. 19B and 21B) is different from Subtype q comprising *Annamia normani*
(Fig. 21A) in the absence of the supraorbital.

To determine the polarity of the morphocline, the conditions of these 22
characters found in other cyprinoid fishes are shown (Fig. 22). In group (B)
consisting of the family Catostomidae, 1) the preethmoid is present, 2) the lateral
ethmoid is immovable, 3) the supraethmoid-ethmoid complex is firmly joined to the
frontals, 4) the supraorbital is present or absent, 5) the frontals are paired, 6) the
orbitosphenoid is often fused with its fellow to form a single element, 7) the
epiotic is present, 8) the fronto-parietal fontanelle is present, 9) the parietal-
pterotic bridge is absent, 10) the deep subtemporal fossa is present, 11) the frontal
is separated from the parasphenoid, 12) the orbitosphenoid borders the
pterosphenoid, 13) the pterosphenoid borders the prootic, 14) the pterotic is

Table 3.　Comparison of six cranial charaters in the subfamily Noemacheilinae (Type C). ep, epiotic; os, orbitosphenoid; pa, parietal; pe, preethmoid; pt, pterotic; pv, prevomer; sec, supraethmoid-ethmoid complex; sp, sphenotic.

Subtype	Character						Species
	pe	pa-pt bridge	Contact between pa and pt	Contact between sp and ep	pv and sec	os	
f	present	absent	present	absent	separate	separate	*Lefua echigonia* *L. nikkonis* *L. costata*
g			absent				*Noemacheilus stoliczkai*
h				present			*N. toni* *N. postventralis* *N. barbatulus*
i		present					*N. pleurotaenia*
j						fused	*N. fasciolata*
k		absent					*N. pulcher*
l	absent				fused		*N. masyae* *N. angorae jordanicus* *N. tigris* *N. pantera* *N. evezardi*
m		present					*N. botia* *N. savona* *N. rupecula* *N. breviceps* *N. fowlerianus* *N. fasciatus*

Table 4.　Comparison of three cranial characters in the subfamily Homalopterinae (Type D). fon, fronto-parietal fontanelle; sf, deep subtemporal fossa; sor supraorbital.

Subtype	Character			Species
	fon	sf	sor	
n	present	present	present	*Homaloptera smithi*
o	absent			*Sinogastromyzon puliensis*
p	present	absent	absent	*Hemimyzon formosanum* *Crossostoma lacustre*
q			present	*Annamia normani*

separated from the pterosphenoid, 15) the parietal borders the sphenotic, 16) the parietal overlaps with the pterotic, 17) the sphenotic is separated from the epiotic, 18) the sphenotic is separated from the supraoccipital, 19) the exoccipital meets

	A	B	C
1. Preethmoid	present, absent	present	present, absent
2. Movability of lateral ethmoid	present, absent	absent	absent
3. Articulation between supra-ethmoid-ethmoid complex and frontals	socket-like not socket-like	not socket-like	not socket-like
4. Supraorbital	present, absent	present, absent	present, absent
5. Frontal	single, paired	paired	paired
6. Orbitosphenoid	single, paired	single, paired	single, paired
7. Epiotic	present, absent	present	present
8. Fronto-parietal fontanelle	present, absent	present	present, absent
9. Parietal-pterotic bridge	present, absent	absent	absent
10. Deep subtemporal fossa	present, absent	present	present
11. Contact between frontal and parasphenoid	present, absent	absent	absent
12. Contact between orbitosphenoid and pterosphenoid	present, absent	present	present
13. Contact between pterosphenoid and prootic	present, absent	present	present
14. Contact between pterosphenoid and pterotic	present, absent	absent	absent
15. Contact between parietal and sphenotic	present, absent	present	present, absent
16. Contact between parietal and pterotic	present, absent	present	present
17. Contact between sphenotic and epiotic	present, absent	absent	absent
18. Contact between sphenotic and supraoccipital	present, absent	absent	absent
19. Contact between both exo-ccipital	present, absent	present	present
20. Prevomer and supraethmoid-ethmoid complex	separate, fused	separate	separate
21. Opisthotic	present, absent	present	present, absent
22. Contact between orbitosphenoid and supraethmoid-ethmoid complex	absent	present	present


```
1.  present
2.  absent
3.  firm
4.  ?
5.  paired
6.  ?
7.  present
8.  present
9.  absent
10. present
11. absent
12. present
13. present
14. absent
15. present
16. present
17. absent
18. absent
19. present
20. separate
21. present
22. present
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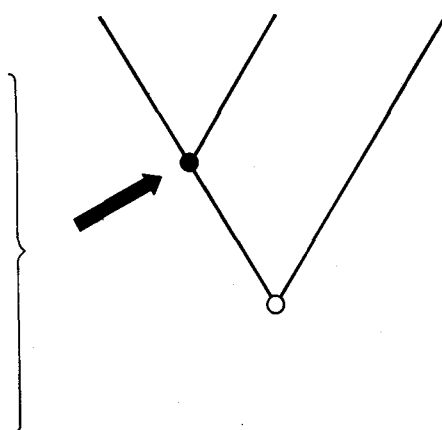
Fig. 22. Character analysis of the cobitoid cranium. The most primitive conditions of 22 characters in group (A) are shown as the conditions in the common ancestor (●) of groups (A) and (B). A, the superfamily Cobitoidea and most members of the subfamily Gobioninae of the family Cyprinidae; B, the family Catostomidae; C, other cyprinoid fishes except members of groups (A) and (B).

its fellow, 20) the prevomer is not fused with the supraethmoid-ethmoid complex, 21) the opisthotic is present, 22) the orbitosphenoid is separated from the supra-ethmoid-ethmoid complex (Sagemehl, 1891; Gregory, 1933; Ramaswami, 1957; Weisel, 1960; Lo and Wu, 1979).

On the other hand, the conditions in group (C) which comprises other cyprinoid fishes except members of groups (A) and (B) are the same as those in group (B) in most of 22 characters (see Sagemehl, 1891; Gregory, 1933; Ramaswami, 1952a, 1952b, 1955a, 1955b; Harrington, 1955; Sorescu, 1970a, 1970b, 1972; 1975; 1978; Dixit and Bisht, 1972a; Buhan, 1974; Hubbs et al., 1974; Barbour and Miller, 1978; Howes, 1978, 1979, 1980). However, group (C) is different from group (B) in the following four features: 1) the preethmoid is absent in some cyprinids (Harrington, 1955; Ramaswami, 1955a, Buhan, 1974), 8) the fronto-parietal fontanelle is usually absent with some exceptions of the cyprinid genera *Gobiobotia* etc. (Ramaswami, 1955b), 15) the parietal is separated from the sphenotic in some cyprinids (Ramaswami, 1955a, 1955b; Howes, 1978; Barbour and Miller, 1978), 21) the opisthotic is absent in some cyprinids (Barbour and Miller, 1978; Howes, 1978, 1980).

When these cyprinoid cranial data including those of the superfamily Cobitoidea are applied to the criterion for the determination of polarity, the

Table 5. Polarities of 22 characters in the cobitoid cranium.

Character	Most primitive condition	Most derived condition
1. preethmoid	present	absent
2. movability of lateral ethmoid	absent	present
3. articulation between supraethmoid-ethmoid complex and frontals	firm	movable
4. supraorbital	?	?
5. frontal	paired	single
6. orbitosphenoid	?	?
7. epiotic	present	absent
8. fronto-parietal fontanelle	present	absent
9. parietal-pterotic bridge	absent	present
10. deep subtemporal fossa	present	absent
11. contact between frontal and parasphenoid	absent	present
12. contact between orbitosphenoid and pterosphenoid	present	absent
13. contact betwen pterosphenoid and prootic	present	absent
14. contact between pterosphenoid and pterotic	absent	present
15. contact between parietal and sphenotic	present	absent
16. contact between parietal and pterotic	present	absent
17. contact between sphenotic and epitoic	absent	present
18. contact between sphenotic and supra-occipital	absent	present
19. contact between exoccipitals	present	absent
20. relation between supraethmoid-ethmoid complex and prevomer	separate	fused
21. opisthotic	?	?
22. contact between orbitosphenoid and supraethmoid-ethmoid complex	absent	present

most primitive conditions of 22 characters in the superfamily Cobitoidea are shown
as character conditions in the common ancestor of groups (A) and (B) (Fig. 22).
Thus, it became clear that the common possession of two character conditions, the
absence of opisthotic and the presence of the contact between the orbitosphenoid and
the supraethmoid-ethmoid complex, by all examined members of the superfamily in-
dicate synapomorphy showing that the superfamily is a monophyletic group. On the
other hand, the most primitive conditions of two other characters, the supraorbital
and the orbitosphenoid, are undeterminable because conditions of these characters
shared by three groups are identical (Fig. 22, also see the section 1 of the chapter
IV). After the determination of the most primitive conditions of remaining
characters excluding above four, the polarity of each morphocline is judged as Table
5. From these results, the relationships among previously defined 16 types and
subtypes (Subtypes i and q are regarded to be equivalent to Subtypes h and p
respectively because of the undetermination of polarities in the supraorbital and
the orbitosphenoid) can be shown as four main evolutionary trends which cor-
respond with four subfamilies, Botiinae, Cobitinae, Noemacheilinae and Homalop-
terinae, of the superfamily Cobitoidea (Figs. 23–26). In these trends, two
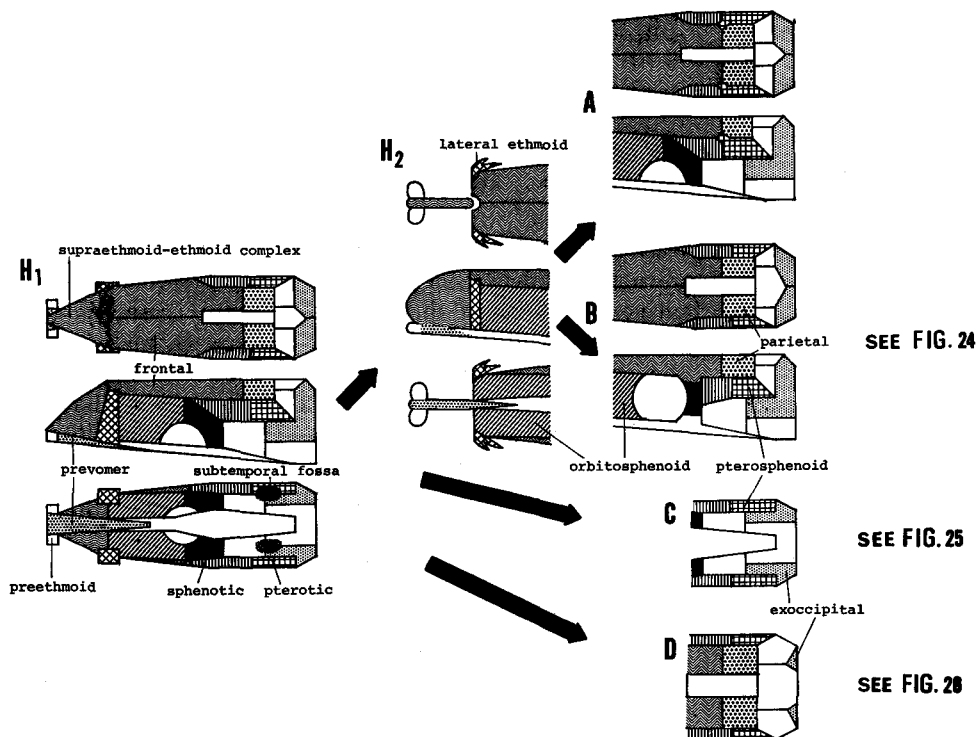
Fig. 23. Four main evolutionary trends of the cobitoid cranium. H_1, H_2 represent
hypothetical morphotypes. H_2 shows the anterior part of the cranium. A, B, C and D
indicate the posterior part of the cranium. H_1, H_2: top, dorsal view; middle, lateral
view; bottom, ventral view. C, ventral view. D, dorsal view. For explanations,
see text.
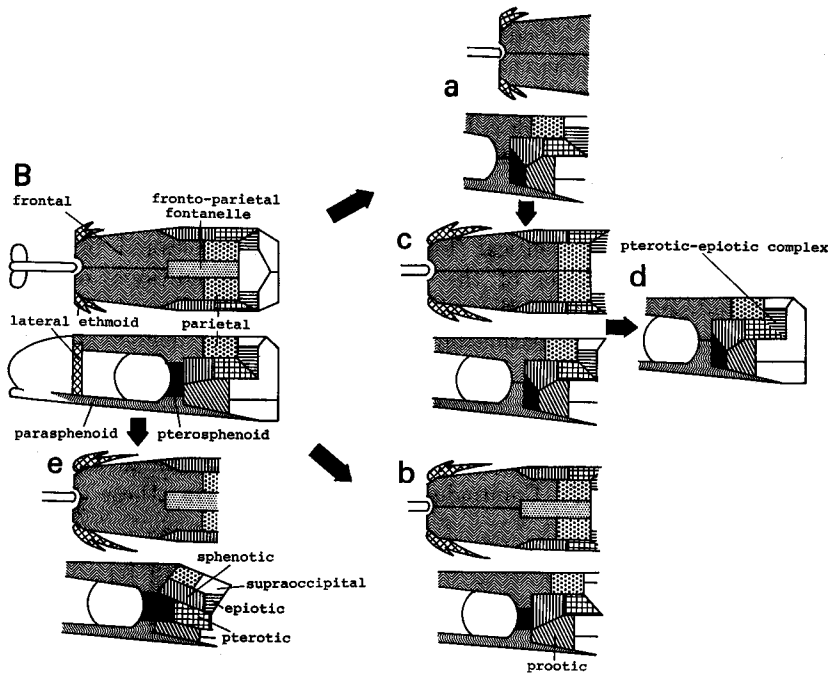
Fig. 24. Evolutionary trends of the cobitine cranium. B, a, b, c, e: above, dorsal view; below, lateral view. d, lateral view. For explanations, see text.

morphotypes are hypothesized (Fig. 23: H_1 and H_2). One of them (H_1), which disagrees with any of previously defined morphotypes of the cobitoid cranium, represents the most primitive conditions of the cobitoid cranium presumed from the cranial character analysis. The other (H_2) indicates several character conditions shared by the cobitid morphotypes A and B.

The first trend represented by the fishes of the subfamily Botiinae is displayed as the disappearance of the contact between the parietal and the sphenotic (Fig. 23: $H_2 \rightarrow A$) succeeding the changes of following five characters: the disappearance of the preethmoid, the occurence of the movable lateral ethmoid, the appearance of the socket-like articulation between the supraethmoid-ethmoid complex and the frontals, the disappearance of the deep subtemporal fossa, and the fusion between the prevomer and the supraethmoid-ethmoid complex (Fig. 23: $H_1 \rightarrow H_3$).

The second trend is represented by members of the subfamily Cobitinae. In this trend, previous five characters first change like the first trend (Fig. 23: $H_1 \rightarrow H_2$), and then the separation between the orbitosphenoid and the pterosphenoid occurs (Fig. 23: $H_2 \rightarrow B$). The following phases of this trend are recognized as three different steps (Fig. 24). In the first step, the frontal first borders the parasphenoid (B→a), the fronto-parietal fontanelle disappears (a→c), and finally the epiotic is fused to the pterotic (c→d). In the second step, the pterosphenoid is separated from the prootic (B→b). Among three steps, the third is the most peculiar (B→e). In this step, the frontal is wholly fused with its fellow on the middorsal line, the

parietal is separated from the pterotic, the sphenotic meets the supraoccipital, the pterotic borders the pterosphenoid, and the sphenotic meets the epiotic. As discussed below, the last feature of this step, the contact of the sphenotic with the epiotic, is also found in the third evolutionary trend, but it differs from that of the third trend in its mode.

The third trend is represented by the fishes of the subfamily Noemacheilinae. In this trend, the parietal is first separated from the pterotic by the extension of the cartilaginous part (Fig. 25: f→g). Then, the epiotic borders the sphenotic (g→h). The contact between both bones also occurs within the second evolutionary trend (Fig. 24: B→e). However, it basically differs from that of the second trend in its mode. In the third trend, the epiotic extends forward to meet the posterior edge of the sphenotic (Fig. 25, h). In the second trend, on the other hand, the contact between the sphenotic and the epiotic is established by an alternative way: the backward extension of the sphenotic, that is found in a cobitine *Acanthopsis choirorhynchos* (Fig. 24, e). Thus, it is considered that the contact between the sphenotic and the epiotic independently occurs in both evolutionary trends. The following phases of the third trend are recognized as two different steps. In one step, the parietal has the secondary contact with the pterotic due to the formation of the parietal-pterotic bridge (Fig. 25: h→j), and finally the preethmoid, the prevomer and the supraethmoid-ethmoid complex are fused to each other to form a large single element (j→m). In the other step, the prevomer is first fused with the supraethmoid-ethmoid complex (h→k). The following phases of this step are somewhat complicated. In the change from k to m (Fig. 25), the parietal-pterotic bridge is formed in addition to the fusion between the preethmoid and the prevomer. On the other hand, in the change from k to l (Fig. 25), the preethmoid is fused with the prevomer. Finally, the contact between the parietal and the pterotic is established by the formation of the bridge (Fig. 25: l→m).

The last evolutionary trend is represented by the fishes of the subfamily Homalopterinae. In this trend, the exoccipital is first separated from its fellow (Fig. 23: H_1→D), and then the fronto-parietal fontanelle disappears (Fig. 26: n→o) or the deep subtemporal fossa disappears (Fig. 26: n→p).
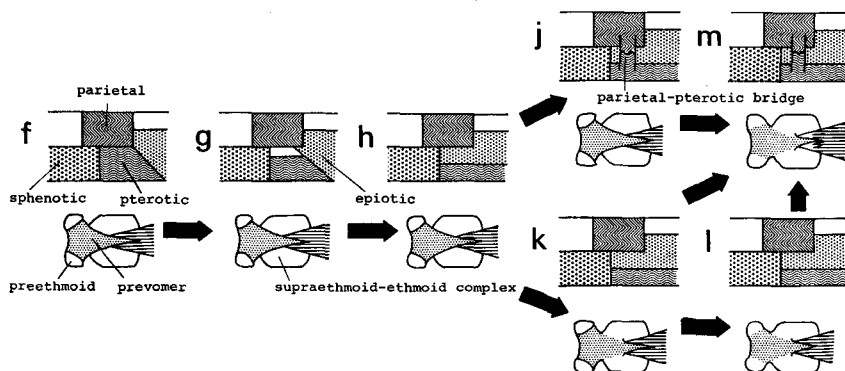
Fig. 25. Evolutionary trends of the noemacheiline cranium. For explanations, see text.

Regarding several features participating in these evolutionary trends of cobitoid cranium, it is interesting that some aspects on the osteological definition of the subfamily Noemacheilinae and the phylogenetic position of the subfamily Homalopterinae are discussed here.

As features characterizing only the subfamily Noemacheilinae, Regan (1911) proposed that the mesethmoid (=supraethmoid-ethmoid complex) is firmly united to the frontals, and also Berg (1940) showed that the mesethmoid, the vomer (=prevomer) and the lateral ethmoid are immovably connected with the frontals and the orbitosphenoid. They have recognized the subfamily as a natural group on the basis of these features. However, these features are rather common among
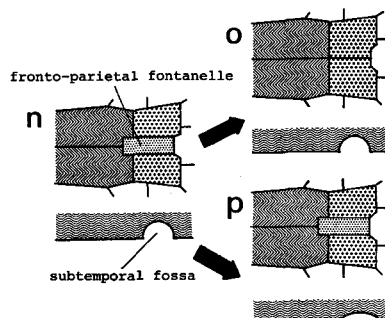
Fig. 26.   Evolutionary trends of the homalopterine cranium.
         For explanations, see text.

other cyprinoid fishes (Ramaswami, 1952a, 1952b, 1955a, 1955b, 1957; Harrington, 1955; Weisel, 1960; Lo and Wu, 1979; Wu et al., 1979), and they are judged as the primitive conditions from the present analysis of cranial characters (fig. 22). It, therefore, is concluded that Regan's (1911) and Berg's (1940) definitions of the subfamily are invalid from the cladistic view point.

On the other hand, Hora (1932) classified the family Homalopteridae, though it is reduced to a subfamily of the new family Homalopteridae in the present study, into two subfamilies Homalopterinae and Gastromyzoninae on the basis of conditions of the paired fin rays and the subtemporal fossa. He hypothesized that fishes of the subfamily Homalopterinae having the deep subtemporal fossa, have evolved from some cyprinid ancestors while fishes of the subfamily Gastromyzoninae having the shallow fossa, have originated from cobitids. Later, Hora (1950) raised both subfamilies to independent families according to his previous hypothesis (1932). This system has been traditionally accepted by Indian ichthyologists (Ramaswami, 1952c, 1952d; Silas, 1952). However, it does not always accepted by many investigators (Greenwood et al., 1966; Lundberg and Marsh, 1976). Though the presence of the deep subtemporal fossa has been regarded as the most important feature by Hora (1932), it is judged as the primitive condition in the present analysis of the cranial characters (Fig. 22). Thus, it is considered that the deep subtemporal fossa is not reasonable as an evidence for the ancestor-descendant relationships between the families Cyprinidae and Homalopteridae proposed by Hora (1950). In addition, there is an

evidence against Hora's conclusion. Hora's conclusion is inconsistent because *Hemimyzon formosanum*, a member of Hora's Homalopteridae, has the shallow fossa. On the other hand, Ramaswami (1952c) provided some cranial evidences to support Hora's hypothesis that homalopterid fishes are cyprinid descendants: 1) the supraethmoid-ethmoid complex firmly articulated with the frontals, 2) the orbitosphenoid, the pterosphenoid and the parasphenoid enclosed the orbital foramen, 3) the prootic, the pterotic and the exoccipital generally accomodated the subtemporal fossa, and 4) the absence of the opisthotic. But, the first three of them are judged to be the primitive conditions in the present analysis (Fig. 22) and thus never serve as supporters of his hypothesis. Although the last feature is judged as the derived condition, it is also found in fishes of the subfamilies Botiinae, Cobitinae and Noemacheilinae of the superfamily Cobitoidea. Thus, Ramaswami's (1952c) consideration are also rejected. In conclusion, it is considered that Hora's (1932) hypothesis is questionable.

2. MANDIBULAR ARCH (Figs. 27–32; Table 6)

Mandibular arch consists of the premaxillary, the maxillary, the dentary, the anguloarticular, the coronomeckelian, the retroarticular, the kinethmoid, the prepalatine, the second preethmoid and the sesamoid bone.

Premaxillary (pmx) is a slightly curved bone having a large anterior ascending process (asp) which is distally connected to the dorsal end of the kinethmoid by a strong ligament. Mediodorsally the bone is somewhat expanded. In *Crossostoma lacustre*, a member of the subfamily Homalopterinae, the distal end of the anterior ascending processes of both sides are fused to each other (Fig. 29F), while in other cobitoid fishes examined, they are firmly attached to each other. In fishes of the subfamily Botiinae and some members of the subfamily Noemacheilinae such as *Noemacheilus pulcher*, *N. botia*, *N. masyae*, *N. fasciolata*, *N. savona*, and *N. evezardi*, the bone anteroventrally forms the anterior process (anp) (=processus dentiformis) (Fig. 27G). In *Botia hymenophysa*, *B. modesta* and *B. dayi*, members of the subfamily Botiinae, the anterior process is laterally bent to form the rounded space with its fellow from the opposite side (Fig. 29B).

Maxillary (mx) is an irregularly shaped thin bone which mediolaterally bears a downward process. The process is well developed in fishes of the subfamily Homalopterinae. The bone anteroventrally froms a large downward process which connects with its fellow from the opposite side below the premaxillary, and anteriorly, into a large knob-like process. In fishes of the subfamily Botiinae, the posterior surface of the anterior knob-like process is distally subdivided into two small projections; one of them is articulated with the prepalatine, and the other, with the second preethmoid (Fig. 29A, B). In fishes of the subfamilies Noemacheilinae and Homalopterinae except *Annamia normani* and *Crossostoma lacustre*, it is dorsally articulated with the prepalatine and ventrally with the second preethmoid (Fig. 29 D, E). In fishes of the subfamily Cobitinae and two homalopterines, *A. normani* and *C. lacustre*, it is articulated only with the second preethmoid (Fig. 29 C, F).

Dentary (d) is the largest bone in the mandibular arch. The bone posteromedially forms a pocket which receives the anterior part of the anguloarticular, post-
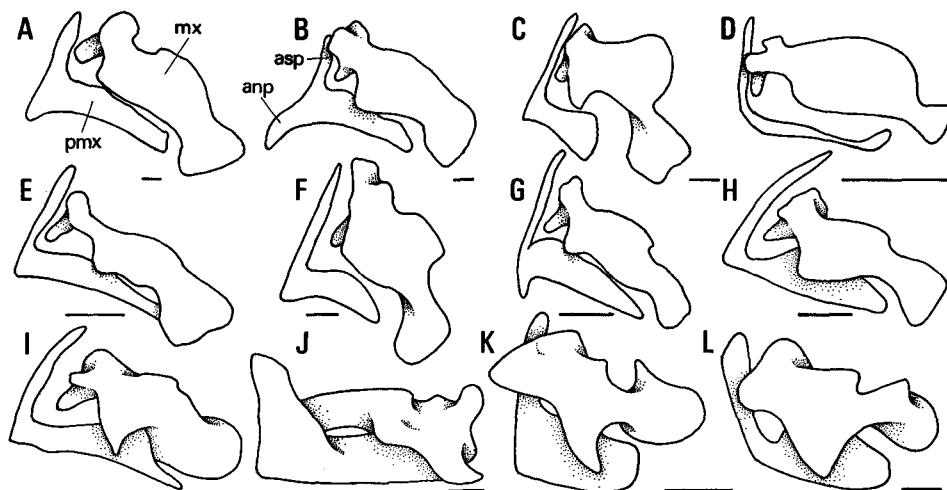
Fig. 27. Upper jaws of cobitoid fishes. A, *Leptobotia curta*; B, *Botia hymenophysa*; C, *Misgurnus fossilis*; D, *Acanthophthalmus anguillaris*; E, *Lefua costata*; F, *Noemacheilus barbatulus*; G, *N. savona*; H, *Homaloptera smithi*; I, *Hemimyzon formosanum*; J, *Sinogastromyzon puliensis*; K, *Annamia normani*; L, *Crossostoma lacustre*. anp, anterior process of premaxillary; asp, ascending process of premaxillary; mx, maxillary; pmx, premaxillary. Scales indicate 1 mm.

erodorsally into a large coronoid process, and medially, into the small projection attaching to the anterior end of the Meckel's cartilage. In fishes of the subfamilies Cobitinae, Noemacheilinae and Homalopterinae, the anterior part of the bone slightly curves ventrally (Fig. 28 C-J), while in fishes of the subfamily Botiinae, it is straight (Fig. 28A, B). In *Hemimyzon formosanum* and *Sinogastromyzon puliensis*, members of the subfamily Homalopterinae, the coronoid process is well developed (Fig. 28G, H).

Anguloarticular (aa) is a large flat bone which is partly overlapped with the posterior part of the dentary. The bone posteriorly forms the articular surface for the condyle of the quadrate, and medially, the small projection attaching to the posterior end of the Meckel's cartilage.

Coronomeckelian (co) is a small triangular thin bone attaching to the dorsomedial side of the anguloarticular. In fishes of the subfamily Cobitinae, the bone is absent (Fig. 28C), while in other cobitoid fishes, it is present (Fig. 28 A, B, D-J).

Retroarticular (ra) is a small irregularly shaped lumpy bone which is firmly joined to the posteroventral surface of the anguloarticular. Posteriorly the bone is ligamentously connected to the anterior part of the interopercle.

Kinethmoid (ke) is a single small rod-shaped bone. Dorsally, the bone is ligamentously connected to the distal end of the ascending process of the premaxillary, and ventrally, to the anteroventral part of the supraethmoid-ethmoid complex. In *Annamia normani* and *Crossostoma lacustre*, members of the subfamily Homalopterinae, the bone is larger and more rounded than those of other cobitoid fishes examined (Fig. 29F).

Prepalatine (ppl) is a small cylindrical bone. The bone is anteriorly articulated
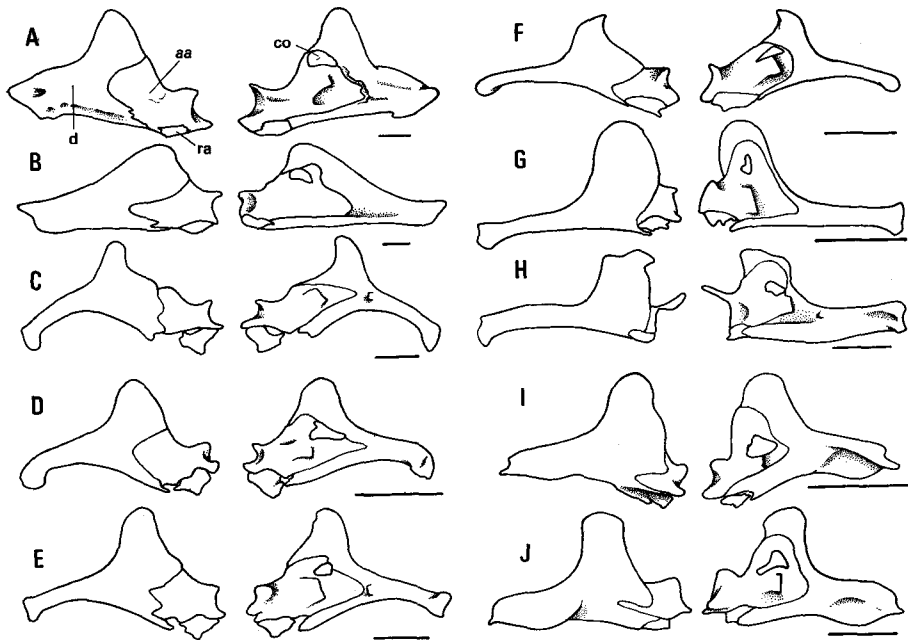
Fig. 28.   Lower jaws of cobitoid fishes.   A, *Leptobotia curta*; B, *Botia hymenophysa*; C,
Misgurnus fossilis; D, *Lefua costata*; E, *Noemacheilus barbatulus*; F, *Homaloptera
smithi*; G, *Hemimyzon formosanum*; H, *Sinogastromyzon puliensis*; I. *Annamia normani*;
J, *Crossostoma lacustre*. aa, anguloarticular;   co, coronomeckelian;   d, dentary;   ra,
retroarticular.   Scales indicate 1 mm.

with the posterodorsal surface of the anterior part of the maxillary, and
posteriorly, with the anterior facet of the autopalatine.   In fishes of the
subfamily Cobitinae and two members of the subfamily Homalopterinae, *Annamia
normani* and *Crossostoma lacustre*, the bone is absent (Fig. 29 C, F).

Second preethmoid (2nd pe) is a small cylindrical bone.   The bone is
anteriorly articulated with the posteroventral surface of the anterior part of the
maxillary.   In fishes of the subfamily Noemacheilinae such as *Lefua echigonia*, *L.
nikkonis*, *L. costata*, *Noemacheilus toni*, *N. postventralis*, *N. barbatulus*, *N. stoliczkai*,
N. pleurotaenia, *N. fasciolata* and *N. pulcher*, the bone is posteriorly articulated
with the preethmoid, while in fishes of the subfamily Botiinae and members of the
subfamily Noemacheilinae such as *Noemacheilus botia*, *N. masyae*, *N. savona*, *N.
fasciatus*, *N. rupecula*, *N. angorae jordanicus*, *N. tigris*, *N. pantera* and *N.
evezardi*, it is articulated with the ventrolateral portion of the supraethmoid-ethmoid
complex. In fishes of the subfamily Cobitinae, the bone is posteriorly divided into the
dorsal and ventral processes; the former is articulated with the anteroventral part
of the autopalatine and the latter is articulated with the ventrolateral part of the
supraethmoid-ethmoid complex.

Sesamoid bone (sb) is a small bone lying over the second preethmoid.   In
fishes of the subfamily Botiinae, the bone is present (Fig. 29 A, B), while in other
cobitoid fishes examined, it is absent (Fig. 29 C-F).
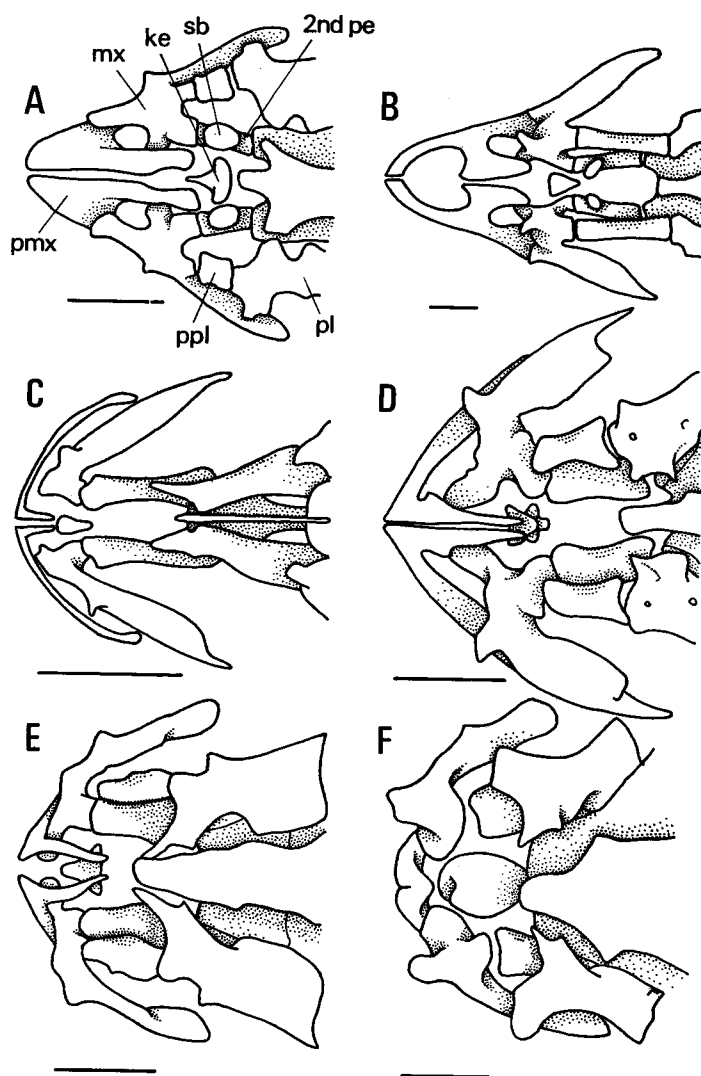
Fig. 29. Dorsal view of mandibular arches of cobitoid fishes. A, *Leptobotia curta*; B, *Botia hymenophysa*; C, *Acanthophthalmus kuhli*; D, *Noemacheilus pulcher*; E, *Homaloptera smithi*; F, *Crossostoma lacustre*. ke, kinethmoid; mx, maxillary; pl, autopalatine; pmx, premaxillary; ppl, prepalatine; sb, sesamoid bone; 2nd pe, second preethmoid. Scales indicate 1 mm.

DISCUSSION

The mandibular arch has been considered as the phylogenetically important part in that it has been taken part in the evolution of the feeding mechanism (Schaeffer and Rosen, 1961; Gosline, 1971). Several investigators have studied

the cobitoid mandibular arch (Sagemahl, 1891; Starks, 1926; Ramaswami, 1948, 1952c, 1952d, 1953).   One of them, Ramaswami (1952c, 1952d, 1953) paid attention to the anterior part of the skull because the superfamily Cobitoidea has a peculiar ossified second preethmoid bone.   However, the phylogenetic significance of the bone has never been evaluated.

Among cobitoid fishes examined here, differences were found in the relation between the premaxillaries on both sides, in the absence or presence of the coronomeckelian, the absence or presence of the sesamoid bone and the absence or presence of the ossified prepalatine (Table 6).   On the basis of the combinations among conditions of these four characters, the cobitoid mandibular arch is divided into five morphotypes (Table 6).   Type A including *Annamia normani*, a member of the subfamily Homalopterinae, is characterized by the presence of the coronomeckelian, the absence of the sesamoid bone, the absence of the ossified prepalatine and the distal ends of both premaxillaries separated from each other.   Type B differs from Type A only by the presence of the ossified prepalatine, and it includes the fishes of the subfamily Noemacheilinae and some members of the subfamily Homalopterinae such as *Homaloptera smithi*, *Hemimyzon formosanum* and *Sinogastromyzon puliensis*.   Type C, including the fishes of the subfamily Botiinae, is distinguished from Type B only by the presence of the sesamoid bone.   Type D, including the fishes of the subfamily Cobitinae, is different from Type A only by the absence of the coronomeckelian.   Type E, including a homalopterine *Crossostoma lacustre*, differs from Type A only in that the premaxillaries on both sides are distally fused with each other.

In order to judge the most primitive conditions of above five characters, including the peculiar feature of the presence of the ossified second preethmoid,

Table 6.   Comparison of several characters of the mandibular arch in cobitoid fishes.

Morpho-type	Character				Subfamily and Species
	distal ends of pre-maxillaries	coronomeckelian	sesamoid bone	prepalatine	
A	separate	present	absent	absent	Homalopterinae *Annamia normani*
B			absent	present	Noemacheilinae all members examined Homalopterinae *Homaloptera smithi*, *Hemimyzon formosanum*, *Sinogastromyzon puliensis*
C			present		Botiinae all species examined
D		absent	absent	absent	Cobitinae all members examined
E	fused	present			Homalopterinae *Crossostoma lacustre*

	A		B	C
1. Each premaxillary	separate fused		separate	separate
2. Coronomeckelian	present absent		present	present absent
3. Sesamoid bones	present absent		absent	absent
4. Prepalatine	present absent		absent	absent
5. Ossified second preethmoid	present absent		absent	absent

1. separate
2. present
3. absent
4. absent
5. absent
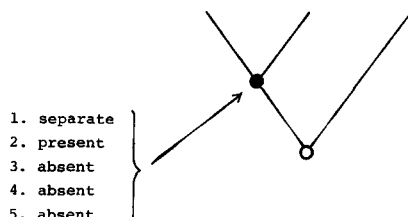
Fig. 30. Character analysis of the cobitoid mandibular arch. The most primitive conditions of five characters in group (A) are shown as the conditions of the common ancestor (●) of groups (A) and (B).

other cyprinoid fishes were examined (Fig. 30). In group (B), the conditions of these characters are: 1) the presence of the free distal ends of premaxillaries on both sides, 2) the presence of the coronomeckelian, 3) the absence of the sesamoid bone, 4) the absence of the ossified prepalatine, and 5) the absence of the ossified second preethmoid (Weisel, 1960; Lo and Wu, 1979). On the other hand, the
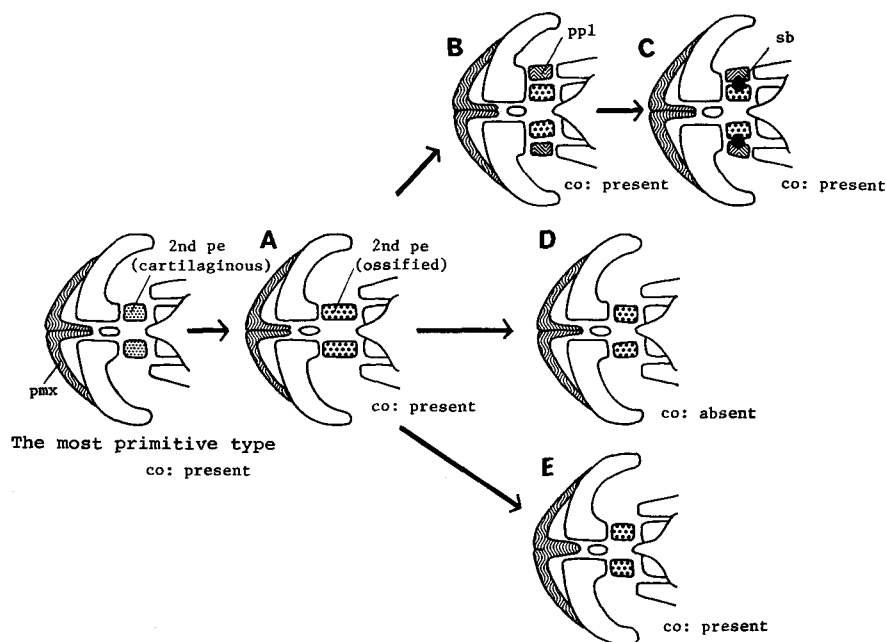
Fig. 31. Evolutionary trends of the cobitoid mandibular arch. For abbreviations, see Figs. 28 and 29. For explanations, see text.

character conditions of group (C) are the same as those of group (B) with an exception that the coronomeckelian is absent in a cyprinid *Gobiobotia brevibarba* (Girgis, 1952; Ramaswami, 1952a, 1952b, 1955a, 1955b; Harrington, 1955; Dixit and Bisht, 1972a; Nelson, 1973; Howes, 1978, 1979, 1980; Wu et al., 1979).

When these cyprinoid conditions of five characters are applied to the criterion (Fig. 30), it can be easily determined that the most primitive conditions of these characters in group (A) are as follows: 1) the separated distal ends of the premaxillaries on both sides, 2) the presence of the coronomeckelian, 3) the absence of the sesamoid bone, 4) the absence of the ossified prepalatine, and 5) the absence of the ossified second preethmoid.

Thus, from the morphoclines of above characters, the relationships among five previously defined morphotypes can be shown as three evolutionary trends in the cobitoid mandibular arch (Fig. 31). They are the appearances of the ossified prepalatine (A→B) and subsequently the sesamoid bone (B→C) in the first trend, the disappearance of the coronomeckelian (A→D) in the second trend, and the fusion of the premaxillaries on both sides (A→E) in the third trend.

For the cobitoid evolution, especially noteworthy is the presence of the ossified second preethmoid, because it is commonly shared by all examined members of the superfamily Cobitoidea.

The appearance of the ossified second preethmoid seems to be closely correlated to the feeding mechanism adopted by the fishes of the superfamily Cobitoidea. Generally, cyprinoid fishes have developed the pipette-like system of the suctorial
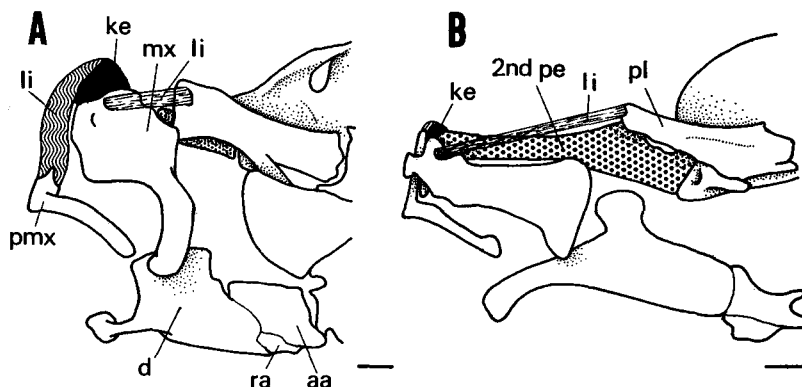
Fig. 32.   Two morphological characteristics in the cyprinoid mandibular arch.   A, a gobion-
ine *Saurogobio dabryi*; B, a cobitine *Acanthopsis choirorhynchos*. aa, anguloarticular; d,
dentary; ke, kinethmoid; li, ligament; mx, maxillary; pl, autopalatine; pmx,
premaxillary; ra, retroarticular; 2nd pe, second preethmoid. In *S. dabryi*, second pre-
ethmoid is cartilage, while in *A. choirorhynchos*, ossified bone. Scales indicate 1 mm.

feeding method with the protrusibility of the mouth (Alexander, 1966, 1969; Gosline, 1973). In connection with the method, the protrusible upper jaw of cyprinoid fishes seems to have first evolved as a mechanism for closing the mouth with the buccal cavity fully expanded (Alexander, 1966, 1969). This mechanism has been accomplished in aid of the kinethemoid which is the unique

feature characterizing the suborder Cyprinoidei.   In addition to this character, there are two morphological characteristics in the anterior region of the skull in a part of cyprinoid fishes: 1) the kinethmoid and the ligament connecting it to the ascending process of the premaxillary are well developed (Fig. 32 A), and 2) the additional bones between the ethmoid part of the skull and the upper jaw are apparent (Fig. 32 B).   The appearance of the ossified second preethmoid in the superfamily Cobitoidea corresponds to the latter.   The bone makes it possible to apply the open mouth to the bottom even by the non-high protrusible mouth having the upper jaw situated anterior to the lower jaw (Fig. 32 B).   From this consideration, it is presumed that the ossified second preethmoid has appeared as a part of the structure for the downward opening of the mouth without any modification of the basic feeding method of cyprinoid fishes, and also that it assures the possibility of the downward opening of the mouth even when the body is situating on the bottom.

This presumption will be discussed again in the section 2 of the chapter VI.

3. HYOID ARCH (Figs. 33–36; Table 7)

Hyoid arch consists of the following elements: the ceratohyal, the epihyal, the dorsal and ventral hypohyals, the interhyal, the branchiostegals and the urohyal.

Ceratohyal (ch) is a flat, pentagonal bone.   Anteriorly it is firmly joined to the ventral and dorsal hypohyals, and posteriorly, to the epihyal (Fig. 33).

Epihyal (eh) is a flat, triangular bone posterior to the ceratohyal.   In *Leptobotia curta* and *Botia dayi*, members of the subfamily Botiinae, it is anterodorsally interlocked with the ceratohyal by a serrated suture (Fig. 33 A), while in other members of the superfamily, it is articulated with the ceratohyal. Posterodorsally, in fishes of the subfamilies Botiinae, Cobitinae and Noemacheilinae, the bone is connected to the proximal end of the interhyal, while in fishes of the subfamily Homalopterinae, it is connected to the ventral portion of the hyomandibular by a strong ligament because of the lack of the interhyal.

Hypohyals (hh) consist of two small lumpy bones, dorsal and ventral, anterior to the ceratohyal.   Medially, they are attached to the sublingual, and laterally, to the ceratohyal. In fishes of the subfamilies Botiinae, Cobitinae and Noemacheilinae, the ventral hypohyal has the posteroventral process connecting to the anterior process of the urohyal by a strong ligament.

Interhyal (ih) is a cylindrical bone connecting the posterior portion of the hyoid arch to the hyomandibular.   In fishes of the subfamily Botiinae except *Leptobotia curta*, it is reduced in size (Fig. 33 B).   In fishes of the subfamily Homalopterinae, the bone is absent* (Fig. 33 G-K).   In most cobitoid fishes examined, if present, it is attached to the lateral side of the posterodorsal part of the epihyal (Fig. 33 A-C, E,F), while in *Acanthophthalmus kuhli* and *A. anguillaris*, members of the subfamily Cobitinae, it is joined to the medial side of the postero-dorsal part of the epihyal (Fig. 33 D).

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* In *Bhavania australia*, *Homaloptera zollingeri* and *Hemimyzon abbreviata*, the rudimentary interhyal is observed (Ramaswami, 1948; McAllister, 1968).
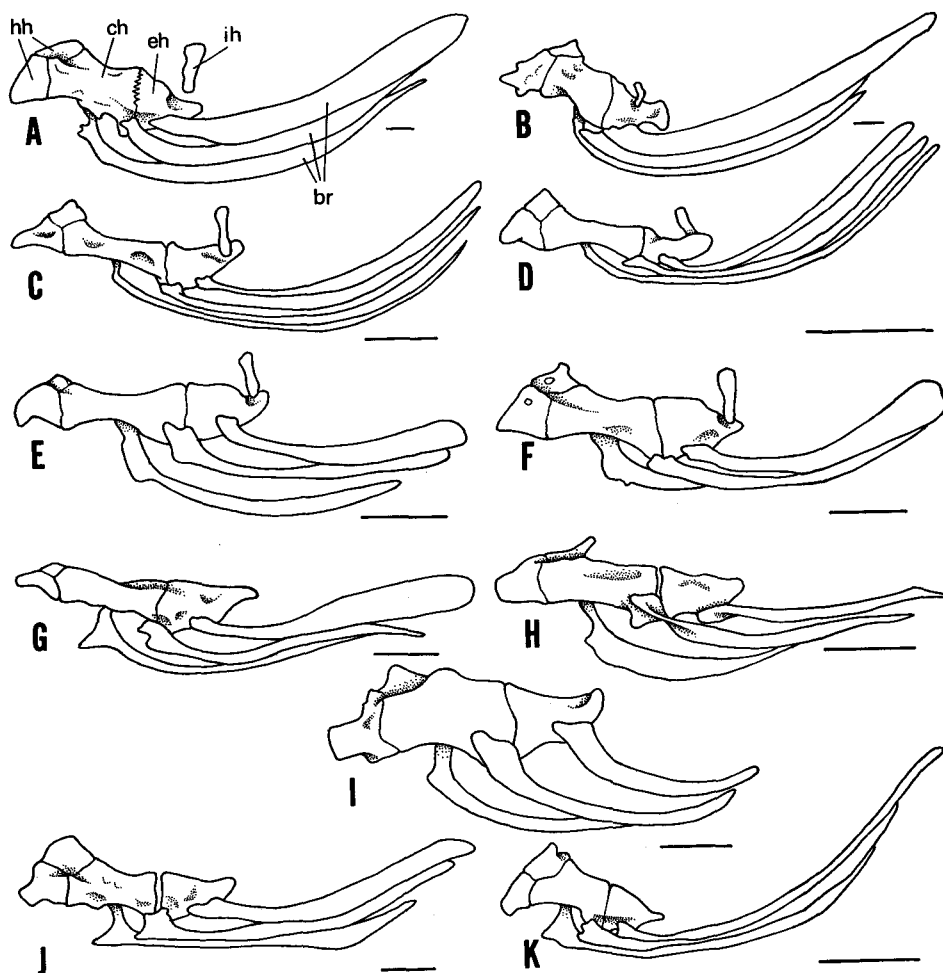
Fig. 33.   Left hyoid arches of 11 cobitoid fishes. A, *Leptobotia curta*; B, *Botia hymenophysa*;
C, *Lepidocephalus guntea*; D, *Acanthophthalmus anguillaris*; E, *Lefua costata*; F, *Noema-
cheilus tigris*; G, *Homaloptera smithi*; H, *Hemimyzon formosanum*; I, *Sinogastromyzon
puliensis*; J, *Annamia normani*; K, *Crossostoma lacustre*. br, branchiostegal; ch,
ceratohyal; eh, epihyal; hh, hypohyal; ih, interhyal.   Scales indicate 1 mm.

Branchiostegals (br) consist of three acinaciform bones.   The first branchi-
ostegal is articulated with the medial side of the ventral margin of the ceratohyal,
and the second and the third, with the lateral side of the ventral margin of the
ceratohyal and the epihyal respectively.   In *Hemimyzon formosanum*, a member of
the subfamily Homalopterinae, the second and third branchiostegals lack the basal
articulations with the ceratohyal and the epihyal due to their outer lateral shift
(Fig. 33 H).

Urohyal (uh) is a single bone situated under the anterior part of basibranchial
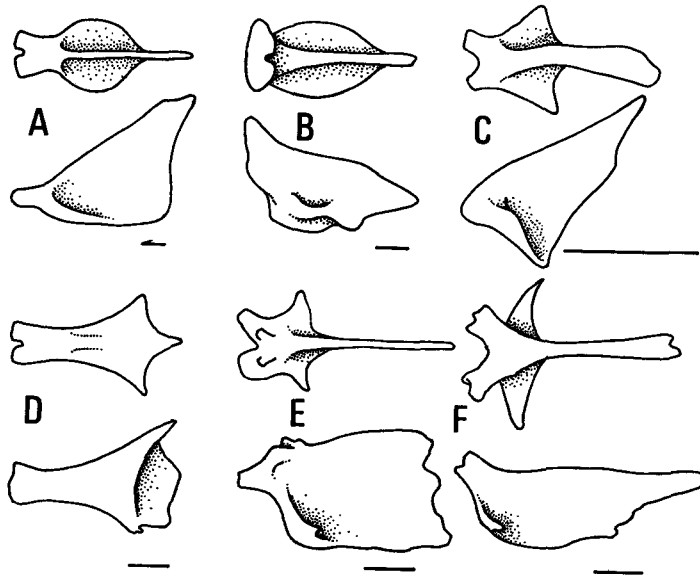
Fig. 34. Urohyals of six cobitoid fishes. A, *Leptobotia curta*; B, *Botia modesta*; C, *Cobitis paludicola*; D, *Acanthopsis choirorhynchos*; E, *Noemacheilus barbatulus*; F, *Sinogastromyzon puliensis*. Upper, dorsal view; lower, lateral view. Scales indicate 0.5 mm.

series.　Anteriorly, it is connected to the ventral hypohyals by strong ligaments, and posteriorly, to the cleithrum by the sternohyoideus muscle. The antero-ventral edge of the bone generally expands laterally to provide the surface where the sternohyoideus muscle is inserted (Fig. 34). In fishes of the subfamily Homalopterinae, this lateral extension of the bone is well-developed (Fig. 34 F). In *Leptobotia curta* and *Botia hymenophysa*, members of the subfamily Botiinae, and fishes of the subfamily Cobitinae, the bone is triangular-shaped with a posterodorsal projection (Fig. 34 A, C, D), while in fishes of the subfamilies Noemacheilinae and Homalopterinae, it is nearly square-shaped (Fig. 34 E, F).

<center>DISCUSSION</center>

In fishes of the superfamily Cobitoidea, the hyoid arch is little used for the analysis of the phylogenetic relationships, although it has been examined by some authors (Ramaswami, 1948, 1952c, 1952d, 1953; McAllister, 1968). Among cobitoid fishes examined, differences were found in the degree of the development of the interhyal (Table 7). According to the developmental degree of the bone, the fishes of the superfamily are classified into three morphotypes. Type A, having well-developed interhyal, includes all members of the superfamily except the fishes of the botiine genus *Botia* and the subfamily Homalopterinae. The second type, Type B, having distinctly reduced interhyal, includes the fishes belonging to the genus *Botia* (Fig. 33 B). The third type, Type C, including fishes of the subfamily Homalopterinae, does not have the interhyal (Fig. 33 G-K).

On the basis of the criterion for the determination of the polarity in the morphocline, the most primitive condition of the cobitoid interhyal is judged (Fig. 35).   In fishes of group (A), the interhyal is either well-developed, distinctly reduced, or absent (Fig. 35).   In fishes of other groups (B) and (C), the bone is well-developed (Ramaswami, 1952a, 1952b, 1955a, 1955b, 1957; Harrington, 1955;

Table 7.   Comparison of cobitoid interhyal.

Morphotype	Interhyal	Subfamily and Genus

A	well-developed	Botiinae
		    Leptobotia
		Cobitinae
		    all genera examined
		Noemacheilinae
		    all genera examined

B	reduced	Botiinae Botia
C	absent	Homalopterinae all genera examined

Weisel, 1960; McAllister, 1968; Dixit and Bisht, 1972a; Howes, 1978, 1979, 1980; Wu et al., 1979; Wu and Lo, 1979).   Thus, it is naturally considered that an evolutionary trend is shown as the relationships among above three types: from well-developed interhyal to the loss of the bone through the distinctly reduced interhyal (A→B→C).

On the other hand, the reduction and the loss of the interhyal may be related to the feeding and the respiration mechanisms.   In fishes of the suborder Cyprinoidei, it is well known that the feeding and the respiration require the development of a negative pressure, namely suction, in the oral and/or branchial cavities (Matthes, 1963; Alexander, 1966; Ballintijn, 1969; Gosline, 1973).   In the expansion of the oral and/or branchial cavities to produce a negative pressure, the hyoid arch has an important role as a lever (Schaeffer and Rosen, 1961). Thus, the distinct reduction and the loss of the interhyal found in fishes of the
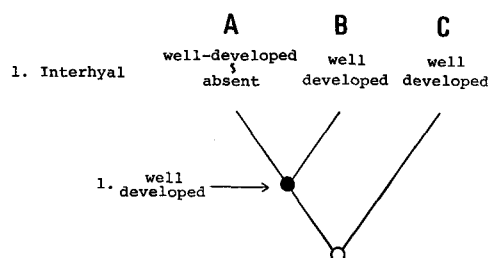
Fig. 35.   Character analysis of the cobitoid interhyal.   The most primitive condition of the character in group (A) is shown as the condition in the common ancestor (●) of groups (A) and (B).

botiine genus *Botia* and the subfamily Homalopterinae may be correlated to the method producing the negative pressure.

The negative pressure is produced by two methods: the lowering of the mouth floor and the lateral swinging of the lateral wall, both of which seem to occur simultaneously (Alexander, 1969; Ballintijn, 1969). The first method is
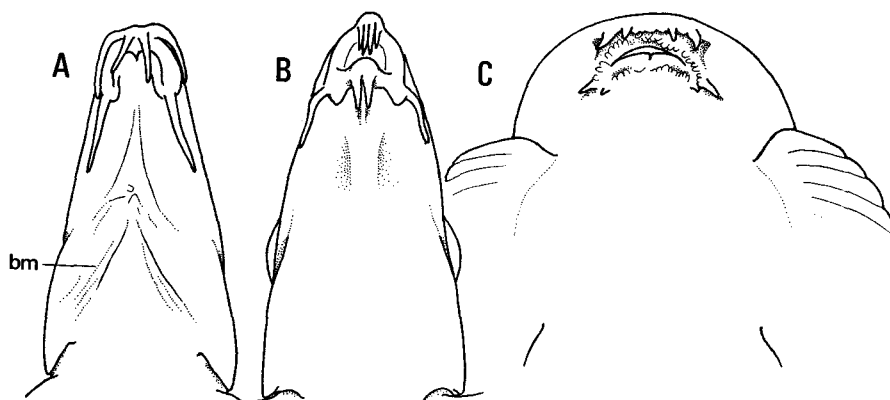
Fig. 36. Ventral view of head in three cobitoid fishes. A, *Leptobotia curta*; B, *Botia macracantha*; C, *Sinogastromyzon puliensis*. bm, branchiostegal membrane.

accomplished by the lowering of the anterior part of the hyoid bar. In the lowering of the hyoid bar, however, the interhyal may be have the least important role, because such movement seems to be established by having only one fulcrum between the hyomandibular and the posteriormost end of the hyoid bar. The second method is accomplished by the combined movements among the suspensorium, the opercular apparatus and the branchiostegals. When the suspensorium is swung laterally to expand the oral and/or branchial cavities, the opercular apparatus is carried laterally and the branchiostegals open like the ribs of a fan (Alexander, 1975). When the branchiostegals are opened incidentally by the lateral swinging of the suspensorium and the opercular apparatus, the hyoid bar is pulled up and back. As Schaeffer and Rosen (1961) suggested, this backward movement of the hyoid bar seems to be allowed by the presence of the interhyal. From this considera-tion, it is presumed that the degree of the lateral swinging in the lateral wall may be dependent upon the length of the interhyal.

In fishes of the botiine genus *Botia* and the subfamily Homalopterinae, the detail mechanisms of the feeding and the respiration are little known (Hora, 1932; Wickler, 1971). However, some movements in the feeding and the respiration may be presumed from some morphological evidences. In fishes of the subfamily Homalopterinae, the branchiostegal membranes supported by the branchiostegals are completely unobservable (Fig. 36 C), and the lateral side of head is stiffened by the extensive lipid-like substances to form an effective sucking disc (Fig. 36 C). In addition to this fact, in *Hemimyzon formosanum*, a member of the same subfamily, the second and third branchiostegals lack the basal articulations with

the hyoid bar. In fishes of the genus *Botia*, the membranes are less-developed (Fig. 36 B).   These facts suggest that in fishes of the genus *Botia* and the subfamily Homalopterinae, the lateral swinging of the lateral wall is restricted. Therefore, it is considered that the reduction or the loss of the interhyal seems to result from the reduction of the lateral swinging in these fishes in the feeding and the respiration.

4. BRANCHIAL APPARATUS (Figs. 37–42; Table 8)

Branchial apparatus includes the following elements: the basibranchial, the ceratobranchial, the epibranchial, the hypobranchial, the infrapharyngobranchial, the basihyal, the sublingual and the lower pharyngeal.

Basibranchials (bb) are a series of flat bones lying on the ventral median line of the branchial cavity. The first two of them are fan-shaped, the third is rod-shaped and the fourth, if present, is rod-shaped (Fig. 37). In fishes of the subfamily Cobitinae, a botiine *Leptobotia curta*, some members of the subfamily Noemacheilinae such as *Noemacheilus postventralis*, *N. pulcher*, *N. angorae jordanicus*, *N. tigris* and *N. fasciatus*, there are four basibranchials (Fig. 37 A, D-F, H; Table 8). In *Botia modesta*, a member of the subfamily Botiinae, there are only two basibranchials (Fig. 37 C). In all other cobitoids examined, there are three basibranchials (Fig. 37 B, G, I, J; Table 8).

Ceratobranchials (cb) comprise four paired elongate bones being essentially identical in shape. Proximally, each bone is articulated with its corresponding epibranchial. Distally, the first to third ceratobranchials are articulated with the corresponding hypobranchials. In *Leptobotia curta*, a member of the subfamily Botiinae, *Noemacheilus postventralis*, a member of the subfamily Noemacheilinae, and *Homaloptera smithi* and *Crossostoma lacustre*, members of the subfamily Homalopterinae, the fourth ceratobranchial is connected to the ossified fourth hypobranchial (Fig. 37 A, F, I), while in all other cobitoid fishes examined, the fourth is in contact with the posterior cartilaginous copula.

Epibranchials (eb) consist of four pairs of small bones. Distally, the first of them is articulated with the first infrapharyngobranchial, and the second and third are joined with the second infrapharyngobranchial. In most members of the super-family, the fourth epibranchial lacks its corresponding infrapharyngobranchial (Fig. 37). In *Leptobotia curta*, *Botia macracantha* and *B. hymenophysa*, members of the subfamily Botiinae, *Noemacheilus postventralis*, a member of the subfamily Noemacheilinae and *Misgurnus anguillicaudatus*, a member of the subfamily Cobitinae, the fourth epibranchial is joined with the third infrapharyngobranchial (Fig. 37 A, B, D, F).

Hypobranchials (hb) are small paired square bones. Medially, the first hypobranchial is articulated with the basibranchial series between the basihyal and the first basibranchial; the second, between the first and the second basibranchials; the third, between the second and third basibranchials. The fourth hypobranchial, if present, is articulated with the posterior part of the third basibranchial. Laterally, each hypobranchial including the fourth one is articulated with its corresponding ceratobranchial. In most cobitoid fishes examined, there are three pairs of the bones. In *Leptobotia curta*, a member of the subfamily Botiinae, *Noemacheilus*
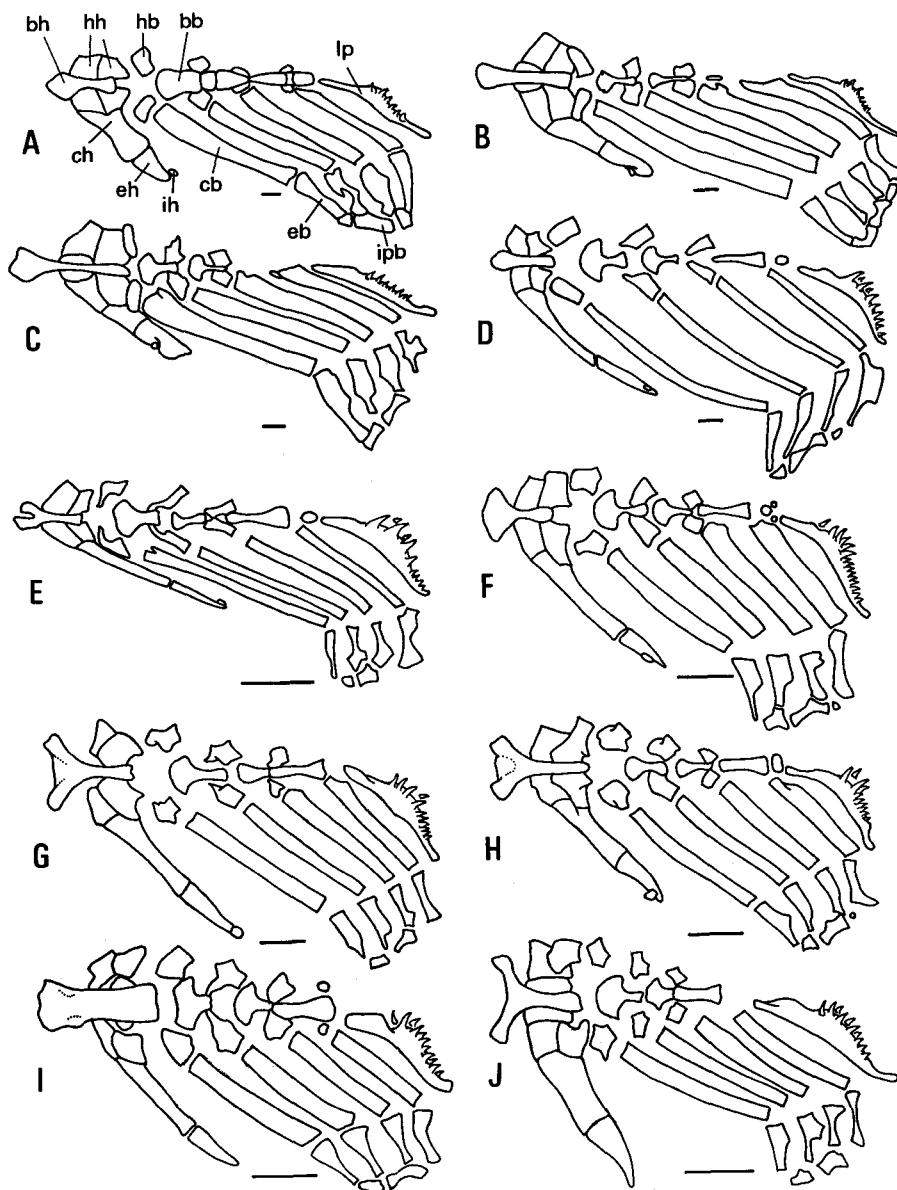
Fig. 37.   Branchial apparatus in cobitoid fishes.   A, *Leptobotia curta* ; B, *Botia hymenophysa*; C, *B. modesta*; D, *Misgurnus anguillicaudatus*; E, *Cobitis paludicola*; F, *Noemacheilus postventralis*; G, *N. barbatulus*; H, *N. pulcher*; I, *Homaloptera smithi*; J, *Hemimyzon formosanum*.   bb, basibranchial; bh, basihyal; cb, ceratobranchial; ch, ceratohyal; eb, epibranchial; eh, epihyal; hb, hypobranchial; hh, hypohyal; ih, interhyal; ipb, infrapharyngobranchial; lp, lower pharyngeal.   Scales indicate 1 mm.

postventralis, a member of the subfamily Noemacheilinae, and *Homaloptera smithi* and *Crossostoma lacustre*, members of the subfamily Homalopterinae, the fourth hypobranchial is present (Fig. 37 A, F, I).

Infrapharyngobranchials (ipb) are small paired bones suspending the branchial apparatus from the ventral floor of the skull. The first infrapharyngobranchial is joined to the first epibranchial; the second, to the second and third epibranchials. The third infrapharyngobranchial, if present, is joined to the fourth epibranchial. In most cobitoid fishes examined, there are two pairs of the bones. The first pair of them are generally smaller than the second. In *Leptobotia curta*, *Botia macracantha* and *B. hymenophysa*, members of the subfamily Botiinae, *Misgurnus anguillicaudatus*, a member of the subfamily Cobitinae, and *Noemacheilus postventralis*, a member of the subfamily Noemacheilinae, the third infrapharyngobranchial is present (Fig. 37 A, B, D, F).

Basihyal (bh) is a flat, Y-shaped or rod-shaped bone representing the anterior-most element of the basibranchial series. In fishes of the subfamilies Botiinae and Cobitinae, and *Noemacheilus rupecula*, a member of the subfamily Noemacheilinae, the bone is rod-shaped (Figs. 37 A-E and 38 A, B). In fishes of the subfamilies Homalopterinae and Noemacheilinae except *N. rupecula*, it is Y-shaped (Figs. 37 F-J and 38 C, D). In fishes of the subfamily Homalopterinae, the bone lies on the dorsal surface of the sublingual (Fig. 38 D).

Sublingual (so) is a small rod-shaped bone locating between the paired hypohyals (Fig. 38). In fishes of the subfamilies Cobitinae, Noemacheilinae and Botiinae except *Leptobotia curta*, there are two ossifications (Fig. 38 A, B, C).
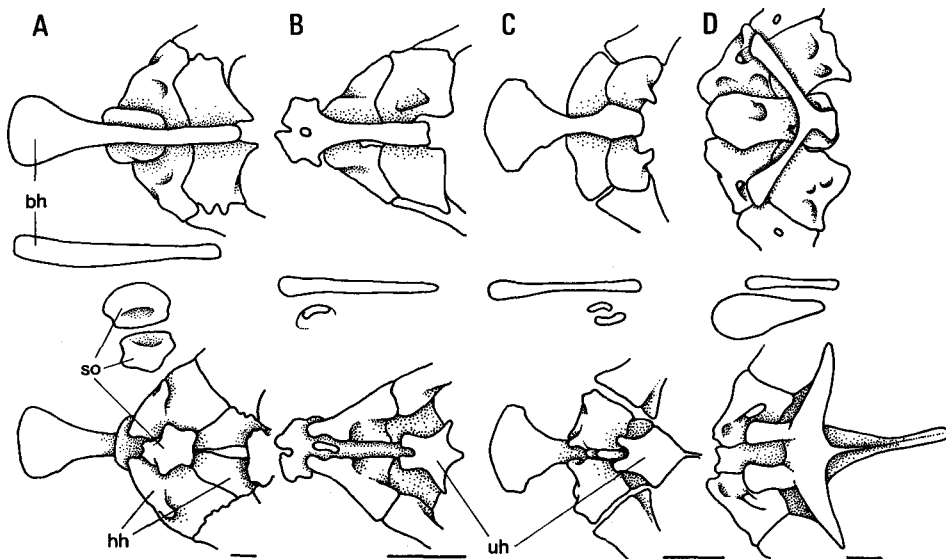
Fig. 38. Anterior part of branchial apparatus in cobitoid fishes. A, *Botia modesta*; B, *Cobitis paludicola*; C, *Lefua costata*; D, *Crossostoma lacustre*. bh, basihyal; hh, hypohyal; so, sublingual; uh, urohyal. Top, dorsal view; middle, lateral view; bottom, ventral view. Scales indicate 0.5 mm.
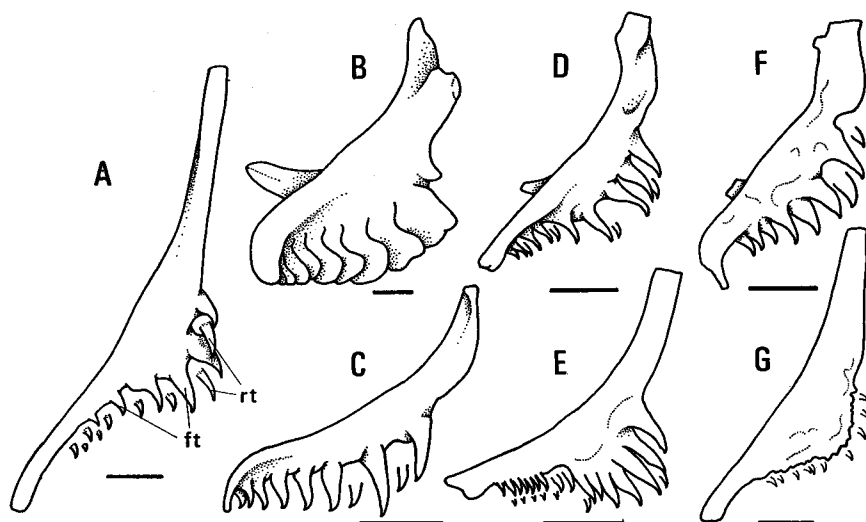
Fig. 39. Lower pharyngeals in cobitoid fishes. A, *Botia hymenophysa*; B, *Misgurnus mizolepis*; C, *Cobitis paludicola*; D, *Noemacheilus pleurotaenia*; E, *Noemacheilus botia*; F, *Homaloptera smithi*; G, *Sinogastromyzon puliensis*. ft, functional tooth; rt, replacement tooth. Scales indicate 0.5 mm.

In a botiine *Leptobotia curta*, the bone is represented as a cartilaginous mass. In fishes of the subfamily Homalopterinae, there is a single relatively large ossification fitting between the paired hypohyals (Fig. 38 D).

Lower pharyngeal (lp) is an elongate arch-like bone bearing a strong ventral process on its ventral surface. On the dorsal surface of the bone, except for a case of a cobitine *Misgurnus mizolepis*, there is a row of 8 to 20 conical teeth. In many specimens examined, there is a replacement tooth (rt) between the functional teeth (ft) (Fig. 39). In *Sinogastromyzon puliensis*, a member of the subfamily Homalopterinae, the teeth on the dorsal surface of the bone consist of only the replacement teeth (Fig. 39 G), and in *Misgurnus mizolepis*, a member of the subfamily Cobitinae, 8 or 9 compressed functional teeth (Fig. 39 B).

DISCUSSION

The branchial apparatus of the superfamily Cobitoidea has been examined by Ramaswami (1948, 1952c, 1952d, 1953) and Nelson (1969). The branchial apparatus, especially sublingual, has been considered as one of the most important characters in elucidating the interfamilial relationships of Berg's family Cobitidae (Nelson, 1969). Moreover, the lack of the first basibranchial has been considered to characterize the family (Nelson, 1969). However, there is still a problem on the identification of basibranchials. It is discussed through the ontogenetic evidences preceding the character analysis of the cobitoid branchial apparatus.

Nelson (1969) defined the first to the third basibranchials on the basis of the relative position of the basibranchials. Thus, he considered that the basibranchial

laid between the paired hyoid elements and the paired first hypobranchials is as the first; the basibranchial laid between the paired first and second hypobranchials as the second; the basibranchial laid between the paired second and third hypobranchials as the third.   According to this definition, it is concluded that the fishes of Berg's family Cobitidae lack the first basibranchial because of the absence of the basibranchial corresponding with the first hypobranchials. However, some evidences from ontogeny of basibranchial series in a cobitid *Misgurnus anguillicaudatus* do not support this conclusion.

In 7.6 mm TL specimen of *M. anguillicaudatus*, the basibranchial series is composed of three cartilaginous copulae (Fig. 40 A).   At 9.5 mm TL, the median cartilaginous copula is subdivided into three smaller cartilaginous masses (Fig. 40 B).   At 11.9 mm TL, the ossification center almost contemporaneously arises on the median part of each cartilaginous mass and the anteriormost copula.   Among the ossification centers on the three masses, there is no distinct difference in the degree of ossification (Fig. 40 C).   Thus, the developmental pattern of the basibranchials in *M. anguillicaudatus*, which is regarded as the lack of the first basibranchial by Nelson (1969), well agrees with those of fishes having the basibranchial corresponding with the first hypobranchials (De Beer, 1937; Bertmar, 1959). Judging from these facts, contrary to Nelson (1969), it is concluded that cobitid fishes also have the first basibranchial and thus typically the complete series of basibranchials consisting of the first to the third.

With regard to characterizing the cobitoid basibranchials, especially noteworthy is the positional relationships of the basibranchials relative to the paired arch elements.   As noted above, fishes of the superfamily Cobitoidea including Berg's Cobitidae have the complete series of basibranchials.
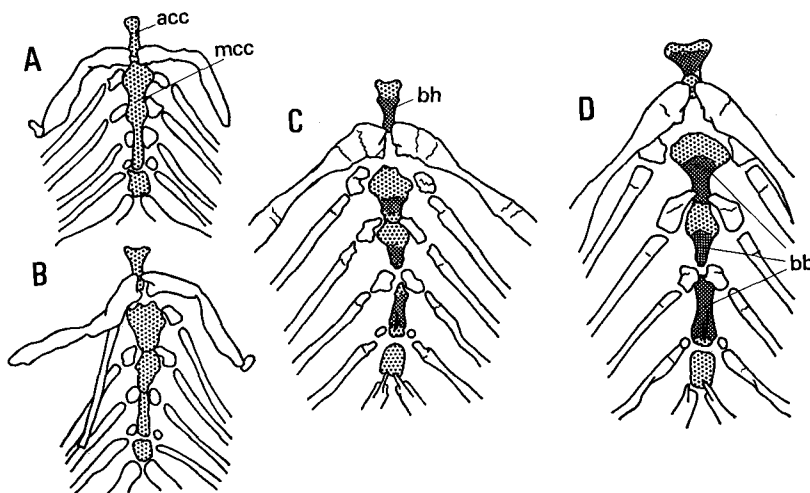
Fig. 40. Ontogenetic development of basibranchial series in a cobitine *Misgurnus anguillicaudatus*. A, 7.6 mm TL; B, 9.5 mm TL; C, 11.9 mm TL; D, 14.7 mm TL. acc, anterior cartilaginous copula; bb, basibranchial; bh, basihyal; mcc, median cartilaginous copula. Roughly dotted part, cartilage; finely dotted part, ossified bone.

Among cobitoid fishes examined, differences are found in the number of basibranchials, hypobranchials and infrapharyngobranchials (Table 8). According to the combinations among the conditions shown in these characters, the cobitoid basibranchial apparatus is classified into seven morphotypes (Table 8). Type A is characterized in having three basibranchials, three pairs of the hypobranchials and two pairs of the infrapharyngobranchials, and includes *Botia dayi*, a member of the subfamily Botiinae, fishes of the subfamily Noemacheilinae except *Noemacheilus postventralis*, *N. pulcher*, *N. angorae jordanicus* and *N. tigris*, and some members of the subfamily Homalopterinae such as *Hemimyzon formosanum*,

Table 8. Comparison of three characters of the branchial apparatus in cobitoid fishes. bb, basibranchial; hb, hypobranchial; ipb, infrapharyngobranchial.

Morphotype	Character			Subfamily and Species
	number of bb	pairs of ipb	4th hb	

A	3	2	absent	Botiinae
				  Botia dayi
				Noemacheilinae
				  Lefua echigonia, L. nikkonis, L. costata, Noemacheilus toni, N. barbatulus N. stoliczkai, N. pleurotaenia, N. botia, N. masyae, N. savona, N. rupecula N. fasciolata, N. breviceps, N. fowlerianus, N. pantera, N. evezardi
				Homalopterinae
				  Hemimyzon formosanum, Sinogastromyzon puliensis, Annamia normani

B			present	Homalopterinae *Homaloptera smithi, Crossostoma lacustre*

C	4		absent	Cobitinae
				  Misgurnus fossilis, M. mizolepis, Cobitis taenia taenia, C. taenia striata, C. takatsuensis, C. biwae, C. koreensis, C. paludicola, Niwaella delicata, N. multifasciata, Sabajenewia aurata vallachica, Acanthopsis choirorhynchos, Acanthopsoides graciroides, Lepidocephalus guntea, Acanthophthalmus kuhli, A. anguillaris
				Noemacheilinae
				  Noemacheilus pulcher, N. angorae jordanicus, N. tigris, N. fasciatus

D	2			Botiinae *Botia modesta*

E	4	3	present	Botiinae
				  Leptobotia curta
				Noemacheilinae
				  Noemacheilus postventralis

F	3		absent	Botiinae *Botia macracantha, B. hymenophysa*
G	4			Cobitinae *Misgurnus anguillicaudatus*

Sinogastromyzon puliensis and *Annamia normani*. Type B including *Homaloptera smithi* and *Crossostoma lacustre*, members of the subfamily Homalopterinae, differs from Type A in having four pairs of hypobranchials. Type C differs from Type A in having four basibranchials and includes fishes of the subfamily Cobitinae except *Misgurnus anguillicaudatus*, and some members of the subfamily Noemacheilinae such as *Noemacheilus pulcher, N. angorae jordanicus* and *N. tigris*. Type D including only *Botia modesta,* a member of the subfamily Botiinae, is distinguished from Type A in having only two basibranchials. Type E, including a botiine *Leptobotia curta* and a noemacheiline *Noemacheilus postventralis*, is characterized in having four basibranchials, four pairs of the hypobranchials and three pairs of the infrapharyngobranchials. Type F including *Botia macracantha* and *B. hymenophysa*, members of the subfamily Botiinae is different from Type A in having three pairs of the infrapharyngobranchials. Type G, including only a cobitine *Misgurnus anguillicaudatus*, differs from Type C in having three pairs of the infrapharyngobranchials.

The most primitive conditions of above characters including the positional relationship between the first three basibranchials and their paired arch elements in the cobitoid branchial apparatus are judged on the basis of the criterion for the determination of polarity (Fig. 41). The conditions of these characters found in group (B) are the presences of the first three basibranchials corresponding to the paired arch elements, two or three basibranchials, two or three pairs of the hypobranchials, and two or three pairs of the infrapharyngobranchials (Weisel, 1960; Lo and Wu, 1979). On the other hand, the conditions of these characters found in group (C) are as follows: the first three basibranchials generally correspond to their paired elements, but in a gyrinocheilid *Gyrinocheilus aymonieri*, the basibranchials are shifted backward relative to the paired arch elements (Ramaswami, 1952a; Wu et al, 1979). Three or four basibranchials, two or three pairs of the infrapharyngobranchials are present (Ramaswami, 1952a, 1952b, 1955a, 1955b; Harrington, 1955; Dixit and Bisht, 1972a; Howes, 1978, 1979, 1980; Wu et al., 1979).

	A	B	C
1. Relation of basibranchials to paired arch elements	corresponded backward shifted	corresponded	corresponded backward shifted
2. Basibranchials	2, 3, 4	2, 3	3, 4
3. Fourth hypobranchial	present absent	absent	absent
4. Infrapharyngobranchials (pairs)	2, 3	2, 3	2, 3

1. corresponded
2. 3
3. absent
4. ?
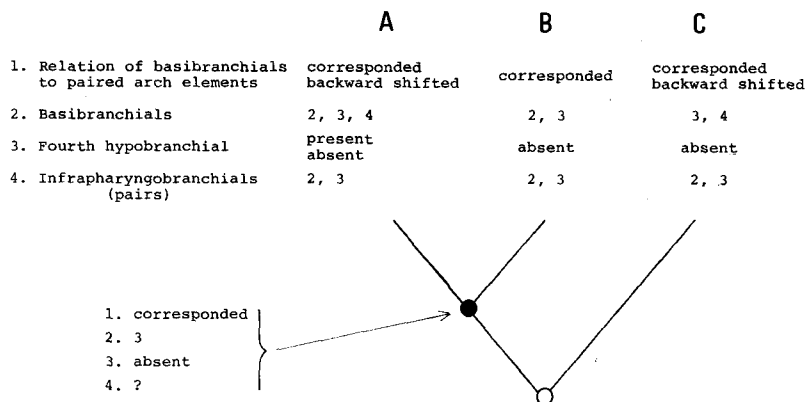
Fig. 41. Character analysis of the cobitoid branchial apparatus. The most primitive conditions of four characters in group (A) are shown as the conditions in the common ancestor (●) of groups (A) and (B).

On the basis of the above criterion, the most primitive conditions of these characters in group (A) are determined as three basibranchials and three hypobranchials (Fig. 41). However, the most primitive condition of the cobitoid infrapharyngobranchial is undeterminable, because the conditions shown in the three groups are identical (Fig. 41). Thus, the number of cobitoid basibranchials advances toward two directions: from 3 to 4 or 2. The number of the cobitoid hypobranchials advances from 3 to 4. Also, the backward shift of the basibranchials relative to the paired arch elements characterizes the superfamily Cobitoidea as the derived state.
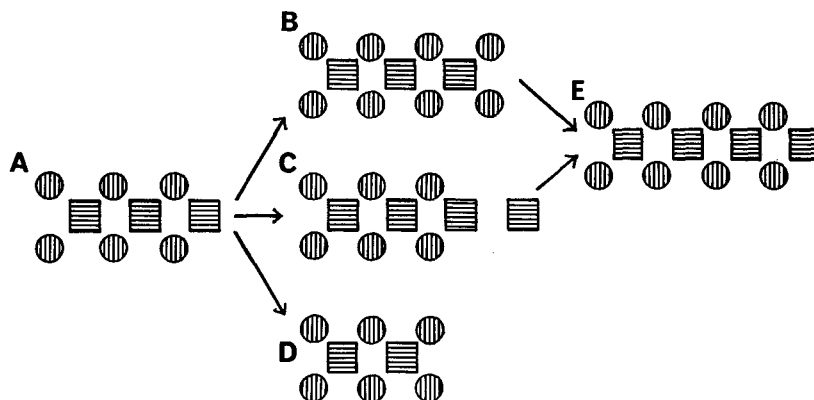
Fig. 42. Evolutionary trends in the cobitoid branchial apparatus. Square, basibranchial; circle, hypobranchial.

On the basis of above two morphoclines, the basibranchials and the hypobranchials, three evolutionary trends are shown as the relationships among five previously defined morphotypes except for Types F and G (Fig. 42) (Types F and G are here dealt as identical with Types A and C respectively because it is impossible to determine the polarity of the infrapharyngobranchial). In the first trend, the fourth hypobranchial occurs (A→B) and then the fourth basibranchial occurs (B→E). In the second trend, the fourth basibranchial occurs (A→C) and then the fourth hypobranchial occurs (C→E). In the third trend, the third basibranchial disappears (A→D).

5. SUSPENSORIUM (Figs. 43–47; Table 9)

Suspensorium includes the following elements: the hyomandibular, the quadrate, the symplectic, the autopalatine, the ectopterygoid, the entopterygoid, the metapterygoid, the opercle, the subopercle, the interopercle, the preopercle and the suprapreopercle. Dermopalatine is absent.

Hyomandibular (hy) is a flat rectangular bone. Dorsally it bears two articular processes suspending the suspensorium from the skull: the anterior articular process fits into the facet formed by the anterior part of the sphenotic, the posterior part of the pterosphenoid and the anterodorsal margin of the prootic;

the posterior one fits into the facet formed by the posterior part of the sphenotic, the posterodorsal margin of the prootic and the ventral margin of the pterotic. Posterodorsally the bone forms a small condyle articulating with the opercle. In fishes of the subfamilies Botiinae, Noemacheilinae and Homalopterinae, and a cobitine genus *Misgurnus*, the anterior border of the bone is concave (Figs. 43, 44A and 45),
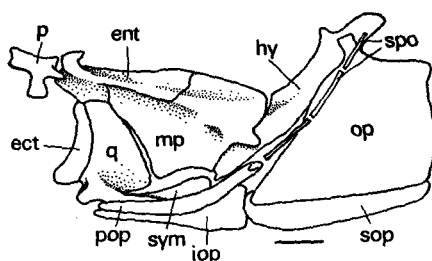
Fig. 43. Suspensorium in a botiine *Botia macracantha*. ect, ectopterygoid; ent, entopterygoid; hy, hyomandibular; iop, interopercle; mp, metapterygoid; op, opercle; p, autopalatine; pop, preopercle; q, quadrate; sop, subopercle; spo, suprapreopercle; sym, symplectic. Scale indicates 1 mm.

while in fishes of the subfamily Cobitinae except *Misgurnus*, it forms an extensive forward process (efp) free from the skull (Fig. 44).

Quadrate (q) is a flat triangular bone which posteroventrally forms a long taper process and anteriorly a condyle for the movable articulation with the anguloarticular.   In fishes of the subfamily Cobitinae except the genus *Misgurnus*, the bone posterodorsally forms the anterior margin of the metapterygoid-quadrate fenestra (mqf) (Fig. 44).

Symplectic (sym) lying among the metapterygoid, the quadrate and the preopercle is a flat triangular bone which anteriorly inserts into the deeply concave part of the quadrate and posteriorly somewhat expands. In fishes of the subfamilies Cobitinae and Noemacheilinae (Figs. 44 and 45 A, B), the bone is narrower and longer than those of fishes of the subfamilies Botiinae and Homalopterinae (Figs. 43 and 45 C-G). In fishes of the subfamily Cobitinae except the genus *Misgurnus*, the bone forms the ventral margin of the metapterygoid-quadrate fenestra (Fig. 44).

Autopalatine (p) is a rod-shaped bone having a ventral process. In fishes of the subfamily Botiinae, the bone is short and stout (Fig. 43), while in fishes of the subfamilies Cobitinae, Noemacheilinae and Homalopterinae, it is slender in shape (Figs. 44 and 45).   Anteriorly, the bone is movably articulated with the prepalatine in fishes of the subfamilies Botiinae and Noemacheilinae and some members of the subfamily Homalopterinae such as *Homaloptera smithi*, *Hemimyzon formosanum* and *Sinogastromyzon puliensis* (Fig. 29 A, B, D, E), while in fishes of the subfamily Cobitinae and some members of the subfamily Homalopterinae such as *Annamia normani* and *Crossostoma lacustre*, it is ligamentously connected to the maxillary (Fig. 29 C, F).   Posteriorly, the bone is articulated with the anterior facet of the entopterygoid. Anteromedially, it is ligamentously connected to the supraethmoid-ethmoid complex, and anterolaterally, to the maxillary.   In *Acanthophthalmus*

kuhli and *A. anguillaris*, members of the subfamily Cobitinae, and fishes of the subfamily Noemacheilinae, the process extending from the ventral part of the bone is relatively reduced (Figs. 44 H, I and 45 A, B).

Ectopterygoid (ect) is a thin flat bone partly overlapping the anterodorsal portion of the quadrate.
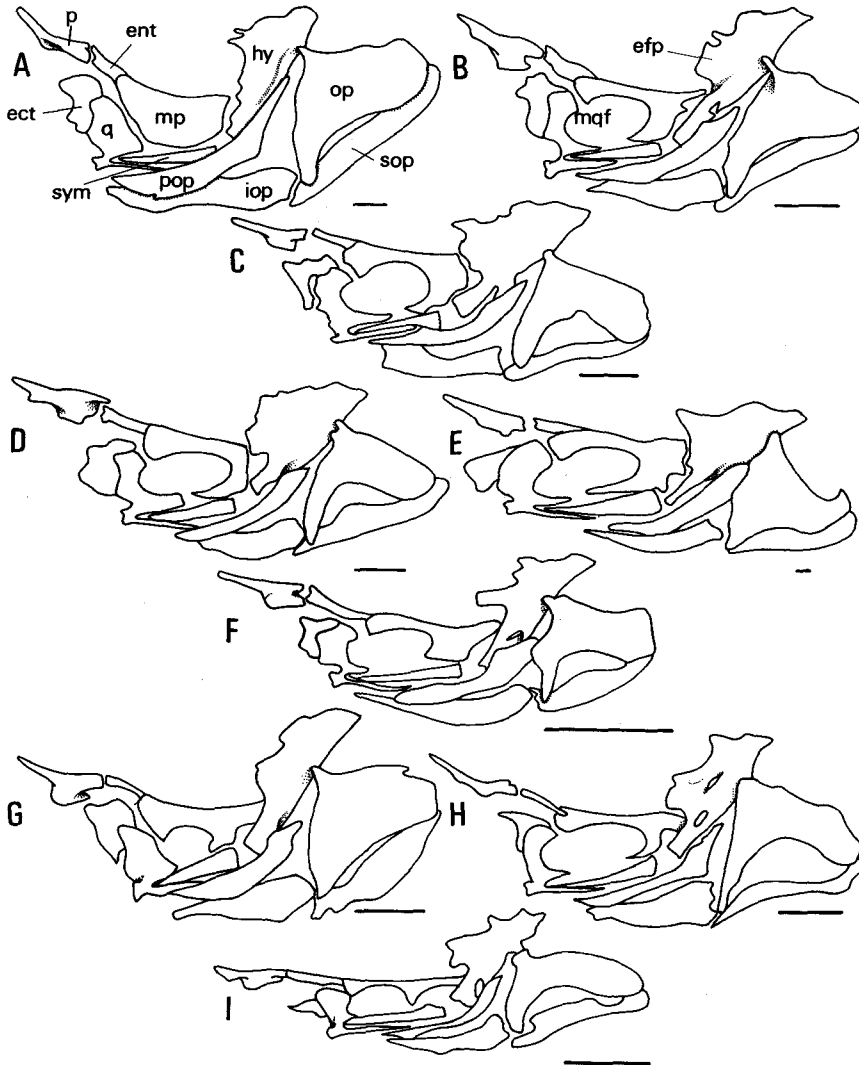
Fig. 44. Suspensoria in cobitine fishes. A, *Misgurnus fossilis*; B, *Cobitis paludicola*; C, *Niwaella multifasciata*; D, *Sabajenewia aurata vallachica*; E, *Acanthopsis choirorhynchos*; F, *Acanthopsoides graciroides*; G, *Lepidocephalus guntea*; H, *Acanthophthalmus kuhli*; I, *Acanthophthalmus anguillaris*. efp, forward process; mqf, metapterygoid-quadrate fenestra. For other abbreviations, see Fig. 43. Scales indicate 1 mm.
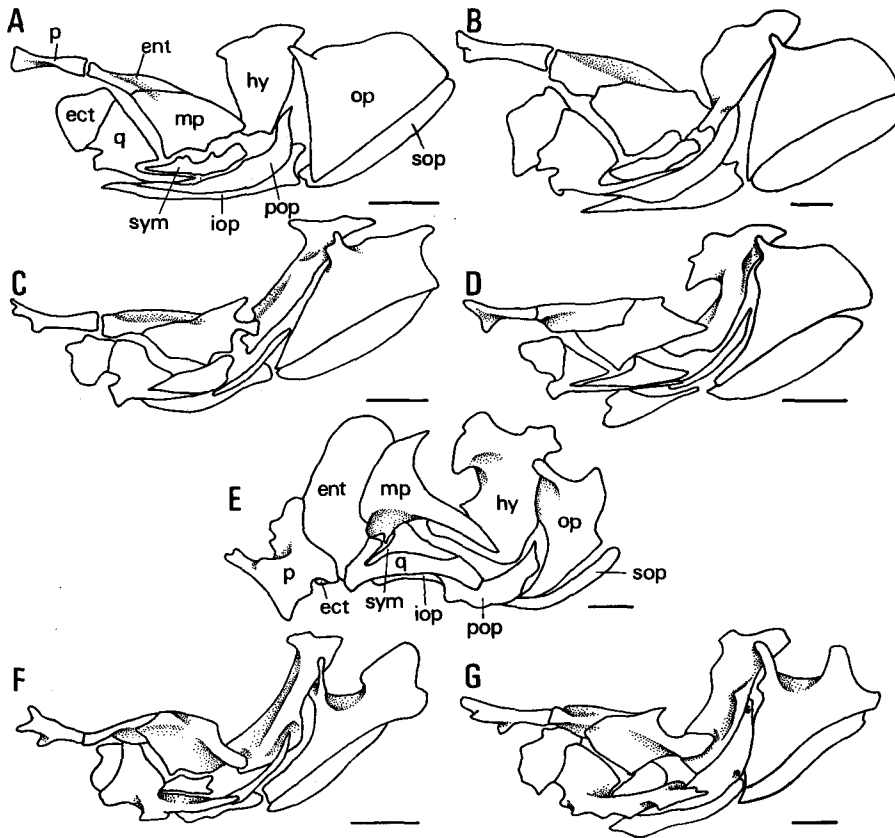
Fig. 45. Suspensoria in homalopterid fishes. A, *Lefua costata*; B, *Noemacheilus barbatulus*;
C, *Homaloptera smithi*; D, *Hemimyzon formosanum*; E, *Sinogastromyzon puliensis*; F,
Annamia normani; G, *Crossostoma lacustre*. Only E is shown from dorsal view. For
abbreviations, see Fig. 43. Scales indicate 1 mm.

Entopterygoid (ent) is a small bone meeting the autopalatine anteriorly and
the metapterygoid posteriorly. In fishes of the subfamilies Botiinae, Noemachei-
linae and Homalopterinae, the bone is an extensive sheet of bone, and the
posteroventral margin of which is firmly attached to the anterodorsal margin of
the metapterygoid (Figs. 43 and 45), while in fishes of the subfamily Cobitinae, it is
reduced into a rod-shaped bone which is movably articulated only with the antero-
medial part of the metapteryogoid (Fig. 44).

Metapterygoid (mp) is a thin flat bone overlapping the entopterygoid
anterodorsally. In fishes of the subfamily Cobitinae except the genus *Misgurnus*,
the ventral margin of the bone forms the metapterygoid-quadrate fenestra (Fig. 44).
In fishes of the subfamilies Botiinae, Noemacheilinae and Homalopterinae, the
dorsal half of the bone is directed medially toward the parasphenoid.

Opercle (op) is a fairly large rectangular or triangular bone. Anteriorly, it has

an articular process articulating with the posterodorsal condyle of the hyomandibular. In fishes of the subfamily Cobitinae, the bone is ventrally concave due to the reduction of the ossification.

Subopercle (sop) is a thin blade-like bone lying ventromedial to the opercle.

Interopercle (iop) is a thin blade-like bone lying ventromedial to the preopercle and the posterior process of the quadrate. Anteriorly, the bone is ligamentously connected to the retroarticular.

Preopercle (pop) is vertically elongated L-shaped bone. The bone is dorsally supported by the hyomandibular, and ventrally, by the posteroventral process of the quadrate. In fishes of the subfamily Botiinae and *Crossostoma lacustre*, a member of the subfamily Homalopterinae, it forms a way for the opercular-mandibular sensory canal.

Suprapreopercles (spo) are a series of small tubular bones lying along the anterior margin of the opercle. In fishes of the subfamily Botiinae, the bones are present (Fig. 43), while in other cobitoids examined, they are absent (Figs. 44 and 45).

DISCUSSION

The suspensorium of the superfamily Cobitoidea has been examined by several authors (Sagemahl, 1981; Berg, 1940; Ramaswami, 1948, 1952c, 1952d, 1953). The metapterygoid-quadrate fenestra, a character of the suspensorium, has been used as one of the taxonomic characters for the Berg's cobitid classification (Berg, 1940; Ramaswami, 1953). On the other hand, as we will discuss below, there has been a controversy concerning the phylogenetic interpretation of this fenestra (Regan, 1911; Greenwood et al., 1966; Gosline, 1973, 1975; Howes, 1976).

Among cobitoids examined here, differences were found in the shape of the entopterygoid and the opercle, and the presence or absence of the metapterygoid-quadrate fenestra and the suprapreopercle (Table 9). On the basis of the combinations among conditions of the four characters, the cobitoid suspensorium is divided into four morphotypes (Table 9). Type A includes fishes of the

Table 9. Comparison of several characters of the cobitoid suspensorium. ent, entopterygoid; mqf, metapterygoid-quadrate fenestra; op, opercle; spo, suprapreopercle.

Morphotype	Character				Subfamily and Genus
	Shape of ent	Ventral margin of op	mqf	spo	
A	extensive sheet-like	straight or convex	absent	absent	Noemacheilinae Homalopterinae
B	reduced rod-shaped	concave			Cobitinae *Misgurnus*
C			present		other genera examined
D	extensive sheet-like	straight or convex	absent	present	Botiinae

subfamilies Noemacheilinae and Homalopterinae. In this type, the entopterygoid
is an extensive sheet of bone, the lower margin of the opercle forms a straight line,
the metapterygoid-quadrate fenestra and the suprapreopercle are absent. Type B
includes fishes belonging to the cobitine genus *Misgurnus*. In this type, the
entopterygoid is a reduced rod-shaped bone, the lower margin of the opercle is
deeply concave due to the reduction of ossification, and the metapterygoid-quadrate
fenestra and the suprapreopercles are absent. Type C, including fishes of the
subfamily Cobitinae except the genus *Misgurnus*, differs from Type B only in
having the metapterygoid-quadrate fenestra. Type D, including fishes of the
subfamily Botiinae, differs from Type A only in having the suprapreopercle.

Since the most primitive conditions of these characters are judged according to
the criterion for the determination of polarity (Fig. 46), the conditions of these

		A	B	C
1.	Suprapreopercle	present absent	present absent	present absent
2.	Shape of entopterygoid	flat rod	flat	flat
3.	Shape of opercle	concave convex	convex	convex
4.	Metapterygoid-quadrate fenestra	present absent	absent	present absent

1. ?
2. flat
3. convex
4. absent
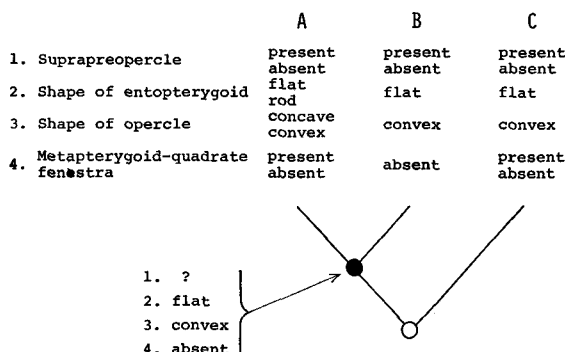
Fig. 46. Character analysis of the cobitoid suspensorium. The most primitive conditions
of four characters in group (A) are shown as the conditions in the common ancestor
(●) of groups (A) and (B).

characters found in other cyprinoid fishes are described below. In group (B), the
entopterygoid is an extensive sheet of bone, the opercle is well developed and
ventrally convex or straight in shape, the metapterygoid-quadrate fenestra is
absent, and the suprapreopercle is generally absent with the exception of
Hypentherium nigricans (personal observation) (see Nelson, 1949; Ramaswami,
1957; Weisel, 1960; Smith and Koehn, 1971; Lo and Wu, 1979). On the other
hand, in group (C), the entopterygoid is an extensive sheet of bone, the opercle is well
developed and ventrally convex or straight in shape, and the metapterygoid-quadrate
fenestra is generally absent (see Girgis, 1952; Ramaswami, 1952a, 1952b, 1955a,
1955b; Harrington, 1955; Dixit and Bisht, 1972a; Howes, 1978, 1979, 1980). How-
ever, the fenestra is present in some cyprinids such as *Chela*, *Opsariichthys*, *Zacco* and
Macrochirichthys (Regan, 1911; Greenwood et al., 1966; Gosline, 1975; Howes, 1976,
1980). The suprapreopercle is typically absent except for *Leuciscus* and *Alburnus*
(Lekender, 1949; Harrington, 1955).

On the basis of the above criterion, the most primitive conditions of these
characters in group (A) are determined as follows (Fig. 46): the entopterygoid is
an extensive sheet of bone; the opercle is well developed and ventrally convex or
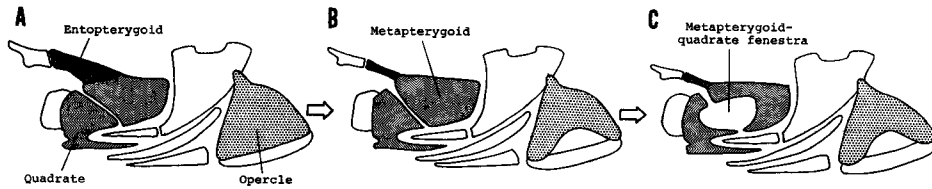
Fig. 47.　Evolutionary trend of the cobitoid suspensorium.　For explanations, see text.

straight; the metapterygoid-quadrate fenestra is absent. However, the most primitive condition of the suprapreopercle is undeterminable, because conditions of the character shared by the three groups are all identical (Fig. 46). Thus, three morphoclines shown in the entopterygoid, the opercle and the metapterygoid-quadrate fenestra are naturally considered below. The entopterygoid is advanced from an extensive sheet of bone to a reduced rod-shaped bone; the ventral margin of the opercle, from convex or straight to deeply concave; the metapterygoid-quadrate fenestra, from its absence to its presence.

According to the three morphoclines, the relationships among three morphotypes (A, B and C) (Type D is dealt as Type A because of the inhability to determine the polarity of the suprapreopercle) can be shown as the reduction of the entopterygoid and the opercle (A→B) preceding the occurrence of the meta-pterygoid-quadrate fenestra (B→C). Finally it is considered that the evolutionary trend in the cobitoid suspensorium is A→B→C (Fig. 47).

This evolutionary trend provides a basis of my comments on the phylogenetic interpretation of the metapterygoid-quadrate fenestra. With regard to its phylogenetic interpretation, there have ever been two opposing opinions: the presence of the fenestra is primitive (Greenwood et al., 1966) or derived (Gosline, 1973, 1975; Howes, 1976). From the fact that this fenestra is common in characoid fishes, Greenwood et al. (1966) interpreted that its presence may be primitive for all cyprinoids. If characoids are ancestral to cyprinoids, this interpretation may be possible. However, there seems to be no evidence to support it (Gosline, 1973; Roberts, 1973). Thus, their idea seems to be rejected.

To the contrary, emphasizing the functional significance of this fenestra, Gosline (1973, 1975) and Howes (1976) interpreted its presence as derived. The present author at least agrees with them in that its presence is interpreted as derived, but thinks that their explanations on the morphocline in the fenestra include some difficulties.

In 1973, Gosline stated that the fenestra provided the increased space for the contraction of the adductor mandibulae. If so, the degree of the development of this muscle must be correlated with the occurrence or actual size of the fenestra. The actual size, however, appears to have little to do with the degree of the development of this muscle (Howes, 1976). Thus this explanation is unreasonable. Later, Gosline (1975) added that the fenestra also provided an additional space for the vertical movement of the hyoid bar. Nevertheless, this explanation also seems to be not acceptable. The fulcrums in the vertical movement of the bar lie on the proximal and distal ends of the interhyal. The distal end of the interhyal is

connected to not the quadrate nor the metapterygoid but to the ventral part of the hyomandibular by a strong ligment. On the other hand, the proximal end of the interhyal is connected to the dorsal part of the epihyal. Therefore, the fenestra appears to be not taken part in any movement of the hyoid bar. Howes (1976) agrees with Gosline (1973, 1975) in emphasizing the functional significance of the fenestra. He explained that its presence provided a greater mobility on the suspensorial elements, enabling them to reorientate more readily to the stresses induced by a highly developed muscle system. However, he does not provide any evidence for this explanation.

In conclusion, this author's interpretation of the fenestra based on the criterion for the determination of polarity agrees with those of Gosline (1973, 1975) and Howes (1976) in that the presence of the fenestra is considered as derived. However, their functional explanations as the reasons for the appearance of the fenestra are not still accepted.

6. PECTORAL GIRDLE AND FIN (Figs. 48–55; Tables 10 and 11)

Pectoral girdle consists of the following elements: the cleithrum, the supracleithrum, the postcleithrum, the posttemporal, the supratemporal, the mesocoracoid, the coracoid, the scapula and the radial.

Cleithrum (cl) lying just posteromedial to the opercle is the largest bone of the girdle. It laterally develops the lateral cleithral lamina where the superficial abductor muscle is inserted, and medially the ventral cleithral lamina where the superficial adductor muscle is inserted. In fishes of the subfamily Cobitinae, the lateral and ventral cleithral laminae are reduced (Fig. 48 D-F). In fishes of the subfamily Homalopterinae, the bone is ventrally enlarged to form the horizontal plane which is firmly attached to its fellow ventromedially. In fishes of the subfamilies Botiinae, Cobitinae and Noemacheilinae, the dorsolateral part of the cleithrum is laterally articulated with the ventromedial part of the supracleithrum, while in fishes of the subfamily Homalopterinae, it is directly attached to the epiotic.

Supracleithrum (scl) is a blade-like bone attaching to the dorsolateral part of the cleithrum. In fishes of the subfamily Cobitinae except *Misgurnus anguillicaudatus*, the upper end of the bone is articulated with the distal part of the posttemporal, while in *M. anguillicaudatus*, it is directly attached to the epiotic. In fishes of the subfamily Homalopterinae, the lateral surface of the bone bears a groove for the lateral line passing from the head to the body.

Postcleithrum (pcl) is a narrow splint-like bone lying posterior to the cleithrum. In fishes of the subfamily Cobitinae, most members of the subfamily Noemacheilinae, and some members of the subfamily Homalopterinae such as *Homaloptera smithi*, *Annamia normani* and *Crossostoma lacustre*, the bone is absent (Figs. 48 D–H and 49 A, D, E), while in fishes of the subfamily Botiinae, some members of the subfamily Noemacheilinae such as *Noemacheilus botia*, *N. pulcher*, *N. masyae* and *N. fasciatus*, and two members of the subfamily Homalopterinae such as *Hemimyzon formosanum* and *Sinogastromyzon puliensis*, it is present (Figs. 48 A-C, I and 49 B, C).

Posttemporal (pt) is a slender bone bearing a single upper process articulating
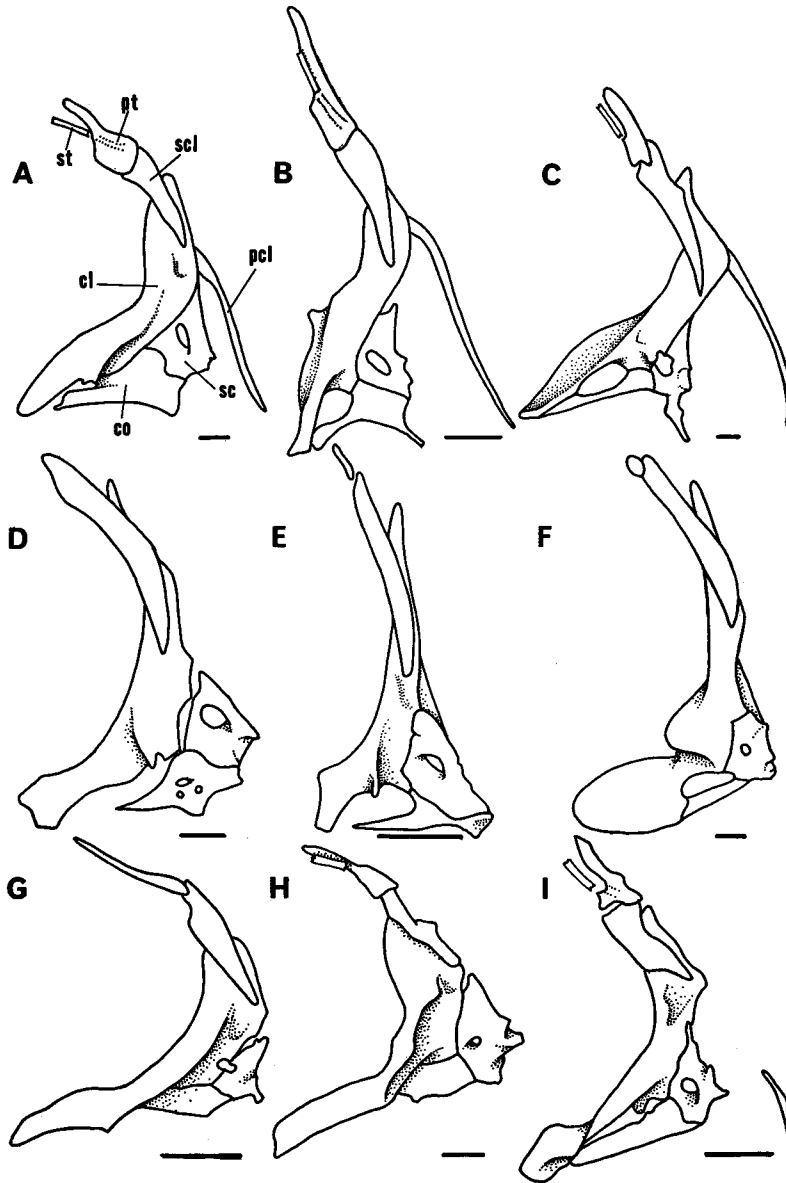
Fig. 48. Lateral view of pectoral girdles in fishes of the subfamilies Botiinae, Cobitinae and Noemacheilinae. A, *Leptobotia curta*; B, *Botia macracantha*; C, *B. hymenophysa*; D, *Misgurnus anguillicaudatus*; E, *Cobitis paludicola*; F, *Acanthopsis choirorhynchos*; G, *Lefua costata*; H, *Noemacheilus barbatulus*; I, *N. masyae*. cl, cleithrum; co, coracoid; pcl, postcleithrum; pt, posttemporal; sc, scapula; scl, supracleithrum; st, supratemporal. Scales indicate 1 mm.
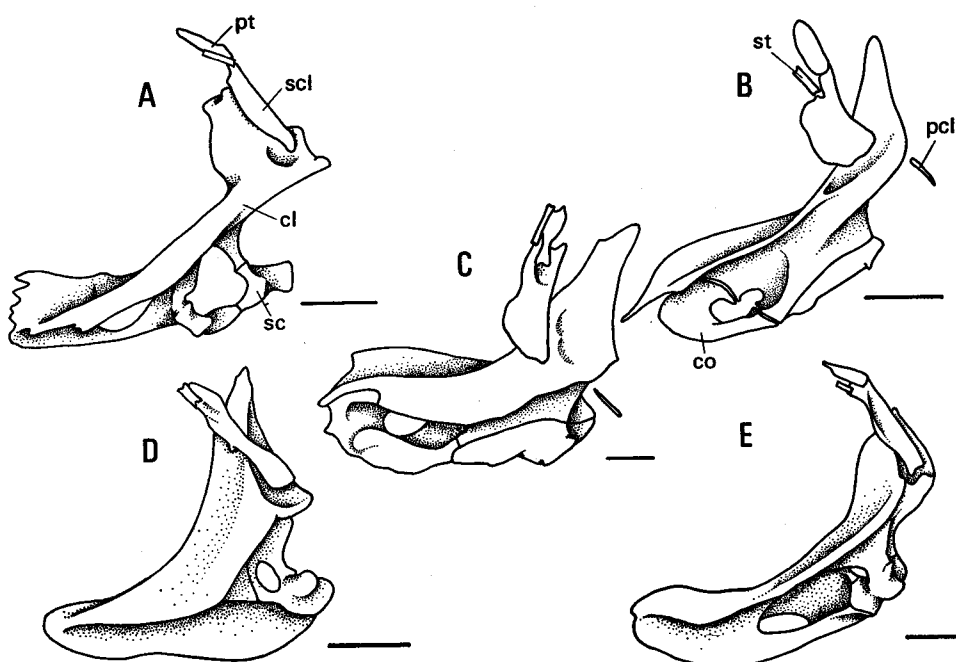
Fig. 49.   Lateral view of pectoral girdles in homalopterine fishes.   A, *Homaloptera smithi*;
B, *Hemimyzon formosanum*; C, *Sinogastromyzon puliensis*; D, *Annamia normani*; E,
Crossostoma lacustre.   For abbreviations, see Fig. 48.   Scales indicate 1 mm.
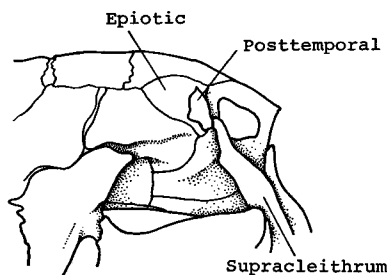
Fig. 50.   Posttemporal part of the pectoral girdle in a cobitine *Misgurnus*
anguillicaudatus (42 mm in total length)

with the skull.   Ventrally the bone is articulated with the upper part of the
supracleithrum.   In *Misgurnus anguillicaudatus*, a member of the subfamily
Cobitinae, and *Annamia normani*, a member of the subfamily Homalopterinae,
the bone is absent* (Figs. 48 D and 49 D).   In a small specimen (42 mm in total

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* Mester-Bacescu (1970) noted that a cobitine *Misgurnus fossilis* lacks the posttemporal.
  In the present observations, however, this species (93.3 mm in SL specimen) has the
  posttemporal attached to the epiotic.

length) of *M. anguillicaudatus*, the posttemporal is rigidly attached to the epiotic (Fig. 50). In fishes of the subfamily Cobitinae except *M. anguillicaudatus*, the bone is reduced in size and firmly attached to the groove forming by the epiotic and the sphenotic, while in fishes of the subfamilies Botiinae, Noemacheilinae and Homalopterinae except *Annamia normani*, it is well developed and movably articulated with the epiotic. In fishes of the subfamilies Botiinae and Noemacheilinae except the genus *Lefua*, the bone ventrally forms a groove or tube for the lateral line passing from the head to the body.

Supratemporal (st) is a tubular bone protecting the lateral line. In fishes of the subfamily Cobitinae and the noemacheiline genus *Lefua*, the bone is absent (Figs. 48 D-G), while in other cobitoids examined, it is present.

Mesocoracoid (mco) is a strong blacing bone among the cleithrum, the scapula and the coracoid. In fishes of the subfamilies Botiinae and Cobitinae, the bone is longer and more slender than those of fishes of the subfamilies Noemacheilinae and Homalopterinae (Fig. 51). The distal part of the bone is firmly attached to the medial surface of the cleithrum in fishes of the subfamilies Botiinae and Noemacheilinae, it has a slight contact with the posteromedial part of the cleithrum in fishes of the subfamily Cobitinae, and it is fused with the medial surface of the cleithrum in fishes of the subfamily Homalopterinae (Fig. 51).

Coracoid (co) is an expanded bone lying ventral to the scapula, the cleithrum and the mesocoracoid. Anteroventrally, it narrows to a short rod-shaped process connected to the ventral tip of the cleithrum. In *Crossostoma lacustre*, *Homaloptera smithi* and *Annamia normani*, members of the subfamily Homalopterinae, the process is distally fused with the anterior part of the cleithrum (Fig. 49).
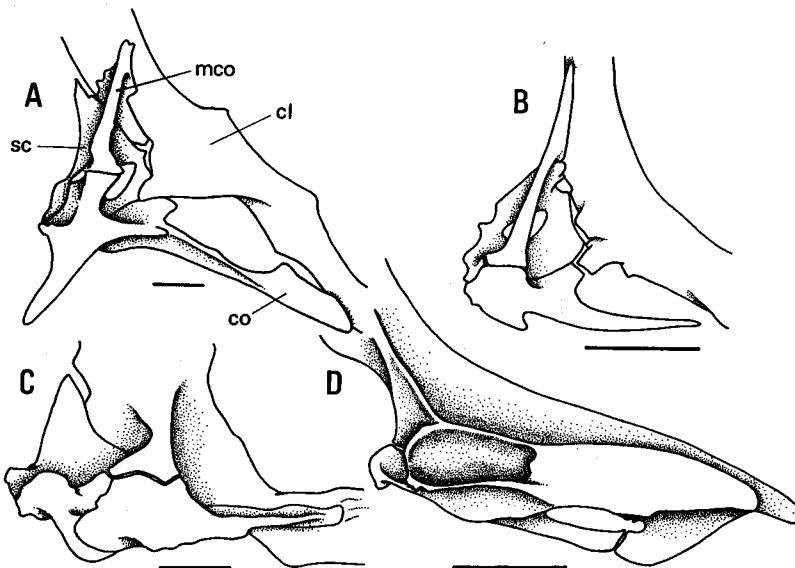
Fig. 51. Medial view of pectoral girdles in cobitoid fishes. A, *Botia hymenophysa*; B, *Cobitis paludicola*; C, *Noemacheilus barbatulus*; D, *Hemimyzon formosanum*. mco, mesocoracoid For other abbreviations, see Fig. 48. Scales indicate 1 mm.

In fishes of the botiine genus *Botia*, the bone develops a strong postventral process (Figs. 48 A-C and 51 A).   In most species belonging to the cobitine genera *Cobitis* and *Misgurnus*, a secondary sexual dimorphism occurs in the size of the bone: the coracoid of adult male is stronger and larger than that of adult female (Fig. 52).
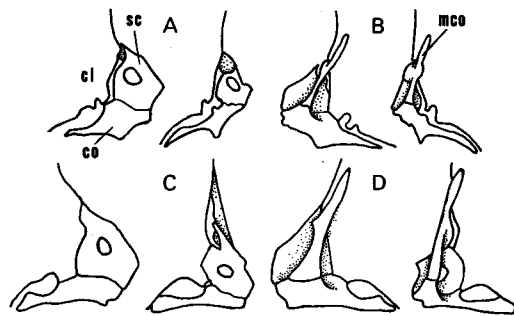
Fig. 52.   Scapula and coracoid of male (left) and female (right) in *Misgurnus anguillicaudatus* (A and B) and *Cobitis biwae* (C and D).   A and C, lateral view; B and D, medial view. For abbreviations, see Figs. 48 and 51.

Scapula (sc) is a nearly triangular bone articulating anterodorsally with the cleithrum and ventrally with the coracoid.   A large central foramen is pierced by the scapula.   In fishes of the noemacheiline genus *Lefua*, this foramen is formed by the scapula and the cleithrum (Fig. 48 G).   Posteriorly the bone forms a saddle-like ridge which supports the first pectoral fin ray.   In most species of the cobitine genera *Cobitis* and *Misgurnus*, a secondary sexual dimorphism occurs in the size of the bone: the scapula of adult male is stronger and larger than that of adult female (Fig. 52).

Radials (r) are flat, square bones supporting pectoral fin rays.   In fishes of the subfamily Cobitinae and *Noemacheilus toni* and *N. barbatulus*, members of the subfamily Noemacheilinae, there are three radials, while in fishes of the subfamilies Botiinae, Homalopterinae and Noemacheilinae except above two species, there are four radials (Table 10)

Pectoral fin consists of unbranched rays and branched rays.   There is a single unbranched ray in fishes of the subfamilies Cobitinae and Noemacheilinae, and *Homaloptera smithi*, *Annamia normani* and *Crossostoma lacustre*, members of the subfamily Homalopterinae; two rays in fishes of the subfamily Botiinae; 11 or 12 rays in a homalopterine *Hemimyzon formosanum*; 10 rays in a homalopterine *Sinogastromyzon puliensis*.   The number of branched rays ranges from 7 to 16 (Table 11).

DISCUSSION

The pectoral girdle of the superfamily Cobitoidea has been used to elucidate the phylogenetic relationships among some members of Berg's family Cobitidae (Starks, 1930; Rendahl, 1930, 1933a; Ramaswami, 1953; Mester-Bacescu, 1970;

Table 10. Comparison of six characters of the cobitoid pectoral girdle. cl, cleithrum; mco, mesocoracoid; pcl, postcleithrum; pt, posttemporal; st, supratemporal; r, radial.

Morpho-type	Character						Subfamily and Species
	cl	pcl	Relation between mco and cl	pt	st	r	
A	moderate	present	separate	present	present	4	Botiinae 　Leptobotia curta, Botia macracantha, B. hymenophysa, B. modesta, B. dayi Noemacheilinae 　Noemacheilus botia, N. masyae, N. pulcher, N. fasciatus
B	moderate	absent	separate	present	present	4	Noemacheilinae 　Noemacheilus postventralis, N. stoliczkai, N. pleurotaenia, N. savona, N. fasciolata, N. breviceps, N. fowlerianus, N. rupecula, N. angorae jordanicus, N. tigris, N. pantera, N. evezardi
C	moderate	absent	separate	present	present	3	Noemacheilinae 　Noemacheilus toni, N. barbatulus
D	moderate	absent	separate	present	absent	4	Noemacheilinae 　Lefua nikkonis, L. costata, L. echigonia
E	reduced	absent	separate	present	absent	3	Cobitinae 　Misgurnus fossilis, M. mizolepis, Cobitis taenia taenia, C. taenia striata, C. biwae, C. takatsuensis, C. koreensis, C. paludicola, Niwaella delicata, N. multifasciata, Sabajenewia aurata vallachica, Acanthopsis choirorhynchos, Acanthopsoides graciroides, Lepidocephalus guntea, Acanthophthalmus kuhli, A. anguillaris
F	reduced	absent	separate	absent	absent	3	Cobitinae 　Misgurnus anguillicaudatus
G	well-developed	present	fused	present	present	4	Homalopterinae 　Hemimyzon formosanum, Sinogastromyzon puliensis
H	well-developed	absent	fused	present	present	4	Homalopterinae 　Homaloptera smithi
I	well-developed	absent	fused	absent	absent	4	Homalopterinae 　Crossostoma lacustre, Annamia normani

Table 11.   The number of branched pectoral fin rays in cobitoid fishes.

Number of branched rays	Subfamily and Species
7	Cobitinae *Acanthopsoides graciroides, Lepidocephalus guntea, Acanthophthalmus anguillaris*
8	Cobitinae *Cobitis taenia taenia, C. taenia striata, C. biwae, C. takatsuensis, C. koreensis, C. paludicola, Niwaella delicata, N. multifasciata, Sabajenewia aurata vallachica* Noemacheilinae *Noemacheilus rupecula*
9	Botiinae *Leptobotia curta* Cobitinae *Acanthopsis choirorhynchos* Noemacheilinae *Noemacheilus fasciolata*
10	Cobitinae *Acanthophthalmus kuhli* Noemacheilinae *Noemacheilus pleurotaenia, N. savona, N. breviceps, N. fowlerianus, N. evezardi, N. angorae jordanicus, N. tigris, Vaillantella euepiptera*
11	Cobitinae *Misgurnus fossilis, M. mizolepis, M. anguillicaudatus* Noemacheilinae *Noemacheilus pantera, N. fasciatus*
11 or 12	Noemacheilinae *Lefua echigonia, L. nikkonis, L. costata, Noemacheilus toni, N. postventralis, N. barbatulus, N. stoliczkai, N. botia, N. pulcher*
12	Homalopterinae *Hemimyzon formosanum*
13	Botiinae *Botia hymenophysa, B. modesta, B. dayi* Homalopterinae *Sinogastromyzon puliensis*
14	Homalopterinae *Annamia normani*
15	Botiinae *Botia macracantha*
15 or 16	Homalopterinae *Homaloptera smithi, Crossostoma lacustre*

Mester, 1973). However, the cobitoid pectoral anatomy is still too meager to reconstruct the phylogeny of the superfamily.

Among cobitoid fishes examined, differences were found in the degree of the development of the cleithrum, the presence or absence of the supratemporal, the presence or absence of the posttemporal, the presence or absence of the postcleithrum, the number of radials, and the relation between the mesocoracoid and the cleithrum (Table 10). On the basis of the combinations among conditions of these characters, the cobitoid pectoral girdle is divided into nine morphotypes (Table 10). In the first type, Type A, the posttemporal, the supratemporal and the postcleithrum are present, the cleithrum is moderate in shape, the number of radials are four, and the mesocoracoid is free from the cleithrum. This type consists of fishes of the subfamily Botiinae and some members of the subfamily Noemacheilinae such as *Noemacheilus botia*, *N. pulcher*, *N. masyae* and *N. fasciatus*. Type B is distinguished from Type A only by the absence of the postcleithrum, and includes many members of the subfamily Noemacheilinae such as *Noemacheilus postventralis*, *N. stoliczkai*, *N. pleurotaenia*, *N. savona*, *N. fasciolata*, *N. breviceps*, *N. fowlerianus*, *N. rupecula*, *N. angorae jordanicus*, *N. tigris*, *N. pantera* and *N. evezardi*. Type C including two members of the subfamily Noemacheilinae, *Noemacheilus toni* and *N. barbatulus*, is different from Type B only in having three radials. Type D differs from Type B only by the absence of the supratemporal, and includes fishes of the noemacheiline genus *Lefua*. Type E is similar to Type A in having the posttemporal and the mesocoracoid separated from the cleithrum. In this type, however, the postcleithrum and the supratemporal are absent, the cleithrum is reduced or distinctly reduced in shape, and the number of radials is three. This type comprises fishes of the subfamily Cobitinae except *Misgurnus anguillicaudatus*. Type F including only *M. anguillicaudatus* differs from Type E only by the absence of the posttemporal. Type G is distinguished from Type A in having the enlarged cleithrum and the mesocoracoid fused with the cleithrum, although it is similar to the latter type in other features. This type is composed of *Hemimyzon formosanum* and *Sinogastromyzon puliensis*, members of the subfamily Homalopterinae. Type H is different from Type G only by the absence of the postcleithrum, and consists of *Homaloptera smithi* and *Crossostoma lacustre*, members of the subfamily Homalopterinae. The last type, Type I, comprising only *Annamia normani*, a member of the subfamily Homalopterinae, differs from Type G only by the absence of the posttemporal.

In order to judge the most primitive conditions of these characters on the basis of the criterion for the determination of polarity (Fig. 53), the conditions of these characters found in other cyprinoid fishes are described below. In group (B), 1) the cleithrum is moderate in shape, 2) the supratemporal is present, 3) the posttemporal is present, 4) the postcleithrum is present, 5) there are four radials, and 6) the mesocoracoid is separated from the cleithrum (Weisel, 1960; Brousseau, 1976; Lo and Wu, 1979). On the other hand, conditions of group (C) are the same as those of group (B) except two characters: 2) the supratemporal is generally present except for the case of a cyprinid, *Coreoleuciscus splendidas* (personal observations), 4) the posttemporal is generally present with some exceptions of some cyprinids such as *Gobiobotia brevibarba* etc. (Sorescu, 1968; personal observations) (also see, Starks, 1930; Ramaswami, 1952a, 1952b, 1955a, 1955b;

Harrington, 1955; Sorescu, 1968; Dixit and Bisht, 1972b; Howes, 1978, 1979, 1980).

According to the above criterion, the most primitive conditions of these characters in group (A) are determined as follows (Fig. 53): 1) the cleithrum is moderate in shape, 2) the supratemporal is present, 3) the posttemporal is present, 4) the postcleithrum is present, 5) the radials are four in number, and 6) the
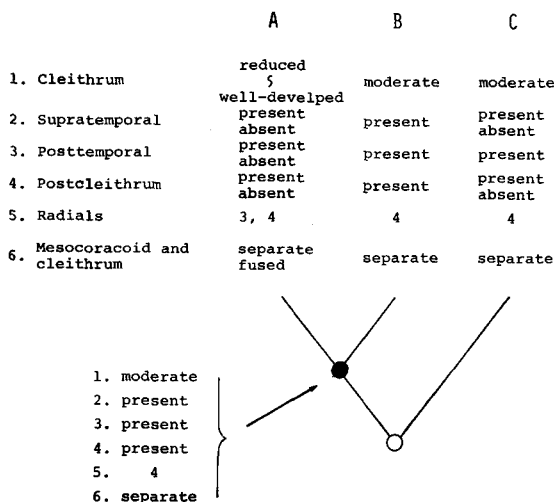
Fig. 53. Character analysis of the cobitoid pectoral girdle. The most primitive conditions of six characters in group (A) are shown as the conditions in the common ancestor (●) of groups (A) and (B).

mesocoracoid is separated from the cleithrum. Thus, from these conditions, the directions of morphoclines in six characters mentioned above are determined. The cleithrum is advanced from moderate shape to reduced one; the supratemporal, the posttemporal and the postcleithrum, from their presence to their absence; the number of radials, from four to three; the relation between the mesocoracoid and the cleithrum, from their separation to their fusion.

According to these six morphoclines, the relationships among the nine morpho-types in the cobitoid pectoral girdle are shown as two evolutionary trends (Fig. 54). In the first trend, the postcleithrum firstly disappears (A→B). Two different steps were recognized in the following phases of the trend. In one step, the disappearance of the supratemporal (B→D) precedes the decrease of radial counts and the reduction of the cleithrum (D→E), while in the other, the reduction of radials in number (B→C) precedes the disappearance of the supratemporal and the reduction of the cleithrum (C→E). Following these phases, the posttemporal finally disappears (E→F). On the other hand, in the second trend, the enalrge-ment of the cleithrum and the distal fusion of the mesocoracoid with the cleithrum (A→G), the disappearance of the postcleithrum (G→H), and the disappearance of the posttemporal (H→I) occur in that order.

In order to presume the cobitoid evolutionary history, it is interesting that
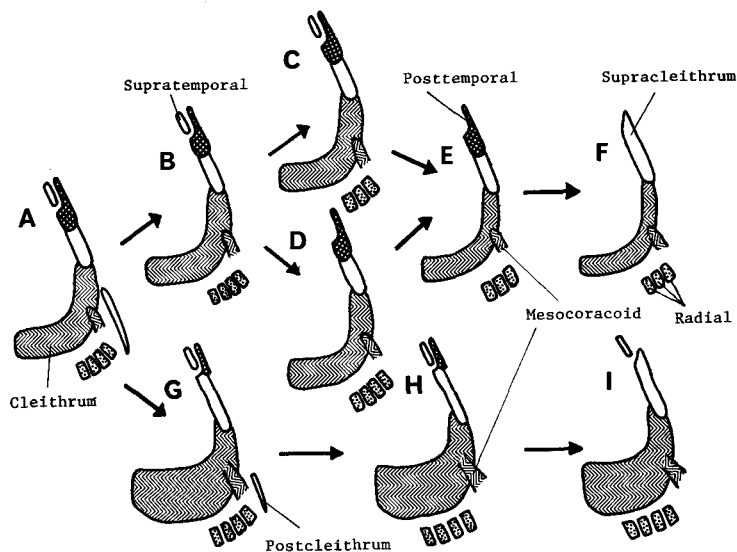
Fig. 54. Evolutionary trends of the cobitoid pectoral girdle.

the reduction and loss of the posttemporal and the degree of the development of the cleithrum are discussed from their functional aspects.

The posttemporal tends to independently disappear in both evolutionary trends (Fig. 54).   This bone is considered to have two functions: the ossified cover for the lateral line extending between head and body, and the buffer for the lateral flection of head relative to body (Gosline, 1971, 1977).

In fishes of the subfamily Cobitinae which represent the most advanced phase (E→F) of the first evolutionary trend, two peculiarities are found.   One is the loss of the lateral line extending between head and body (Fig. 55).   Necessarilly, this brings about the disappearance of the function of the posttemporal as an ossified cover for the lateral line.   The other is the presence of the well-developed pharyngeal processes (Fig. 55 B).   The processes inserted below the anterior vertebrae firmly attach the skull to a few anterior vertebrae (Fig. 55), and thus they may bring about the further reduction of the flexibility between the skull and anterior vertebrae. The reduction and loss of the flexibility seem to be parallel to those in the posttemporal part of the pectoral girdle (Gosline, 1977).   Therefore, the second function of the posttemporal, the buffer for the lateral flection of head relative to body, is also probably reduced.

On the other hand, in fishes of the subfamily Homalopterinae which represent the most advanced phase (H→I) of the second evolutionary trend, two morphological peculiarities are also found.   One is the disassociation of the posttemporal from the lateral line (Fig. 49).   In homalopterine fishes examined here, the lateral line is associated with the supracleithrum instead of the post-temporal (Fig. 55 C).   Thus, the function of the posttemporal as a cover for the lateral line disappears.   The other is the direct contact of the cleithrum to the skull

(Fig. 55 C).   In homalopterine fishes, the cleithrum tends to anteriorly attach to the posteroventral part of the skull, and posteriorly to the anterior part of the gasbladder capsule by extensive connective tissure.   The skull, the pectoral girdle and the gasbladder capsule seem to functionally serve as a rigidly combined unit disappeared the flexibility of head and anterior vertebrae.   Thus, the function of the posttemporal as the buffer for the lateral flection may be reduced.
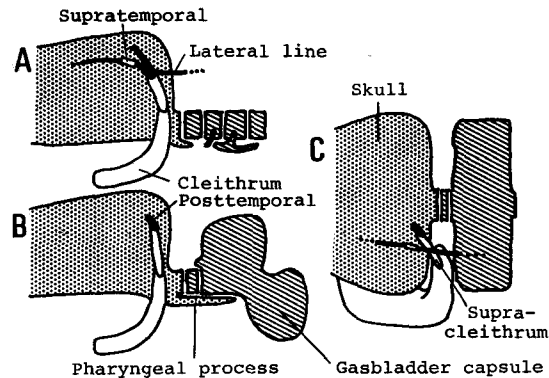
Fig. 55.   Diagram showing pectoral girdle, skull and anterior vertebrae.   A, generalized cyprinoid fish; B, cobitine fish; C, homalopterine fish.

From above discussion, it became clear that the reduction and loss of the posttemporal occurring in the most advanced phase of both evolutionary trends may be closely related to the reduction and loss of the original functions of the posttemporal.

Secondly, on the degree of the development of the cleithrum, the condition of the bone is derived toward the opposing directions in both evolutionary trends.

In the first trend, the bone becomes reduced (Fig. 54: C or D→E).   The reduction of the bone, which occurs in fishes of the subfamily Cobitinae, is mostly reflected by the reductions of the lateral and ventral cleithral laminae which provide surfaces for the superficial abductor and adductor muscles which take part in the movement of successive fin rays (Winterbottom, 1974; Brousseau, 1976) (Fig. 48).   In fishes of the subfamily, a morphological characteristic is present: the elongated body (Fig. 69).   It appears to be related to locomotion.   The most common method of locomotion found in the fishes of the subfamily is swimming by the waveform lateral flexures of the body.   When these fishes move only by such a swimming method, the amphitude of the locomotor wave is high and remains almost constant throughout the body (Aleev, 1963).   Thus, as Gosline (1971) pointed out, the various requirement of the locomotor are distributed along the length of the body, and hence there is little differentiation of fins.   Under such a situation, the importance of the pectoral fin as a stabilizer seems to be reduced.   From this consideration, it is presumed that the reduction of the pectroal girdle, especially the cleithrum, is closely related to the swimming method adopted by the fishes of the subfamily Cobitinae.

In the second trend, on the other hand, the cleithrum becomes enlarged

(Fig. 54: A→G). The enlargement of the bone, which occurs in fishes of the subfamily Homalopterinae, is mostly reflected by the formation of the horizontal plane. The plane is medially attached to its fellow to form the flattened ventral surface. It has been thought that fishes of the subfamily Homalopterinae have the ability of adhesion as an adaptation to the torrential habitat (Hora, 1932; Wickler, 1971). Adhesion to the substratum is partly effected by the close application of the flattened and smooth ventral surface (i.e. the sucking disc) of the body (Hora, 1932). In this connection, it is presumed that the horizontal plane of the cleithrum takes part in the formation of the effective sucking disc.

These presumptions will be also discussed in the chapter VI.

7. WEBERIAN APPARATUS AND GASBLADDER CAPSULE (Figs. 56–62; Table 12)

Weberian apparatus consists of four Weberian ossicles and the first to fourth vertebral elements.

Weberian ossicles include the claustrum, the scaphium, the intercalarium and the tripus.

Claustrum (cla), lying lateral to the anterolateral base of the neural complex, is the anteriormost element of the Weberian ossicles. The bone is anterolaterally depressed to form a bowl-like portion meeting the median side of the scaphium.

Scaphium (sca) is a cup-shaped bone meeting medially the anterior part of the claustrum. The convex posterolateral surface of the bone is raised for the attachment of ligament extending from the intercalarium.

Intercalarium (inc) is a small rod-shaped bone lying between the scaphium and the tripus (Fig. 56 C, D). In *Leptobotia curta*, a member of the subfamily Botiinae, the bone is proximally inserted into a fossa situated below the third neural complex (Fig. 57 A), while in fishes of the superfamily except *L. curta*, it does not have any contact with the first to the fourth vertebral elements of the Weberian apparatus.

Tripus (tr) is the posteriormost element of Weberian ossicles. Anteriorly, the bone is ligamentously connected to the intercalarium, posteriorly to the anterior portion of the gasbladder, and medially articulated with the lateral part of the second-third compound centrum. The bone is a thin triangular bone having the posterior twisted part in fishes of the subfamily Botiinae (Fig. 56 A), a thin flat triangular bone in fishes of the subfamily Cobitinae (Fig. 56 B, C), and a thin Y-shaped bone in fishes of the subfamilies Noemacheilinae and Homalopterinae (Fig. 56 D-F).

First to four vertebral elements include the first to fourth centra, the second lateral process, the third neural arch, the neural complex, the fourth parapophysis, the fourth neural arch and spine, and the ossa suspensoria.

First centrum (c 1) laterally forms a pair of short lateral processes connecting to the upper end of the cleithrum by a strong ligament.

Second centrum (c 2) is fused with the third centrum (c 3) to form a compound centrum.

Second lateral process produced from the lateral part of the second centrum, is proximally branched to form the second horizontal process (hp 2) and the
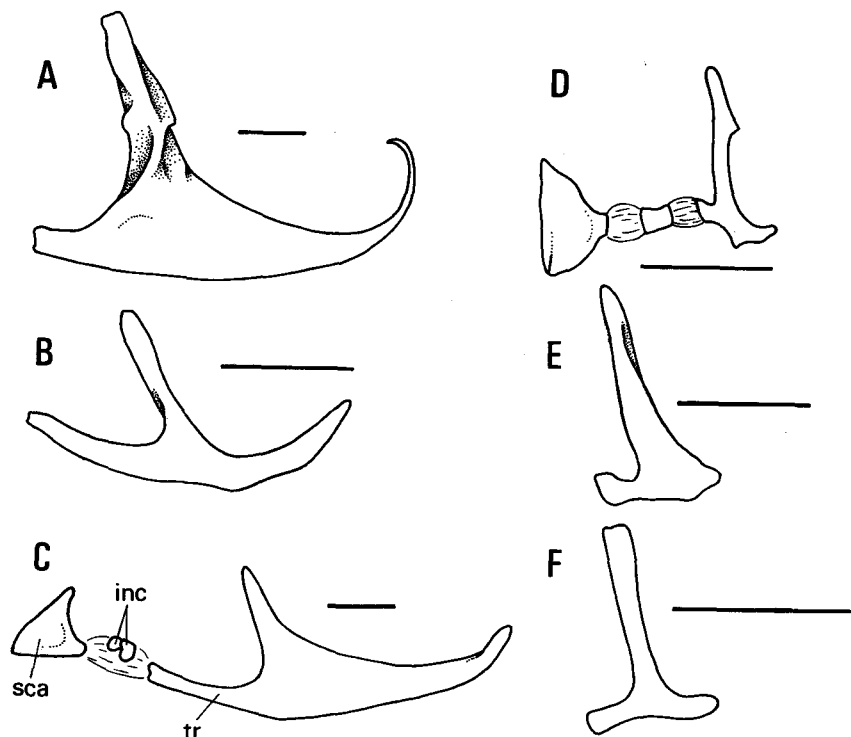
Fig. 56. Tripus of cobitoid fishes.   A, *Leptobotia curta*; B, *Cobitis paludicola*; C, *Acanthopsis choirorhynchos*; D, *Noemacheilus botia*; E, *Crossostoma lacustre*; F, *Hemimyzon formosanum*. tr, tripus; inc, intercalarium; sca, scaphium.   Scales indicate 0.5 mm.

second descending process (dp 2) (Fig. 62 A). In fishes of the subfamily Botiinae except *Botia dayi*, the second descending process lies in a fibrous membrane covering the anterior sac of the gasbladder, while the second horizontal process is excluded from the membrane.   In a botiine *Botia dayi*, the second descending process is posteriorly expanded to fuse with the anterior edge of the fourth descending process, and forms the anterior part of the gasbladder capsule (Figs. 57 D and 62 B).   In fishes of the subfamily Cobitinae, both processes do not have any contact with the gasbladder, nor incorporated in the gasbladder capsule made of the fourth horizontal and descending processes (Figs. 58 and 62 C).   In fishes of the subfamilies Noemacheilinae and Homalopterinae, both processes form the anterodorsal and anteroventral surfaces of the gasbladder capsule (Figs. 59, 60 and 62 D, E).   In all members examined here of the subfamilies Noemacheilinae and Homalopterinae except a noemacheiline genus *Lefua* and two homalopterine genera *Annamia* and *Crossostoma*, the second horizontal process is posteriorly sutured with the fourth horizontal process (Figs. 59 and 60).   On the other hand, in fishes of the genus *Lefua*, the former process is separated from the latter in short distance (Fig. 59 A), and in fishes of the genera *Annamia* and *Crossostoma*, the former is posteriorly fused with the anterior edge of the latter process (Fig.
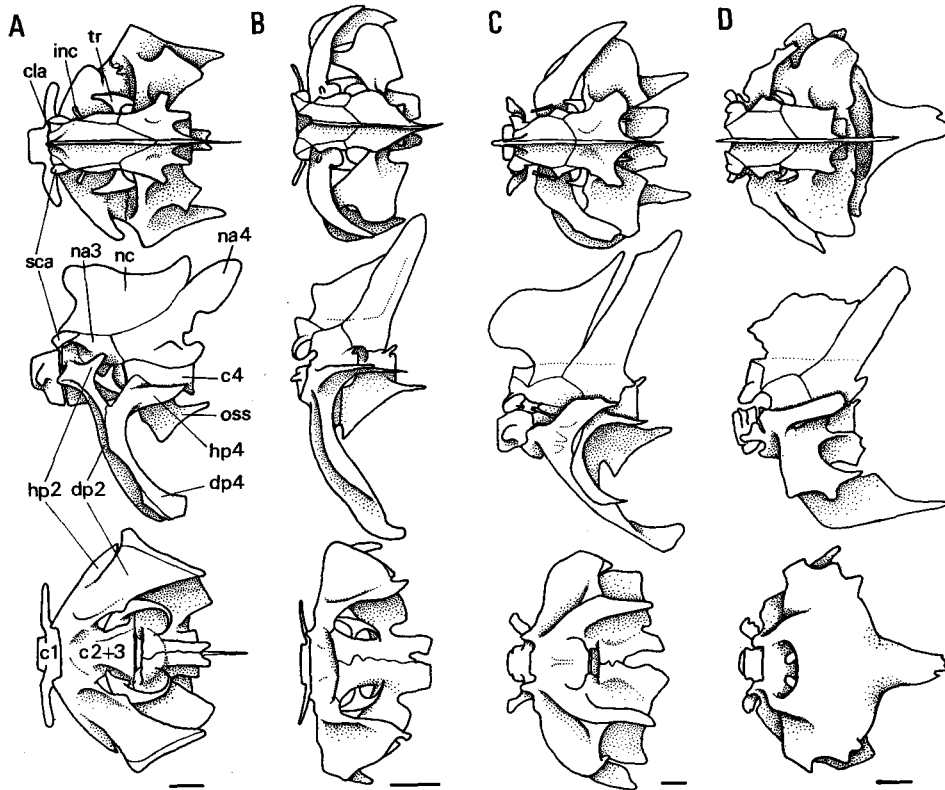
Fig. 57. Weberian apparatus of fishes of the subfamily Botiinae. A, *Leptobotia curta*; B, *Botia macracantha*; C, *Botia modesta*; D, *Botia dayi*. c, centrum; cla, claustrum; dp, descending process; hp, horizontal process; inc, intercalarium; na 3, third neural arch; na 4, fourth neural arch and spine; nc, neural complex; oss, ossa suspensoria; sca, scaphium; tr, tripus. Top, dorsal view; middle, lateral view; bottom, ventral view. Scales indicate 1 mm.

60 B). In fishes of the subfamily Homalopterinae, the anterolateral part of the second descending process is firmly attached to the posterior surface of the cleithrum, while in all other cobitoids examined, it is separated from the cleithrum.

Third neural arch (na 3), overlapping the second-third compound centrum, is anteriorly attached to the claustrum, dorsally to the neural complex, posteriorly to the fourth neural arch and spine.

Neural complex (nc) is posteriorly attached to the fourth neural arch and spine, anteroventrally to the claustrum, and posteriorly to the third neural arch.

Fourth parapophysis, produced from the fourth centrum, is proximally branched to form the fourth horizontal process (hp 4) and the fourth descending process (dp 4) (Fig. 62 A). The former process is proximally expanded to form a large horizontal plate covering the dorsal surface of the anterior sac of the gasbladder. In fishes of the subfamily Botiinae except *Botia dayi*, both processes

lay in a fibrous membrane covering the anterior sac of the gasbladder, while in *B. dayi*, they cover the anterior sac to form the gasbladder capsule in cooperation with the second horizontal process (Figs. 57 D and 62 B).   In fishes of the subfamily Cobitinae, both processes form the gourd-like capsule bearing laterally two pairs of large openings, ventrally a pair of downward projections (Figs. 58 and 62 C) and posteriorly a small opening.   In fishes of the subfamilies Noemacheilinae and Homalopterinae, in cooperation with the ossa suspensoria (oss), the second horizontal and descending processes, both processes form the laterally
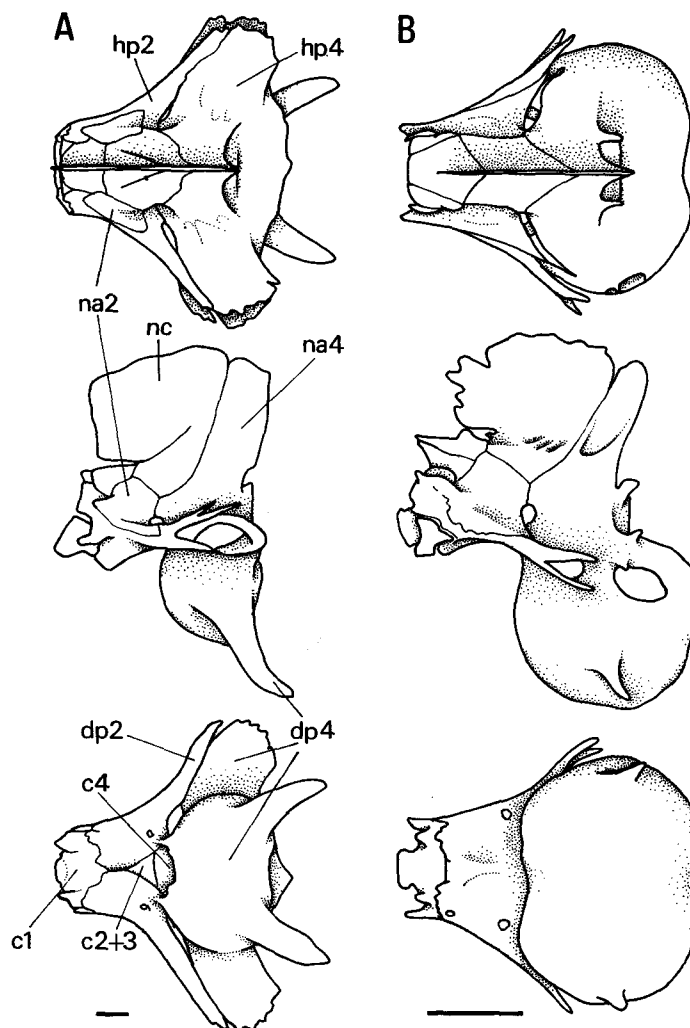
Fig. 58.   Weberian apparatus of two species of the subfamily Cobitinae.   A, *Acanthopsis choirorhynchos*; B, *Cobitis paludicola*.   Top, dorsal view; middle, lateral view; bottom, ventral view.   For abbreviations, see Fig. 57.   Scales indicate 1 mm.
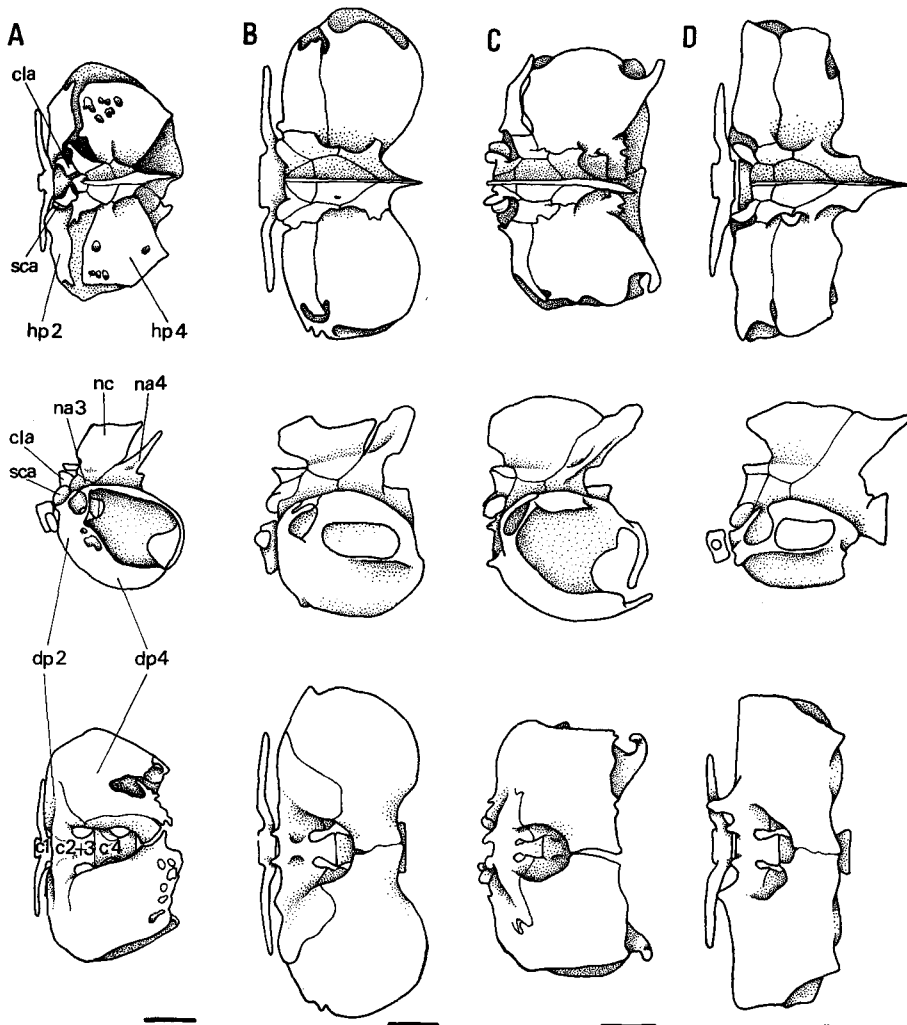
Fig. 59. Weberian apparatus of four noemacheiline fishes. A, *Lefua echigonia*; B, *Noemacheilus barbatulus*; C, *N. pleurotaenia*; D, *N. savona*. For abbreviations, see Fig. 57. Top, dorsal view; middle, lateral view; bottom, ventral view. [Scales indicate 1 mm.

divided capsule bearing laterally two pairs of large openings (Figs. 59 and 60). In most members of the subfamily Noemacheilinae examined, the horizontal plate which is made of the fourth horizontal process is posteriorly extended to form a complete capsule (Figs. 59 B, D and 62 E), while in some members of the same subfamily such as *Lefua echigonia*, *L, nikkonis*, *L. costata*, *Noemacheilus pleurotaenia* and *N. pulcher*, the posterior wall of the capsule made of the horizontal plate is incomplete (Figs. 59 A, C and 62 D).

Fourth neural arch and spine (na 4) is anterodorsally attached to the
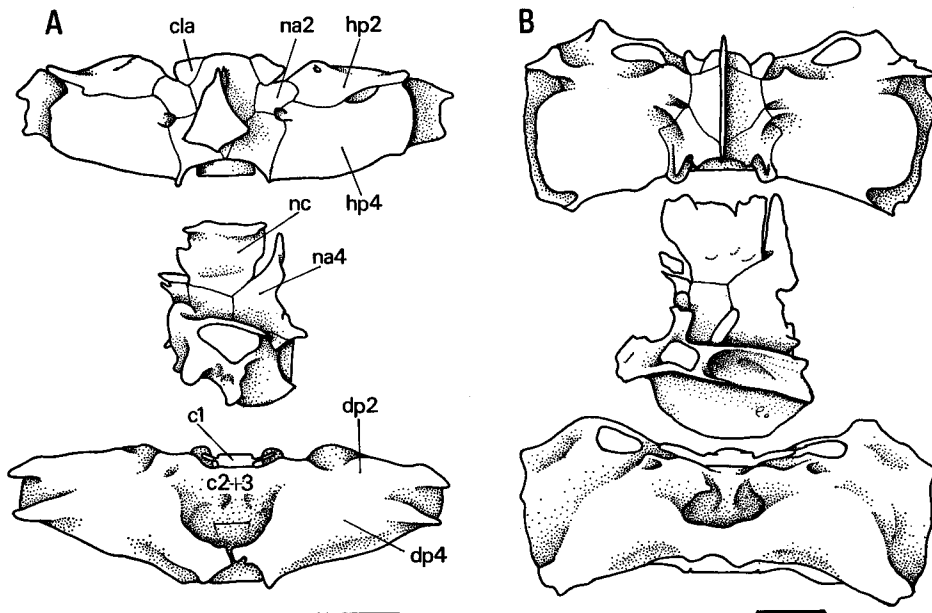
Fig. 60. Weberian apparatus of two species of the subfamily Homalopterinae. A, *Hemimyzon formosanum*; B, *Crossostoma lacustre*. Top, dorsal view; middle, lateral view; bottom, ventral view. For abbreviations, see Fig. 57. Scales indicate 1 mm.

neural complex, anteroventrally to the third neural arch, and ventrally to the fourth centrum.

Ossa suspensoria (oss) are a pair of thin downward processes originated from the ventral side of the fourth centrum, and sutured with each other in the midventral line. The posterior flange of the ossa suspensoria is posteriorly extended to attach to the tunica externa of the gasbladder.

DISCUSSION

The Weberian apparatus is the most peculiar feature characterizing ostariophysan fishes. The cobitoid Weberian apparatus has been examined by several authors (Chranilov, 1927; Ramaswami, 1952c, 1952d, 1953; Alexander, 1962, 1964b; Wu et al., 1981). In the superfamily Cobitoidea, especially the functional aspect of the apparatus has been interested because of the formation of the bony capsule (Alexander, 1964b). Also, the shapes of the capsule and the tripus have been used for the elucidation of the intrafamilial relationships among members of the superfamily except the subfamily Homalopterinae. However, the similarity of both characters between the subfamilies Noemacheilinae and Homalopterinae has been neglected (Ramaswami, 1952c, 1952d, 1953). This problem will be discussed below. On the other hand, from the present observations, it became clear that the fusion between the second and third centra is a shared common feature in all examined members of the superfamily. It is analyzed below whether this feature supports the monophyly of the superfamily or not.

Among cobitoid fishes examined here, differences were found in the shape of the tripus, the presence or absence of the second horizontal process taking part in the formation of the capsule, the presence or absence of the second descending process taking part in the formation of the capsule, the presence or absence of the fourth horizontal process forming the posterior surface of the capsule, and the presence or absence of the subdivided capsule (Table 12). On the basis of the

Table 12. Comparison of several characters of the Weberian apparatus in cobitoid fishes. tr, tripus; hp 2, 2nd horizontal process; dp 2, 2nd descending process; hp 4, 4th horizontal process; s-c, subdivided capsule.

Morpho-type	Character					Subfamily and Species
	tr	hp 2 forming capsule	dp 2 forming capsule	hp 4 forming capsule	s-c	
A	triangular	absent	absent	absent	absent	Botiinae *Leptobotia curta, Botia modesta, B. hymenophysa, B. macracantha*
B		present		present		Botiinae *Botia dayi*
C		absent				Cobitinae all members examined
D	Y-shaped	present	present	absent	present	Noemacheilinae *Lefua echigonia, L. nikkonis, L. costata, Noemacheilus pulcher, N. pleurotaenia*
E				present		Noemacheilinae *Noemacheilus toni, N. barbatulus, N. stoliczkai, N. postventralis, N. botia, N. masyae, N. savona, N. fasciolata, N. fasciatus, N. tigris, N. rupecula, N. angorae jordanicus, N. pantera, N. evezardi N. fowlerianus, N. breviceps* Homalopterinae all species examined

combinations among conditions of these five characters, the cobitoid Weberian apparatus is classified into five morphotypes (Table 12). The first type, Type A, is characterized in that the tripus is triangular, the second horizontal, and second descending and the fourth horizontal processes are not taken part in the formation of the capsule, and the subdivided capsule is absent. This type includes members of the subfamily Botiinae except *Botia dayi*. The second type, Type B, consisting of only *B. dayi* is almost identical with Type A except that the second descending process and the fourth horizontal process participates in the formation of the capsule. The third type, Type C, is distinguished from Type A only by the presence of the fourth horizontal process forming the posterior surface of the capsule. This

type consists of fishes of the subfamily Cobitinae.   The last two types, Types D and E, are distinctly different from the former three types in having Y-shaped tripus and the subdivided capsule.   Type D differs from Type E in that the fourth horizontal process does not form the posterior surface of the capsule.   The former consists of some members of the subfamily Noemacheilinae such as *Lefua echigonia*, *L. nikkonis*, *L. costata*, *Noemacheilus pleurotaenia* and *N. pulcher*, while the latter is composed of other examined members of the subfamily Noemacheilinae and all members of the subfamily Homalopterinae examined.

In the present study, the most primitive conditions of these characters in the superfamily Cobitoidea is judged according to the criterion for the determination of polarity (Fig. 61).   Thus, the conditions of these characters found in other cyprinoid fishes have to be shown.   In group (B) consisting of the family Catostomidae. 1) the tripus is triangular, 2) the second horizontal process, 3) the second descending process and 4) the fourth horizontal process do not participate in the formation of capsule, 5) the subdivided capsule is not formed, and 6) the fusion between the second and third centra is present or absent (Chranilov, 1927, Krumholz, 1943; Nelson, 1948; Lo and Wu, 1979).   On the other hand, group (C) composed of all other cyprinoids except members of groups (A) and (B) differs from group (B) in two features: 4) the fourth horizontal process forms the posterior surface of the capsule in some cyprinids such as *Gobiobotia* (Ramaswami, 1955b), and 5) the subdivided capsule is found in fishes of the cyprinid genus *Gobiobotia* (Ramaswami, 1955b) (also see, Chranilov, 1927; Krumholz, 1943; Ramaswami, 1952a, 1952b, 1955a, 1955b; Alexander, 1962; Dixit and Bisht, 1972b; Sorescu, 1972; Howes, 1978, 1979; 1980; Wu et al., 1979).

	A	B	C
1. Tripus	triangular Y-shaped	triangular	triangular
2. 2nd horizontal process taking part in the formation of capsule	present absent	absent	absent
3. 2nd descending process taking part in the formation of capsule	present absent	absent	absent
4. 4th horizontal process forming the posterior surface of capsule	present absent	absent	present absent
5. Subdivided capsule	present absent	absent	present absent
6. Second and third centra	separate fused	separate fused	separate fused

1. triangular
2. absent
3. absent
4. absent
5. absent
6. ?

Fig. 61.   Character analysis of the cobitoid Weberian apparatus.   The most primitive conditions of six characters in group (A) are shown as the conditions of the common ancestor (●) of groups (A) and (B).

On the basis of the criterion, the most primitive conditions of these six characters in group (A) are determined as follows: 1) the tripus is triangular, 2) the second horizontal, 3) the second descending and 4) the fourth horizontal processes are not taken part in the formation of the capsule, and 5) the subdivided capsule is absent (Fig. 61). The relation between the second and third centra is underterminable because the conditions of this character found in three groups are all identical. Thus, the directions of morphoclines in five characters are presumed. The shape of tripus changes from triangular to Y-shaped; the second horizontal, the second descending and the fourth horizontal processes forming a part of the capsule, from absent to present; and the subdivided capsule, from absent to present.

According to these five morphoclines, the relationships among five previously defined morphotypes in the cobitoid Weberian apparatus are shown as three evolutionary trends (Fig. 62). A peculiar phenomenon common to these three trends is the formation of the bony capsule covering the anterior sac of gasbladder. the function of capsule have been little studied except for Setter (1929) and Alexander (1962, 1964a, 1964b). When Alexander (1964b) discussed the capsule with reference to the habitat of cobitoid fishes, especially *Noemacheilus*, he inferred that the atrophy of the posterior sac and some reduction of the anterior sac of gasbladder first occurs as the adaptation to a bottom-living habit, and that the bony encapsulation of the anterior sac of bladder occurs second. On the other hand, in his earlier papers (1962, 1964a), he explained that the encapsulation of gasbladder by bone is considered as by-products of swimbladder reduction, and that in the adaptation to a bottom-living habit the reduction of swimbladder is advantageous but the encapsulation is incidental. Thus, he concluded that the bony capsule might
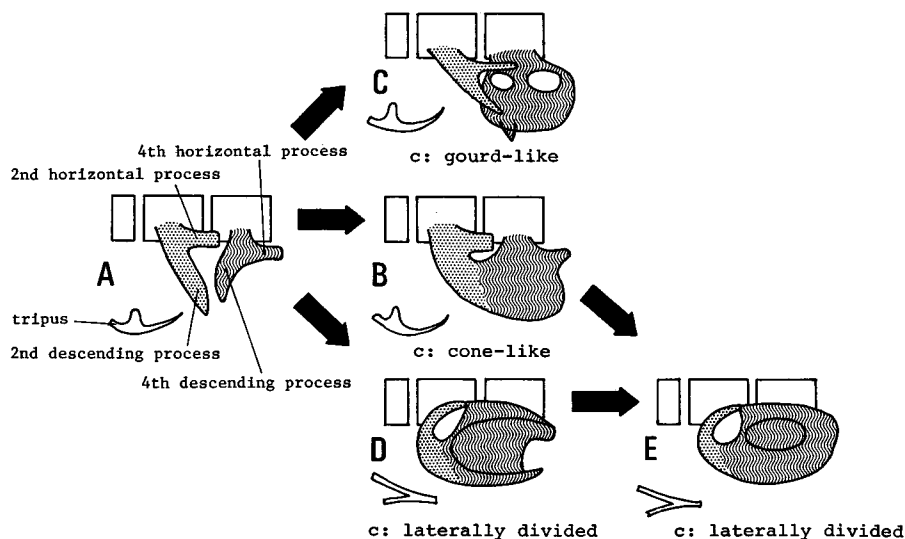
Fig. 62. Evolutionary trends of the cobitoid Weberian apparatus. c, the shape of capsule. For explanations, see text.

serve to isolate the swimbladder from pressure changes originating in the body. However, this conclusion seems to include some difficulties, since the pressure changes originating in the body are never restricted to bottom-living fishes with a reduced swimbladder.   Moreover, differences in the internal pressures between free-swimming forms with well-developed bladder and the bottom-living forms are unknown.   Thus, it may be invalid that the encapsulation of the anterior sac of bladder is regarded simply as by-products of the reduction of bladder, and that it serves as the isolation of swimbladder from the internal pressures, though there is no experiment testing this question.   At this time, our knowledge on the capsule is too meager to discuss its function.   However, the fact that the bony capsule occurs only in bottom-living fishes at least shows that the bottom-living habit has been indispensable to the formation of capsule.   This consideration will be also discussed in the chapter VI.

On the other hand, the third of above three evolutionary trends (A→D→E) provides some clues for the elucidation of the relationships between the subfamilies Noemacheilinae and Homalopterinae (Fig. 62).   The similarity in the structures of the gasbladder capsule and the tripus between both subfamilies has been rather neglected (Hora, 1932, 1950; Ramaswami, 1952c, 1952d, 1953).   On the contrary, the presence of the deep subtemporal fossa has been considered to be phylogenetically important (Hora, 1932, 1950; Ramaswami, 1952c, 1952d, 1953).   However,
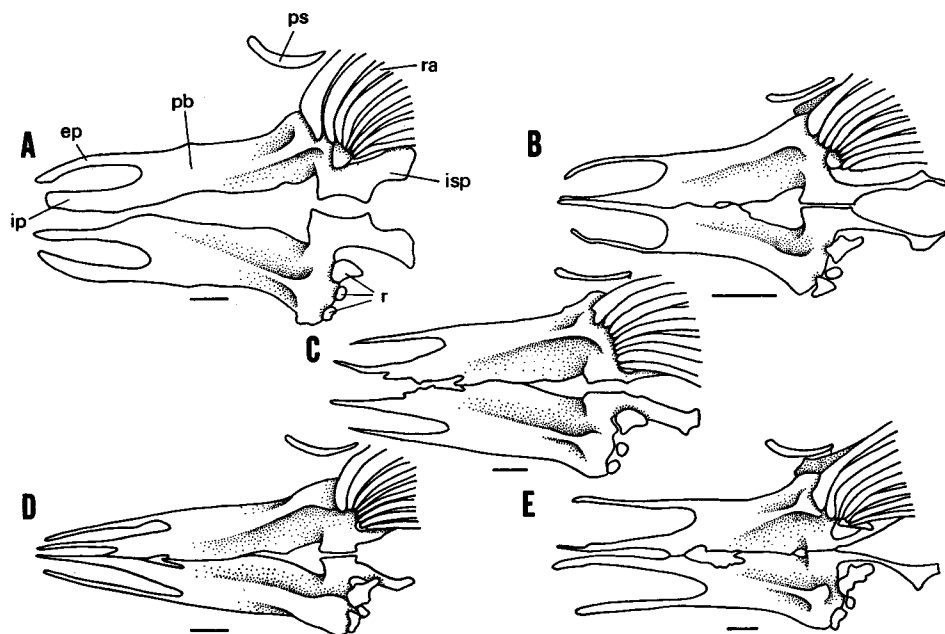
Fig. 63. Ventral view of pelvic girdles in botiine fishes. A, *Leptobotia curta*; B, *Botia macracantha*; C, *B. hymenophysa*; D, *B. modesta*; E, *B. dayi*. ep, external process; ip, internal process; isp, ischiac process; pb, pelvic bone; ps, pelvic splint; ra, fin ray; r, radial.   Scales indicate 1 mm.

this feature which forced many investigators to neglect the similarity in the Weberian apparatus was judged to be invalid from the character analysis of the cranial characters. The present character analysis indicates that the second horizontal and descending processes taking part in the formation of capsule and the Y-shaped tripus shared by all examined members of both subfamilies are derived features in the superfamily Cobitoidea. Therefore, these features show that fishes of both subfamilies form a monophyletic group.

8. PELVIC GIRDLE AND PELVIC FIN (Figs. 63–70; Tables 13 and 14)

   Pelvic girdle consists of the pelvic bone and the radials.
   Pelvic bones (pb) are a pair of flattened elongated bones lying in the ventral plane of the belly. Anteriorly, the bone bears two spine-like processes, internal (ip) and external (ep) processes (Figs. 63–65). Medially, the internal process is attached to its fellow on the median line. However, in a member of the subfamily Noemacheilinae, *Noemacheilus tigris*, and in fishes of the subfamily Homalopterinae, these processes are not very developed (Figs. 65 J and 66). In fishes of the subfamilies Botiinae and Noemacheilinae, and a homalopterine *Homaloptera smithi*, the ischiac process (isp) extends backward from the posteromedian edge of the pelvic bone (Figs. 63, 65 and 66 A), while in other cobitoids examined the process is less developed (Figs. 64 and 66 B-E).
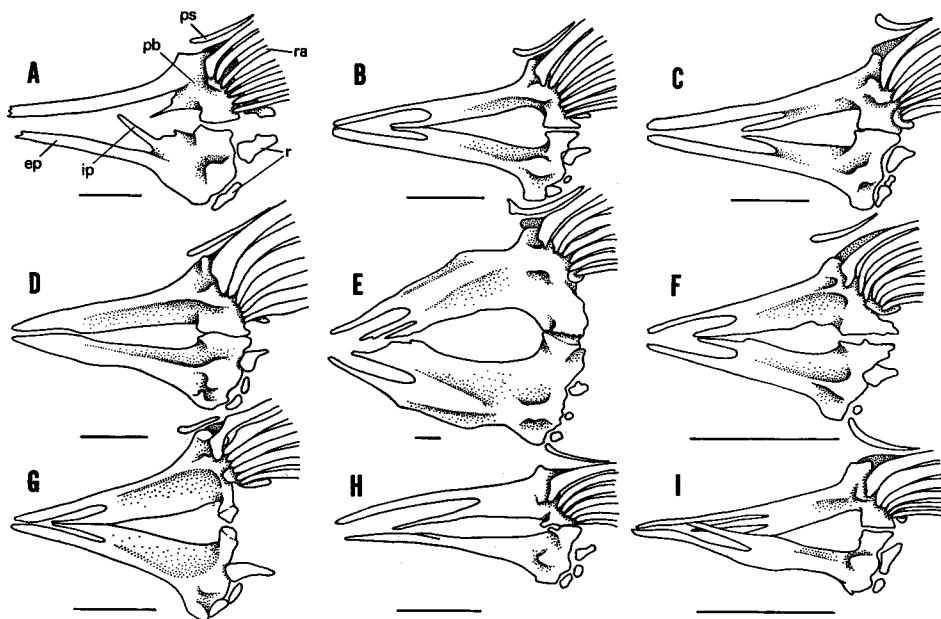
Fig. 64. Ventral view of pelvic girdles in cobitine fishes. A, *Misgurnus fossilis*; B, *Cobitis paludicola*; C, *Niwaella multifasciata*; D, *Sabajenewia aurata vallachica*; E, *Acanthopsis choirorhynchos*; F, *Acanthopsoides graciroides*; G, *Lepidocephalus guntea*; H, *Acanthophthalmus kuhli*; I, *Acanthophthalmus anguillaris*. For abbreviations, see Fig. 63. Scales indicate 1 mm.
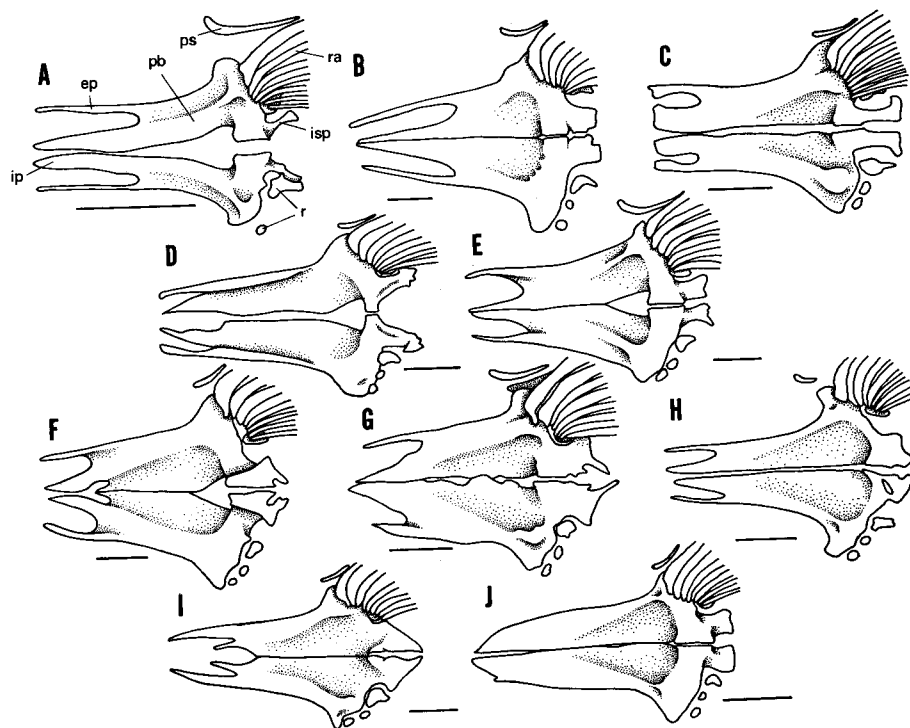
Fig. 65. Ventral view of pelvic girdles in noemacheiline fishes. A, *Lefua costata*; B, *Noemacheilus barbatulus*; C, *N. stoliczkai*; D, *N. pleurotaenia*; E, *N. pulcher*; F, *N. botia*; G, *N. masyae*; H, *N. savona*; I, *N. evezardi*; J, *N. tigris*. For abbreviations, see Fig. 63. Scales indicate 1 mm.

Radials (r) are small bones lying behind the posterior edge of the pelvic bone. In fishes of the subfamily Botiinae, members of the subfamily Noemacheilinae except the genus *Lefua*, members of the subfamily Cobitinae except *Acanthophthalmus anguillaris* and the genera *Misgurnus* and *Acanthopsoides*, and two members of the subfamily Homalopterinae, *Annamia normani* and *Crossotoma lacustre*, three radials are present, the first of which is the largest L-shaped bone and others are lumpy bones (Figs. 63–66). In fishes of the cobitine genera *Misgurnus* and *Acanthopsoides* and *Acanthophthalmus kuhli*, and fishes of the noemacheiline genus *Lefua*, there are two radials (Figs. 64 A, F and 65 A). In *Homaloptera smithi*, *Hemimyzon formosanum* and *Sinogastromyzon puliensis*, members of the subfamily Homalopterinae, there are 5, 6 and 16 radials respectively (Fig. 66 A-C).

Pelvic fin consists of pelvic splint, and unbranched and branched rays.

Pelvic splint (ps) is a curved unsegmented spine-like bone running along the outer surface of the outermost ray. In most members of the superfamily Cobitoidea, it is well developed (Figs. 63–65), while in fishes of the subfamily Homalopterinae it is rudimentary (Fig. 66).

Rays (r) consist of unbranched and branched ones. The unbranched ray is a single in fishes of the subfamilies Botiinae, Cobitinae and Noemacheilinae, and two

Table 13.   The number of pelvic branched and unbranched rays
            in cobitoid fishes.

Fin rays		Subfamily and Species
Unbranched	Branched	
1	5	Cobitinae *Acanthophthalmus anguillaris*
1	6	Cobitinae *Cobitis taenia taenia, C. taenia striata, C. biwae,* *C. takatsuensis, C. koreensis, C. paludicola,* *Niwaella delicata, N. multifasciata, Sabajenewia* *aurata vallachica, Acanthopsis choirorhynchos,* *Acanthopsoides graciroides, Lepidocephalus* *guntea, Acanthophthalmus kuhli* Noemacheilinae *Lefua echigonia, L. nikkonis, L. costata,* *Noemacheilus rupecula*
1	7	Botiinae *Botia modesta, B. dayi* Cobitinae *Misgurnus fossilis, M. anguillicaudatus, M.* *mizolepis* Noemacheilinae *Noemacheilus postventralis, N. stoliczkai, N.* *pleurotaenia, N. botia, N. pulcher, N. masyae,* *N. fasciatus, N. savona, N. fasciolata, N.* *breviceps, N. fowlerianus, N. pantera, N. angorae* *jordanicus, N. tigris*
1	7 or 8	Noemacheilinae *Noemacheilus toni, N. barbatulus*
1	8	Botiinae *Leptobotia curta, Botia hymenophysa, B. macra-* *cantha* Noemacheilinae *Noemacheilus evezardi* Homalopterinae *Crossostoma lacustre*
1	9	Homalopterinae *Annamia normani*
2	7	Homalopterinae *Homaloptera smithi*
4	10	Homalopterinae *Hemimyzon formosanum*
6	15	Homalopterinae *Sinogastromyzon puliensis*

homalopterines *Annamia normani* and *Crossostoma lacustre* (Figs. 63–66; Table 13).
On the other hand, there are two unbranched rays in a homalopterine *Hemimyzon
formosanum*, and six in a homalopterine *Sinogastromyzon puliensis* (Fig. 66 A, B,
C; Table 13).
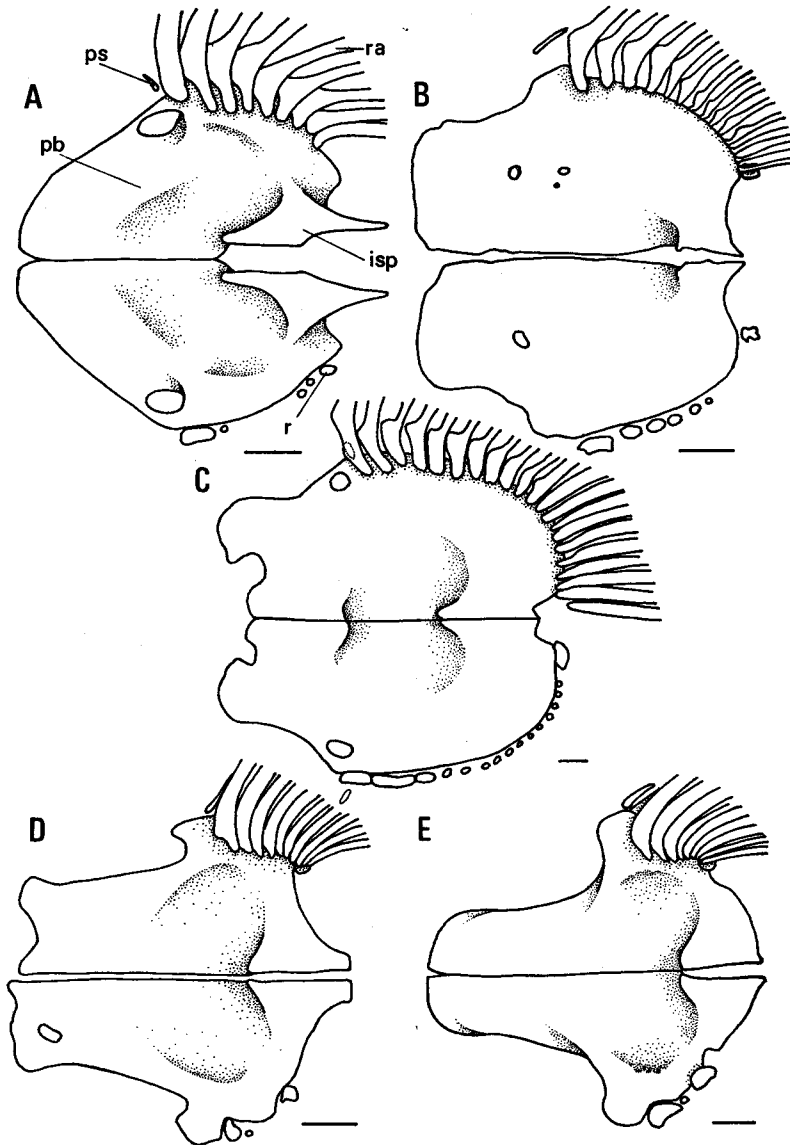
Fig. 66. Ventral view of pelvic girdles in homalopterine fishes. A, *Homaloptera smithi*;
B, *Hemimyzon formosanum*; C, *Sinogastromyzon puliensis*; D, *Annamia normani*; E,
Crossostoma lacustre. For abbreviations, see Fig. 63. Scales indicate 1 mm.

The number of branched rays ranges from 5 to 15 (Table 13).

DISCUSSION

The pelvic girdle and pelvic fin of the superfamily Cobitoidea have been
examined by several authors (Hora, 1932; Sewertzoff, 1934; Chang, 1945; Mester,

1972). They have little regard for the analysis of the phylogenetic relationships, although they are frequently used as the taxonomic characters.

Among cobitoid fishes examined, differences are found in the developmental degree of the pelvic bone and the number of radials (Table 14). On the basis of the combinations among conditions of these characters, the cobitoid pelvic girdle is divided into eight morphotypes (Table 14). Type A is characterized in having moderately developed pelvic bone and three radials. In this type, the fishes of the subfamily Botiinae, members of the subfamily Cobitinae except the genera *Misgurnus*, *Niwaella*, *Acanthopsoides* and *Acanthophthalmus*, members of the

Table 14. Comparison of the shape of pelvic bone and the number of radials in cobitoid fishes.

| Morphotype | Character | | Subfamily and Species |
	Shape of pelvic bone	Number of radials	
A	moderate	3	Botiinae *Leptobotia curta, Botia macracantha, B. hymenophysa, B. modesta, B. dayi* Cobitinae *Cobitis taenia taenia, C. taenia. striata, C. takatsuensis, C. koreensis, C. biwae, C. paludicola, Lepidocephalus guntea, Sabajenewia aurata vallachica, Acanthopsis choirorhynchos* Noemacheilinae *Noemacheilus toni, N. barbatulus, N. postventralis, N. stoliczkai, N. botia, N. pleurotaenia, N. pulcher, N. masyae, N. savona, N. fasciolata, N. breviceps, N. fowlerianus, N. rupecula, N. fasciatus, N. angorae jordanicus, N. tigris, N. pantera, N. evezardi*
B		2	Cobitinae *Acanthopsoides graciroides* Noemacheilinae *Lefua echigonia, L. nikkonis, L. costata*
C	less-developed	3	Cobitinae *Niwaella delicata, N. multifasciata, Acanthophthalmus kuhli*
D		2	Cobitinae *Misgurnus fossilis, M. anguillicaudatus, M. mizolepis, Acanthophthalmus anguillaris*
E	well-developed	3	Homalopterinae *Annamia normani, Crossostoma lacustre*
F		5	Homalopterinae *Homaloptera smithi*
G		6	Homalopterinae *Hemimyzon formosanum*
H		16	Homalopterinae *Sinogastromyzon puliensis*

subfamily Noemacheilinae except the genus *Lefua* are included. Type B, including
a cobitine *Acanthopsoides graciroides* and the fishes of the noemacheiline genus
Lefua, differs from Type A in having two radials. Types C and D are similar to
each other in having the less-developed pelvic bone. However, the former is
distinguished from the latter in the number of radials. Type C, having three
radials, consists of *Niwealla delicata*, *N. multifasciata* and *Acanthophthalmus kuhli*,
while Type D having two radials is composed of cobitines *Misgurnus fossilis*, *M.
mizolepis*, *M. anguillicaudatus* and *Acanthophthalmus anguillaris*. The remaining
four types E, F, G and H are characterized in possessing the well-developed pelvic
bone, and differ from each other in the number of radials. Type E with three
radials includes two homalopterines *Annamia normani* and *Crossostoma lacustre*.
Type F has five radials and includes a homalopterine *Homaloptera smithi*. Type G
with 6 radials and Type H with 16 radials consist of *Hemimyzon formosanum* and
Sinogastromyzon puliensis respectively.

The most primitive cobitoid conditions of the two characters are judged
according to the criterion for the determination of polarity (Fig. 67). In the fishes
of both groups (B) and (C), the pelvic bone is well developed and the number of
radials is three (Sewertzoff, 1934; Dixit and Bisht, 1972b). Thus, it is considered
as the most primitive conditions of these characters in the superfamily Cobitoidea
that the pelvic bone is well-developed and the number of radials is three (Fig. 67).
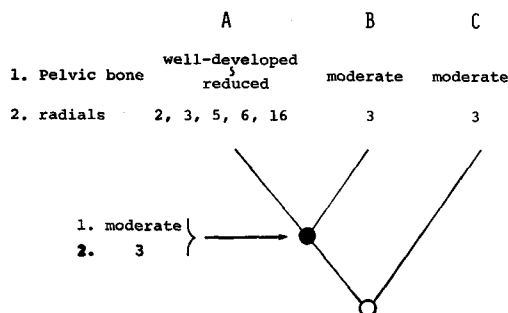
Fig. 67. Character analysis of the cobitoid pelvic girdle. The most primitive conditions
of two characters in group (A) are shown as the conditions of common ancestor (●)
of groups (A) and (B).

On the basis of two morphoclines constructed from these primitive conditions,
the relationships among eight morphotypes are shown as three evolutionary trends
(Fig. 68). The first trend is the decrease of radials in number (C→D) following
the reduction of pelvic bone (A→C). To the contrary, the second trend is the
reduction of pelvic bone (B→D) following the decrease of radial counts (A→B).
The third trend first displays the enlargement of pelvic bone (A→E). Then,
radials increase in number (E→F→G→H). In the cobitoid evolutionary trends,
two tendencies toward opposite directions are shown: 1) the reduction of pelvic
bone and/or the decrease of radial counts, which are represented by the fishes of
the cobitine genera *Misgurnus*, *Niwaella*, *Acanthopsoides* and *Acanthophthalmus*
and a noemacheiline genus *Lefua* (Figs. 64 and 65 A); 2) the enlargement of pelvic

bone and the increase of radials, which are represented by the fishes of the subfamily Homalopterinae (Fig. 66). They are discussed from the functional view points.

The cobitoid group having the reduced pelvic bone and low radial counts has generally an elongated body comparable with other cobitoid groups (Fig. 69). It seems to be related to locomotion. The most common method of locomotion found
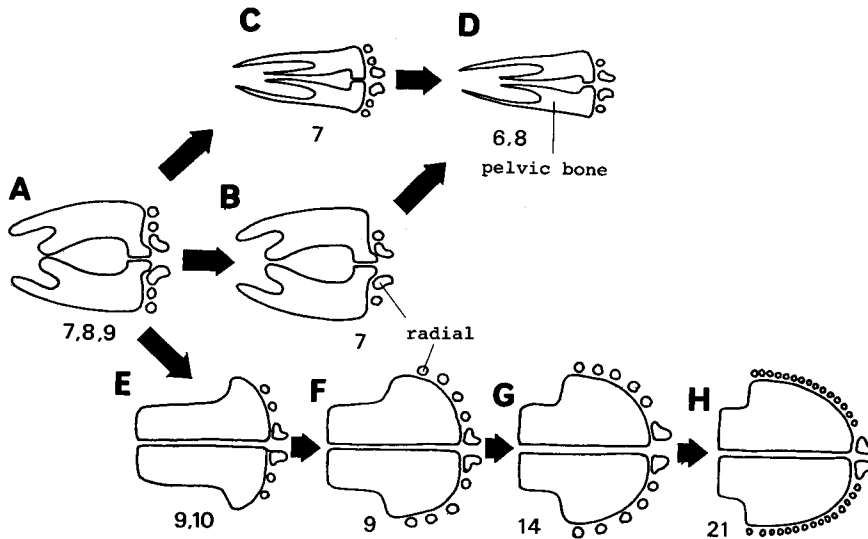
Fig. 68. Evolutionary trends of the cobitoid pelvic girdle. For explanations, see text. Numerals indicate the number of fin rays.
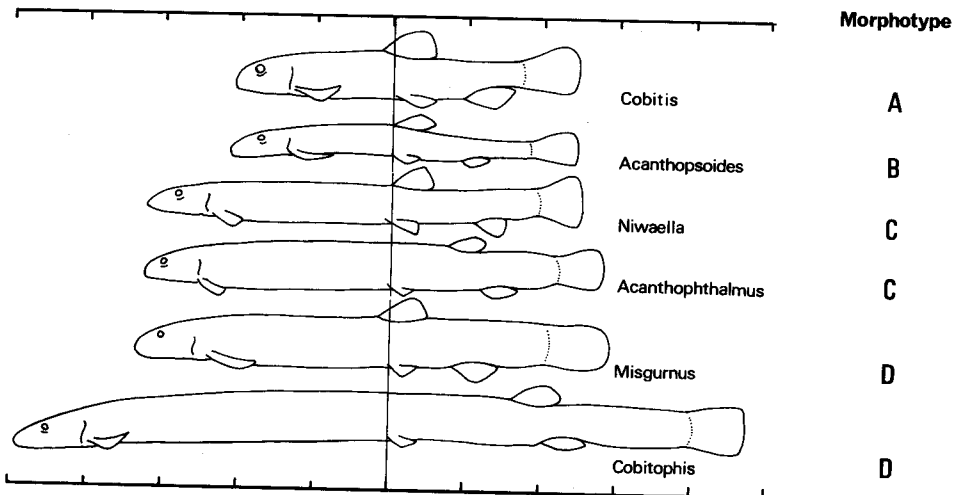
Fig. 69. Comparison of body elongation in six cobitines. In all fishes, the head length is standerized for comparison. For explanations about types, see text and Table 14.
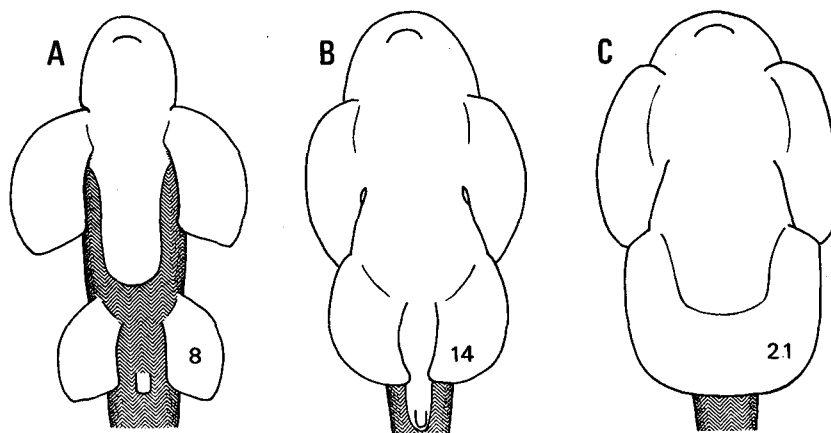
Fig. 70. Squamation of ventral side in three homalopterine fishes. A, *Crossostoma lacustre*;
B, *Hemimyzon formosanum*; C, *Sinogastromyzon puliensis*. Numerals indicate the
number of pelvic fin rays.

in fishes of the superfamily Cobitoidea except the subfamily Homalopterinae is
swimming by the waveform lateral flexures of the body, namely undulation.
Particularly the swimming method of some elongated cobitid fishes such as the genus
Misgurnus, *Niwaella*, *Acanthopsoides* and *Acanthophthalmus* are closely similar to
that of eels which is characterized by the exaggerated sidewise swinging of the body.
When the fish moves only by undulation, the amphitude of the locomotor wave
is high and remains almost constant throughout the body (Aleev, 1963). As
Gosline (1971) pointed out, therefore, the various requirements of locomotor are
distributed along the length of the body. As a result, there is little differentiation
of fins. In the exaggerated undulation method like that of eels, the fins serve as
the supplementary surface of resistance, and thus increase the driving force created
by the trunk (Aleev, 1963). Under such situation, the paired fins, which primarily
have served as the stabilizer or keel, appear to have the least importance among
fins. Aleev (1963) suggested that with the elongation of the body the paired fins
gradually decrease in size until they finally disappear. In fact, in many
elongated fishes which move by the exaggerated undulation method, the paired
fins, especially the pelvic fin, are reduced or disappear (Asano, 1962; McCosker,
1977). Therefore, the reduction of pelvic bone and the decrease of radial counts
found in the fishes of the genera *Misgurnus*, *Niwaella*, *Acanthopsoides* and *Acantho-
phthalmus* may be closely associated with the method of forward movements
adopted by such elongated fishes.

The second tendency represented by the fishes of the subfamily Homalopterinae
appears to be closely related to the adhesion to substances, because homalopterine
fishes inhabit torrential streams and slowly crawl on stones with the aid of the
paired fins (Hora, 1932; Wickler, 1971). In the fishes of the subfamily, the pelvic
fin, having the primary function as the stabilizer, has been considered to have an
additional function or the function of adhesion (Hora, 1932). This function seems

to be accomplished by the formation of the sucking disc. As Hora (1932) and Lundberg and Marsh (1976) pointed out, the effective sucking disc may require the flattened smooth surface and the soft wall surrounded it. In homalopterine fishes, the former is accomplished by the flattened ventral surface of body, the reduced squamation and the large pelvic bone (Figs. 66, 68 and 70). On the other hand, the latter which assists the close application of body to the substance is satisfied by having many fin rays correlated to the number of radials (Table 13; Fig. 68). Thus, as shown in Figs. 68 and 70, the more effective the sucking disc becomes, the more morphological requirements appear to increase. From this consideration, it is presumed that the enlargement of the pelvic bone and the increase in radial counts are correlated to the efficiency in the function of adhesion.

These two presumptions on the cobitoid pelvic evolution will be discussed in the chapter VI again.

9. MEDIAN FINS (Figs. 71–73; Tables 15 and 16)

Dorsal fin: the dorsal fin includes pterygiophores and fin rays.

Each pterygiophore typically consists of an elongated proximal radial (pr), a pair of rod-shaped distal radials (dr) and a rod-shaped medial radial (mr) (Fig. 71). The first pterygiophore comprises only an elongated bipartite proximal radial supporting several spinous rays (Fig. 72; Tables 15 and 16). The second pterygiophore, which supports an unbranched segmented ray, consists of a proximal radial and a pair of distal radials (Fig. 72). All other pterygiophores except terminal one are typical one consisting of a proximal radial, a pair of distal radials and a medial radial, though it is observed in some specimens that the third and/or fourth pterygiophores are the same conditions as the second. The terminal pterygiophore, which supports two last rays, comprises only a proximal radial and a pair of distal radials (Fig. 72). Each proximal radial in the first and second pterygiophores is always inserted into space anterior to each corresponding neural spine. In all other pterygiophores except terminal one, two proximal radials usually insert into interspace between neural spines (Fig. 72).

Fin rays consist of the spinous ray, the unbranched segmented ray and the branched segmented ray. There are 3 to 5 spinous rays in fishes of the subfamily
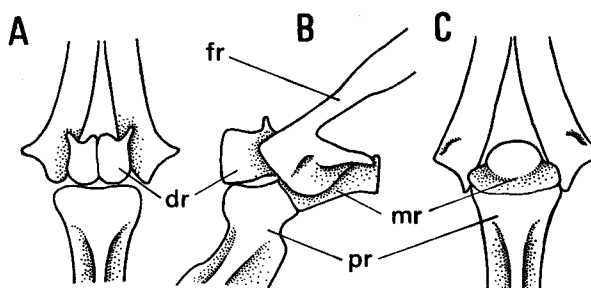
Fig. 71. Fifth dorsal fin ray and its pterygiophore in a botiine *Leptobotia curta*. A, anterior view; B, lateral view; C, posterior view. dr, distal radial; fr, fin ray; mr, medial radial; pr, proximal radial.
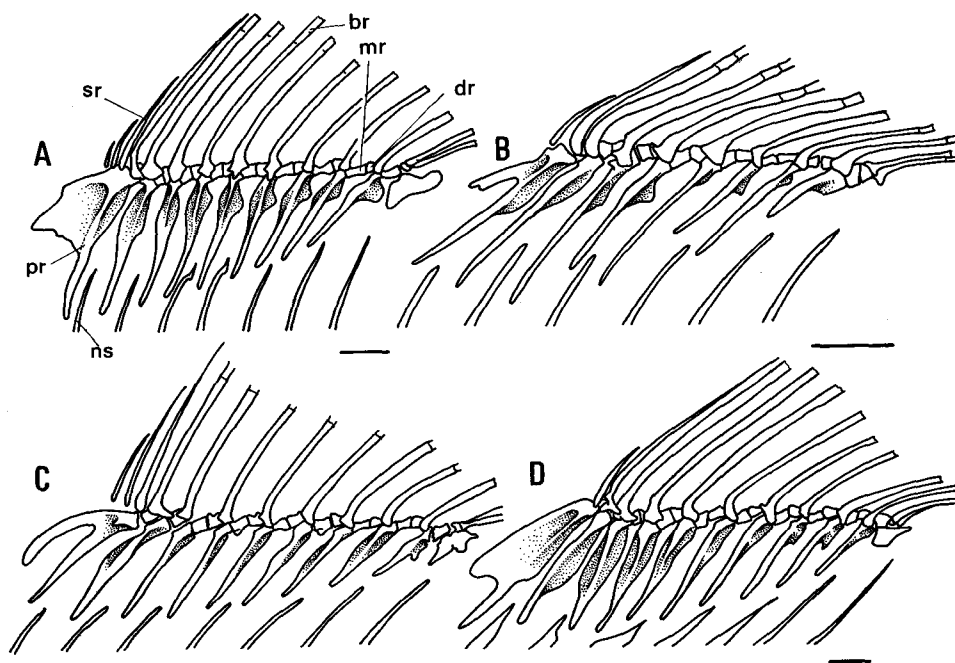
Fig. 72. Dorsal fins in cobitoid fishes. A, *Botia macracantha*; B, *Cobitis paludicola*; C, *Noemacheilus tigris*; D, *Crossostoma lacustre*. br, fin ray; dr, distal radial; mr, medial radial; ns, neural spine; pr, proximal radial; sr, spinous ray. Scales indicate 1 mm.

Botiinae, 1 to 3 in fishes of the subfamily Cobitinae, 2 to 4 in fishes of the subfamily Noemacheilinae, and 1 or 2 in fishes of the subfamily Homalopterinae (Tables 15 and 16). There is an unbranched segmented ray in all cobitoid fishes examined (Fig. 72). The number of branched segmented rays ranges from 9 to 14 in fishes of the subfamily Botiinae, 7 to 12 in fishes of the subfamily Cobitinae, 7 to 13 in fishes of the subfamily Noemacheilinae, and 8 or 9 in fishes of the subfamily Homalopterinae (Tables 15 and 16).

Anal fin: the anal fin includes the pterygiophores and the fin rays.

Each pterygiophore typically consists of the same elements as the dorsal pterygiophore. The first pterygiophore consists of only an elongated bipartite proximal radial supporting several spinous rays (Fig. 73; Tables 15 and 16). The second pterygiophore, which supports an unbranched segmented ray, is composed of an elongated proximal radial and a pair of distal radials (Fig. 73). All other pterygiophores except the terminal one are typical ones consisting of the three elements, though it is observed in some specimens that the third pterygiophore comprises the same elements as the second one. The terminal pterygiophore, which supports two last rays, consists of only a small proximal radial and a pair of distal radials. The proximal radial of the first pterygiophore always inserts into space anterior to the corresponding haemal spine. In all other pterygiophores except the terminal one, two proximal radials usually insert between haemal spines (Fig. 73).

Table 15. Frequency distribution of dorsal and anal fin ray counts in the family Cobitidae.

Species	Dorsal fin													Anal fin					
	Spinous rays					Segmented rays								Spinous rays			Segmented rays		
	I	II	III	IV	V	7	8	9	10	11	12	13	14	I	II	III	5	6	7
Botiinae																			
Leptobotia curta			5						3	2						5		5	
Botia macracantha				1				1								1		1	
B. hymenophysa				4	1							3	2			5		5	
B. modesta			6	2				8								8		8	
B. dayi			5	1						6					3	3		6	
Cobitinae																			
Misgurnus fossilis			5			5										5		3	2
M. anguillicaudatus		11				11									11			11	
M. mizolepis		20				1	19								20			19	1
Cobitis taenia taenia		10	2			1	11								12			11	1
C. taenia striata		13					12	1							13			13	
C. takatsuensis		11				11									11		1	10	
C. biwae		18					18								18			18	
C. koreensis		12					12								12			12	
C. paludicola		4					3	1							4			4	
Niwaella delicata		11				1	10								11			11	
N. multifasciata		10				10									10		10		
Sabajenewia aurata vallachica	1	12					12	1						1	12			12	1
Acanthopsoides graciroides		8					8								8			8	
Acanthopsis choirorhynchos		10									9	1		1	9			10	
Lepidocephalus guntea		5				5									5			5	
Acanthophthalmus kuhli		5				5									5			5	
A. anguillaris		2				2									2			2	
Somileptes gongota		1						1								1		1	

Table 16.   Frequency distribution of dorsal and anal ray counts in the family Homalopteridae.

Species	Dorsal fin											Anal fin						
	Spinous rays				Segmented rays							Spinous rays				Segmented rays		
	I	II	III	IV	7	8	9	10	11	12	13	I	II	III	IV	5	6	7
Noemacheilinae																		
Lefua echigonia		8	6		14								6	8			10	
L. nikkonis		4	6		10								5	5			10	
L. costata		1	6	1	7	1							1	6			7	
Noemacheilus toni			9			9							7	2			9	
N. postventralis		2	22		2	26							1	22	3	1	27	
N. barbatulus			1	2		4								4			4	
N. stoliczkai		5	16	2		6	19						6	16			25	
N. pleurotaenia							1										1	
N. botia			2						1	1			2				2	
N. pulcher		1	24	1					1	8	17	1	23				24	
N. masyae			2					2				1	1				2	
N. fasciolata						1			1				1				1	
N. fasciatus			1					1					1				1	
N. breviceps			20				20						20				20	
N. fowlerianus			12				12						12				12	
N. rupecula		7	3			10						1	9				10	
N. angorae jordanicus			3				3						2	1			3	
N. tigris			3				3						2	1			3	
N. pantera		2	2				4						4				4	
N. evezardi		2	1		2	1						1	1				2	
N. savona		4	6		10							1	9				10	
Homalopterinae																		
Homaloptera smithi		15			15							6	9				15	
Hemimyzon formosanum	1	15			15	1						9	8				16	1
Sinogastromyzon puliensis		1				1						1					1	
Annamia normani	3	4			3	4						2	5			7		
Crossostoma lacustre	2	14			1	15						11	6				17	
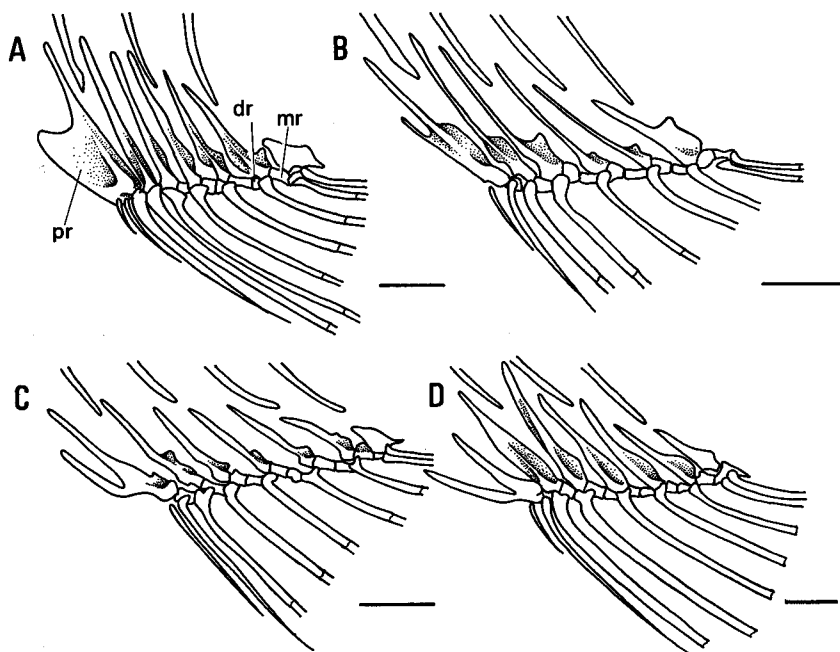
Fig. 73. Anal fins in cobitoid fishes. A, *Botia macracantha*; B, *Cobitis paludicola*; C, *Noemacheilus tigris*; D, *Crossostoma lacustre*. For abbreviations, see Fig. 72. Scales indicate 1 mm.

The fin rays include the spinous ray, the unbranched segmented ray and the branched segmented ray. There are almost always 3 spinous rays (occasionally 2) in fishes of the subfamily Botiinae, 2 (occasionally 1 or 3) in fishes of the subfamily Cobitinae, 2 or 3 (occasionally 1 or 4) in fishes of the subfamily Noemacheilinae, and 1 or 2 in fishes of the subfamily Homalopterinae (Tables 15 and 16). There is a single unbranched segmented ray in all cobitoid fishes examined (Fig. 73). In most cobitoids examined here, the mode of branched segmented ray counts is 6 (Tables 15 and 16). In a cobitine *Niwaella multifasciata* and a homalopterine *Annamia normani*, the number of rays is 5 (Tables 15 and 16).

DISCUSSION

The number of dorsal and anal fin rays has been used for the taxonomic works of various fish groups. Among four cobitoid subfamilies, there are several tendencies in the number of spinous dorsal and anal fin rays. With regard to the spinous dorsal fin ray counts, the fishes of the subfamily Botiinae have always more than three, the fishes of the subfamily Cobitinae have constantly two with a few exceptions, the fishes of the subfamily Noemacheilinae have two or three, and the fishes of the subfamily Homalopterinae have always less than two. On the other hand, with regard to the number of spinous anal fin rays, the fishes of the subfamily Botiinae have two or three, the fishes of the subfamilies Cobitinae and

Noemacheilinae have two in most specimens examined, and the fishes of the sub-family Homalopterinae have one or two. For the present character analysis, the spinous ray conditions of other cyprinoid fishes have to be shown. However, knowledge about them is too meager to analyze. Thus, the number of spinous rays is not used for the phylogenetic analysis of the superfamily Cobitoidea.

On the other hand, the skeletal supports of the median fins have been examined by several authors (Eaton, 1945, in major groups of actinopterygians; Weitzman, 1962, in a characin; Vari, 1978, in terapon perches). Especially the pterygiophore morphology has come to be considered as one of important characters for the phylogenetic works in a scombrid *Thunnus atlanticus* (Potthoff, 1975) and in a scombrolabracid *Scombrolabrax heterolepis* (Potthoff et al., 1980). The present examinations indicate that the pterygiophore structures among cobitoid fishes examined are essentially the same (Figs. 72 and 73). It is impossible to determine whether the cobitoid pterygiophore conditions are primitive or derived according to the present character analysis, because the pterygiophore morphology of other cyprinoid fishes is little known. Thus, in the present study, the dorsal and anal pterygiophores are also not used for the phylogenetic analysis of the superfamily Cobitoidea.

10. VERTEBRAE AND THEIR ACCESSARY BONES (Figs. 74–80; Tables 17–19)

Vertebrae are divided into the abdominal ones defined as those without the haemal spine and the caudal ones defined as those having the haemal spine. The accessary bones includes the pleural rib, the epineural, the epipleural and the parapophysis.

Vertebra anterodorsally produces a pair of prezygapophyses, posterodorsally a pair of neural postzygapophyses, and posteroventrally a pair of haemal postzyga-pophyses. Each of some abdominal vertebrae ventrally produces a pair of the lateral processes (basapophyses) which are distally articulated with the pleural ribs (Fig. 74). In fishes of the subfamily Botiinae, the processes are found on the last four to six abdominal vertebrae; in fishes of the subfamily Cobitinae except *Lepidocephalus guntea* and *Somileptes gongota*, the last one to three; in *G. gongota* and *L. guntea*, all abdominal vertebrae except the first five including the Weberian apparatus; in fishes of the subfamily Noemacheilinae except *Noemacheilus botia*, the last four to six; in *N. botia*, all abdominal vertebrae except the first seven; in two homalopterines *Hemimyzon formosanum* and *Sinogastromyzon puliensis*, about the last ten; in a homalopterine *Crossostoma lacustre*, the last seven to nine; in two homalopterines *Homaloptera smithi* and *Annamia normani*, the last three to four.

The total numbers of vertebrae including the first four of the Weberian apparatus and the last preural centrum in cobitoid fishes examined are shown in Tables 17 and 18. The total number of vertebrae ranges from 31 to 39 in the subfamily Botiinae, from 35 to 66 in the subfamily Cobitinae, from 32 to 43 in the subfamily Noemacheilinae, and from 31 to 38 in the subfamily Homalopterinae (Tables 17 and 18).

In the compositions of the number of abdominal and caudal vertebrae found in cobitoid fishes examined, the fishes of the superfamily are classified into three
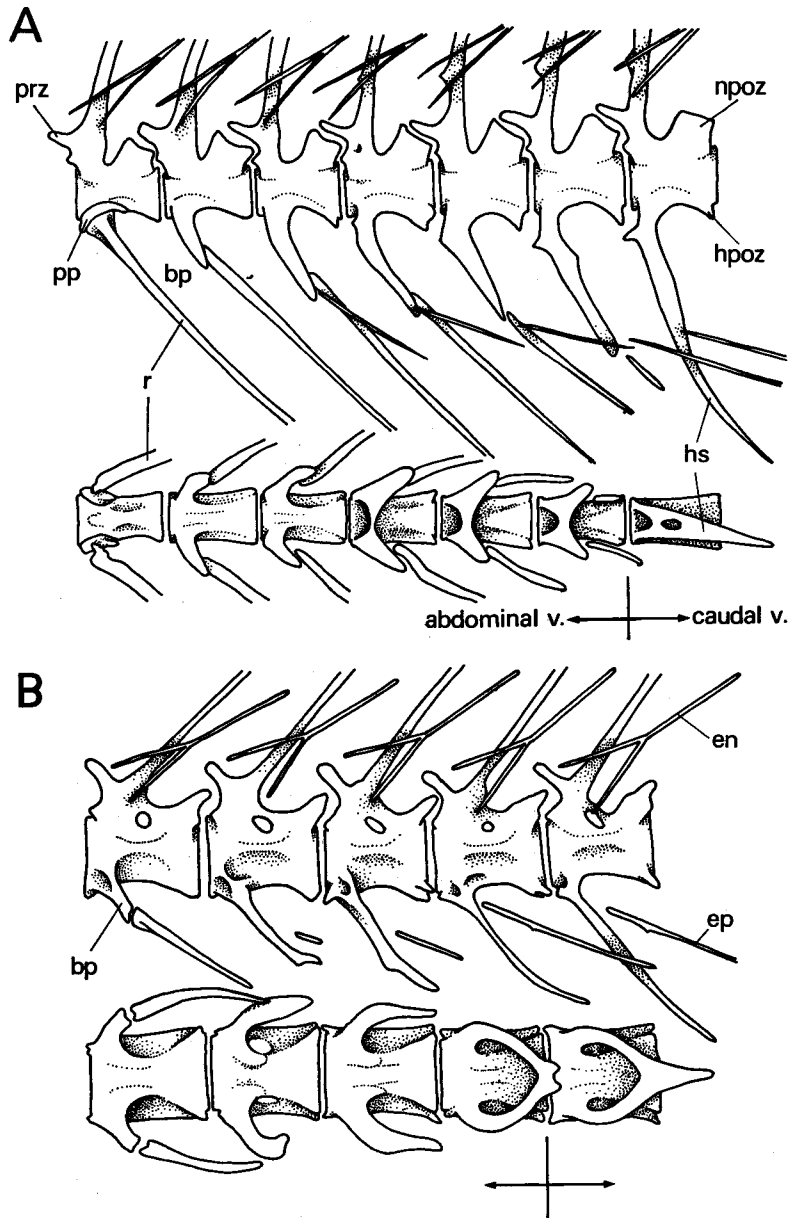
Fig. 74. Several vertebrae and their accessary bones located near the boundary between the abdominal and caudal vertebrae in cobitoid fishes. A, *Botia macracantha*; B, *Misgurnus anguillicaudatus*. bp, basapophysis; en, epineural; ep, epipleural; hpoz, haemal postzygapophysis; hs, haemal spine; npoz, neural postzygapophysis; pp, parapophysis; prz, prezygapophysis; r, pleural rib.

Table 17. Frequency distribution of total vertebral counts in the family Cobitidae.

Species	Total vertebral number																										
	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56 ····	66
Botiinae																											
Leptobotia curta					1	2	1	1																			
Botia macracantha		1																									
B. hymenophysa			1	3	1																						
B. modesta	8																										
B. dayi	1	3	2																								
Cobitinae																											
Misgurnus fossilis																					1	2	2				
M. anguillicaudatus														1	2	6	1										
M. mizolepis																2	9	5	5								
Cobitis taenia taenia											1	1	5	5													
C. taenia striata								1		2	1	6	3	1													
C. takatsuensis													1	9	1												
C. biwae											1	2	7	7	1												
C. koreensis														2	4	6											
C. paludicola										1	1	1	1														
Niwaella delicata																		1	2	1	5	2	1				
N. multifasciata																			1		2	5	2				
Sabajenewia aurata vallachica													4	8	2												
S. romanica															2												
Acanthopsoides graciroides										1	5	1		1													
Acanthopsis choirorhynchos								1		1	3	3		1	1												
Lepidocephalus guntea						5																					
Acanthophthalmus kuhli																			1		4						
A. anguillaris																									1		1
Somileptes gongota				1																							

groups A, B and C (Figs. 75–78): the number of abdominal vertebrae is more than, about equal to or less than those of caudal ones. The first group A is represented by *Cobitis biwae*, *C. takatsuensis*, *C. paludicola*, *M. fossilis*, *M. anguillicaudatus*, *M. mizolepis*, *Niwaella delicata*, *N. multifasciata*, *Acanthopsis*
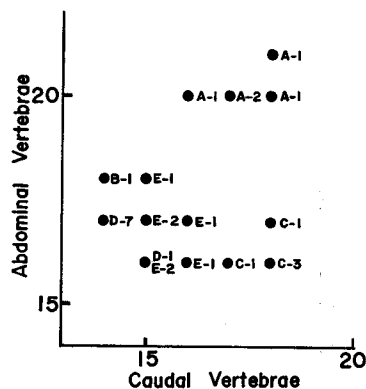
Fig. 75. Vertebral compositions of botiine fishes. A, *Leptobotia curta*; B, *Botia macracantha*; C, *B. hymenophysa*; D, *B. modesta*; E, *B. dayi*.

Table 18. Frequency distribution of total vertebral counts in the family Homalopteridae.

| Species | \multicolumn{14}{c}{Total vertebral number} | Total |
	31	32	33	34	35	36	37	38	39	40	41	42	43	44	
Noemacheilinae															
Lefua echigonia					2	8	4								14
L. nikkonis						1	6	3							10
L. costata						1	3	6							10
Noemacheilus toni							2	7	5						14
N. postventralis								7	16	6					29
N. barbatulus							4								4
N. stoliczkai							9	10	7						26
N. pleurotaenia				1	1										2
N. botia		1		1											2
N. pulcher		2	18	6											26
N. masyae				1	1										2
N. savona			2	5	5										12
N. fasciolata						1									1
N. rupecula												7	4		11
N. angorae jordanicus						1	2								3
N. tigris					1	1	1								3
N. pantera						1	3								4
N. evezardi			3												3
N. fasciatus				1											1
N. breviceps			3		12	5									20
N. fowlerianus					2	4	4	2							12
Homalopterinae															
Homaloptera smithi	2	10	3												15
Hemimyzon formosanum					1	6	8	2							17
Sinogastromyzon puliensis						1									1
Annamia normani		2	3	1											6
Crossostoma lacustre							7	12							19
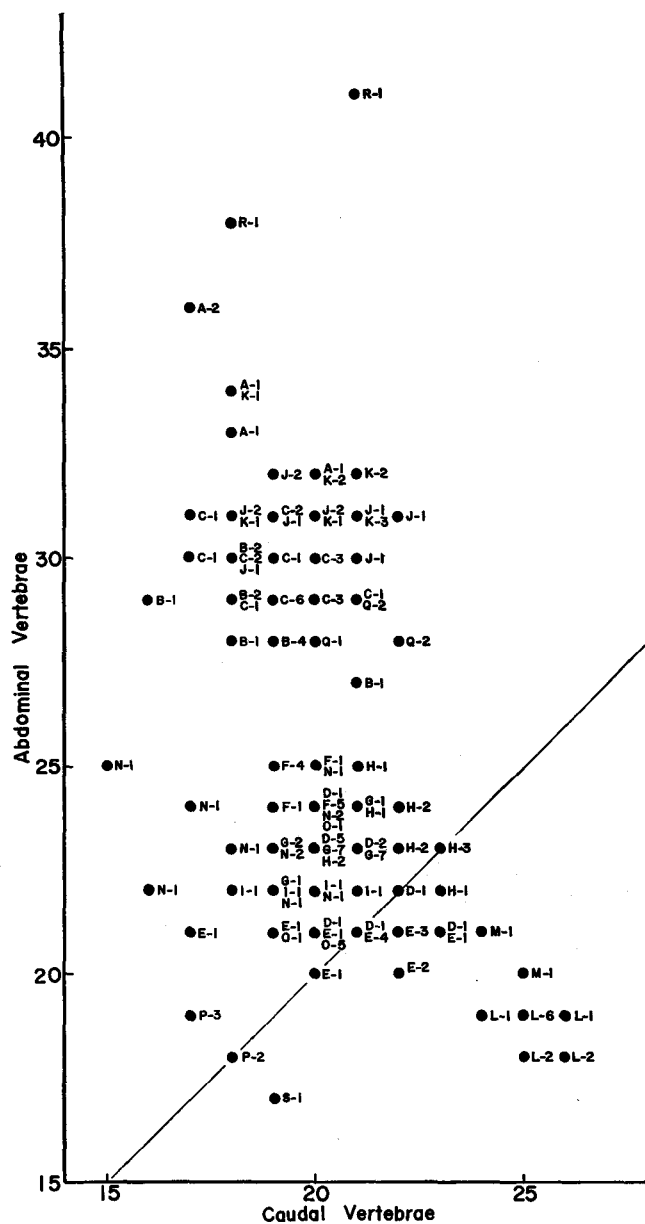
Fig. 76.   Vertebral compositions of cobitine fishes.   A, *Misgurnus fossilis*; B, *M. anguilli-caudatus*; C, *M. mizolepis*; D, *Cobitis taenia taenia*; E, *C. taenia striata*; F, *C. takatsuensis*; G, *C. biwae*; H, *C. koreensis*; I, *C. paludicola*; J, *Niwaella delicata*; K, *N. multifasciata*; L, *Sabajenewia aurata vallachica*; M, *S. romanica*; N, *Acanthopsis choirorhynchos*; O, *Acanthopsoides graciroides*; P, *Lepidocephalus guntea*; Q, *Acanthophthalmus kuhli*; R, *A. angullaris*; S, *Somileptes gongota*.

choirorhynchos, Acanthophthalmus kuhli and *A. anguillaris* in the subfamily Cobitinae, *Lefua costata, L. nikkonis, Noemacheilus toni, N. postventralis, N. barbatulus, N. stoliczkai* and *N. pleurotaenia* in the subfamily Noemacheilinae, the fishes of the subfamily Botiinae except *Botia hymenophysa*, and the fishes of the subfamily Homalopterinae except *Homaloptera smithi* (Figs. 75–78). However, in
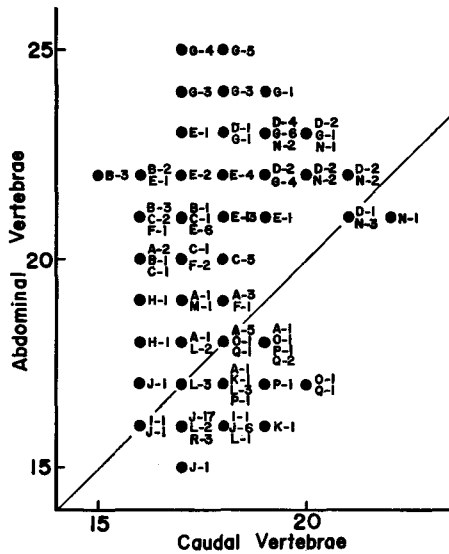
Fig. 77. Vertebral compositions of noemachei-
line fishes. A, *Lefua echigonia*; B, *L.
nikkonis*; C, *L. costata*; D, *Noemacheilus
toni*; E, *N. postventralis*; F, *N. barbatulus*;
G, *N. stoliczkai*; H, *N. pleurotaenia*; I,
N. botia; J, *N. pulcher*; K, *N. masyae*; L,
N. savona; M, *N. fasciolata*; N, *N. rupe-
cula*; O, *N. angorae jordanicus*; P, *N.
tigris*; Q, *N. pantera*; R, *N. evezardi*.
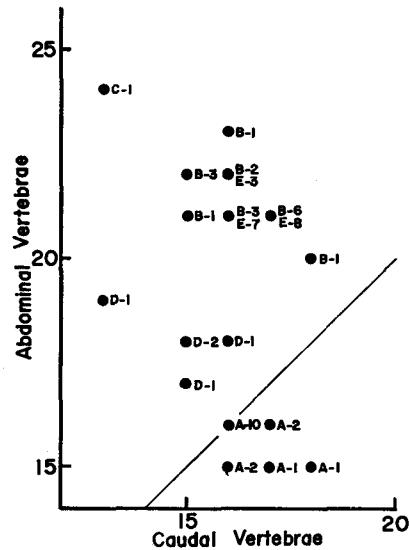
Fig. 78. Vertebral compositions of
homalopterine fishes.
A, *Homaloptera smithi*;
B, *Hemimyzon formosanum*;
C, *Sinogastromyzon puliensis*;
D, *Annamia normani*;
E, *Crossostoma lacustre*.

some cobitines *Cobitis takatsuensis, C. biwae, C. paludicola* and *Niwaella multifasciata* (Fig. 76: F, G, I, K) and some noemacheilines *Noemacheilus toni, N. barbatulus* and *N. stoliczkai* (Fig. 77: D, F, G), their ranges of the composition are partly overlapped those of some members of the group B. The second group B is represented by *Cobitis taenia taenia, C. taenia striata, C. koreensis, Acanthopsoides graciroides* and *Lepidocephalus guntea* in the subfamily Cobitinae, *Lefua echigonia, Noemache-ilus botia, N. pulcher, N. savona, N. fasciolata* and *N. rupecula* in the subfamily Noemacheilinae, and a homalopterine *Homaloptera smithi* (Figs. 76–78). However, in three cobitines *Cobitis taenia taenia, C. koreensis* and *Acanthopsoides graciroides* (Fig. 76: D, H, O) and two noemacheilines *Lefua echigonia* and *Noemacheilus savona* (Fig. 77: A and N), their ranges of the composition are partly overlied with those of some members of the group A. The third group C is represented by *Botia hymenophysa* in the subfamily Botiinae, the fishes of the cobitine genera *Sabajenewia*

and *Somileptes*, and *Noemacheilus angorae jordanicus*, *N. masyae*, *N. tigris*, *N. pantera* and *N. evezardi* in the subfamily Noemacheilinae. However, in the range of the composition, all noemacheilines of this group are partly included in group B (Fig. 77: K, O, P, Q, R).

Pleural rib (r) is an elongated rod-shaped bone running backward and downward into the myocommata. The bones are gradually reduced backwards in size. The last rib is distinctly reduced in every species of the superfamily Cobitoidea. The bones are born by vertebrae from the fifth to the last abdominal in
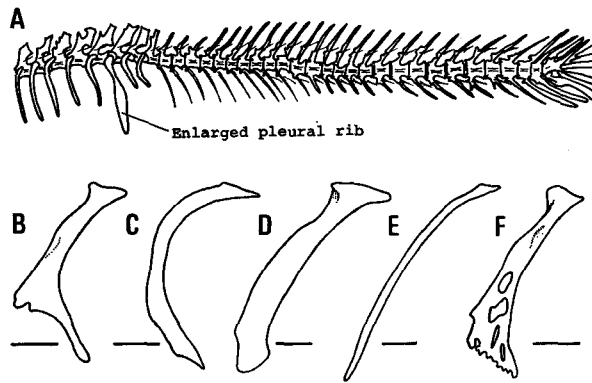
Fig. 79.   Enlarged pleural ribs in homalopterine fishes. A, lateral view of axial skeleton; B, C, D, E and F, posterior view of enlarged rib on left side. A and C, *Hemimyzon formosanum*; B, *Homaloptera smithi*; D, *Sinogastromyzon puliensis*; E, *Crossostoma lacustre*; F, *Annamia normani*. Scales indicate 1 mm.

fishes of the subfamily Botiinae, from the fifth to the last two to four abdominal in fishes of the subfamilies Cobitinae, Noemacheilinae and Homalopterinae. In fishes of the subfamily Homalopterinae, there is an enlarged pleural rib connected to the pelvic bone by a strong ligament (Fig. 79). It is the tenth rib in *Homaloptera smithi*, *Hemimyzon formosanum* and *Sinogastromyzon puliensis*, the twelveth rib in *Annamia normani*, and the thirteenth rib in *Crossostoma lacustre*.

Epineural (en) is a proximally forked spine-like bone running backward and upward into the myocommata from its corresponding vertebra. The bones are born by all vertebrae except the last four or five caudal vertebrae including the first preural centrum (Figs. 74 and 79).

Epipleural (ep) is a typically forked spinous bone running backward and downward into the myocommata from its corresponding vertebra, though the epipleurals corresponding to abdominal vertebrae are unforked. The bones are found from the last two to five abdominal vertebrae to caudal vertebrae except the last four or five vertebrae including the first preural centrum in fishes of the superfamily Cobitoidea except a cobitine *Acanthopsis choirorhynchos*. In *A. choirorhynchos*, all vertebrae except the first six ones bear epipleurals.

Parapophyses (pp) are a pair of small lumpy bones being typically autogenous with the ventrolateral part of the centrum. In fishes of the subfamilies Botiinae, Noemacheilinae and Homalopterinae, the bones are possessed by

Table 19. Comparison of two characters in the cobitoid axial
              skeleton.

| Morphotype | Character | | Subfamily |
	Enlarged rib	Parapophysis	
A	absent	present	Botiinae Noemacheilinae
B		absent	Cobitinae
C	present	present	Homalopterinae

abdominal vertebrae having no lateral process (basapophysis). In fishes of the
subfamily Cobitinae, all parapophyses are fused to centra to form the lateral
processes (basapophyses) (Fig. 74).

<center>DISCUSSION</center>

With regard to the cobitoid vertebrae and their accessary bones, there are
little reports with exceptions of the fishes of the subfamily Homalopterinae (Hora,
1932; Chang, 1945; Liang, 1974), and the fishes of the cobitine genera *Cobitis* and
Niwaella (Sawada and Kim, 1977).

Among cobitoid fishes examined here, differences were found in many
characters. However, the knowledge of other cyprinoid vertebrae and their accessary
bones is too meager, although it is indispensable for the present character analysis.
Thus, in the present study, the analyzable characters were restricted in the enlarged
rib and the parapophysis (Table 19). On the basis of the combinations among
conditions of these two characters, cobitoid vertebrae and their accessary bones are
divided into three morphotypes (Table 19). Type A, consisting of the fishes of the
subfamilies Botiinae and Noemacheilinae is characterized by the absence of the
enlarged rib and the presence of the parapophysis. Type B, including the
fishes of the subfamily Cobitinae, differs from Type A only by the absence of the
parapophysis. Type C differs from Type A only by the presence of the enlarged
rib, and includes the fishes of the subfamily Homalopterinae.
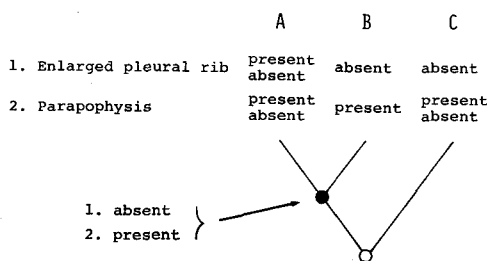
Fig. 80. Character analysis of vertebrae and their accessary bones in cobitoid fishes. The
     most primitive conditions of two characters in group (A) are shown as the conditions of
     the common ancestor (●) of groups (A) and (B).

In the enlarged rib and the parapophysis, their most primitive conditions are judged according to the criterion for the determination of polarity (Fig. 80). The conditions of these characters found in group (B) are the absence of the enlarged rib and the presence of parapophysis on the abdominal vertebrae. On the other hand, the conditions of these characters found in group (C) are as follows (Dixit and Bisht, 1972b; Skelton, 1976; Howes, 1978, 1979, 1980). Though the enlarged rib is always absent, the parapophyses are generally present in most fishes of the group. But in the fishes of the cyprinid genus *Gobiobotia*, it was observed that they are absent to form the lateral processes (basapophyses) (personal observations).

On the basis of the criterion, it was determined that the most primitive conditions of these two characters in group (A) are the absence of the enlarged pleural rib and the presence of the parapophysis. Thus, from the morphoclines of both characters, the relationships among three previously defined morphotypes can be shown as two trends: the fusion of parapophyses to centra (A→B) and the enlargement of pleural rib (A→C).

In these evolutionary trends, the enlargement of pleural rib is functionally noteworthy for the cobiotid evolutionary history. In the fishes of the subfamily Homalopterinae, one of the pleural ribs is enlarged (Fig. 79) and is ligamentously connected to the anterolateral margin of the pelvic bone. These fishes seems to have developed the sucking disc on the ventral surface of the body as an adaptation to the torrential life (Hora, 1932; Chang, 1945, 1948). It is considered that the enlargement of the pelvic bone was a contribution to the development of the disc (see pp. 91–92). When the pelvic bone is compared with the pleural rib in the developmental degree, a relationship between them may be found. In the fishes of the genera *Crossostoma* and *Vanmanenia* having the somewhat developed pelvic bone, the enlarged rib is more or less thicker than the typical one, while in the fishes of the genera *Pseudogastromyzon*, *Lepturichthys*, *Hemimyzon*, *Beaufortia*, *Sinogastromyzon* and *Metahomaloptera* having the greatly enlarged pelvic bone, the enlarged rib is distinctly thick and often distally forked (Chang, 1945). Therefore, the pelvic bone seems to be developed in correlation to the pleural rib. Consequently, it is presumed that the enlarged rib has served as the supporter of the enlarged pelvic bone in order to maintain the increased ventral surface of the disc.

This presumption will be also discussed in the chapter VI.

11. CAUDAL COMPLEX AND FIN (Figs. 81–86; Table 20)

Caudal complex includes the following elements: the second preural centrum, the first preural centrum, the pleurostylar, the neural spine and arch, the last haemal spine and arch, the hypurals, the parhypural, the uroneural, the epural, the principal caudal rays and the procurrent rays.

Second preural centrum (pc 2) is dorsally fused with the last neural spine and arch. In the fishes of the subfamilies Botiinae, Noemacheilinae and Homalopterinae, the bone is ventrally articulated with the last haemal spine and arch (Figs. 81 A-C, 82 and 83), while in the fishes of the subfamily Cobitinae, it is fused with the element (Fig. 81 D-L).
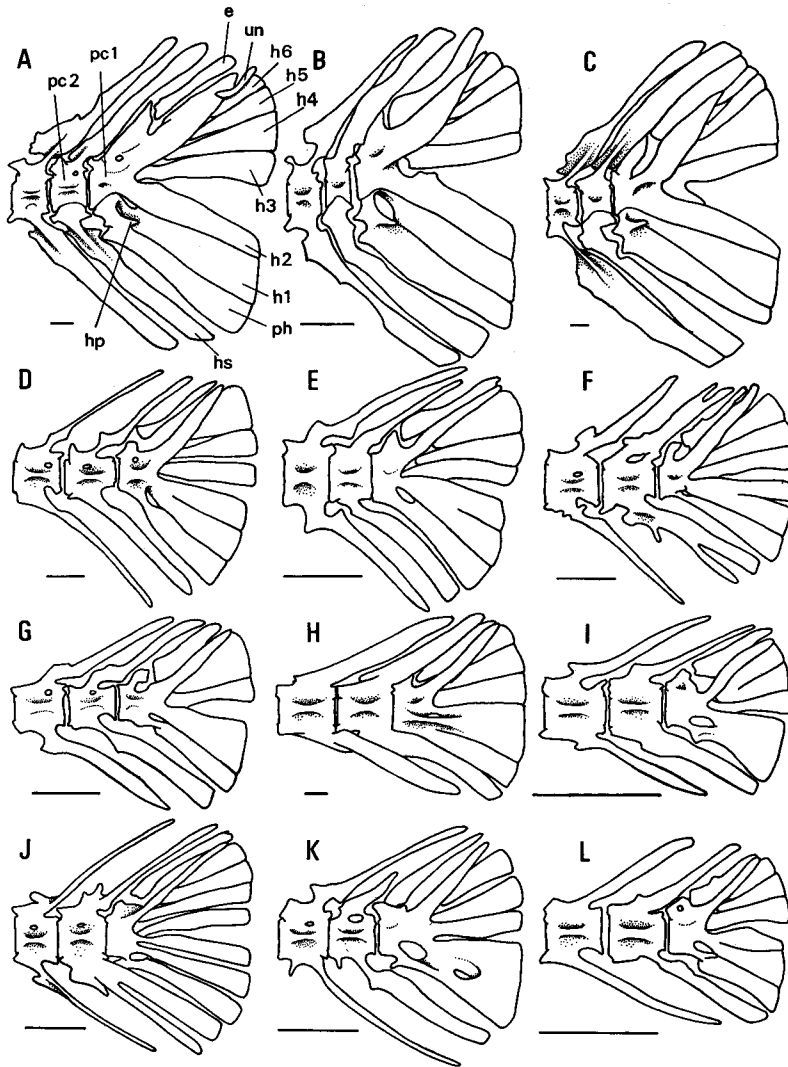
Fig. 81. Caudal complex in cobitid fishes. A, *Leptobotia curta*; B, *Botia macracantha*; C, *B. modesta*; D, *Misgurnus fossilis*; E, *Cobitis paludicola*; F, *Niwaella multifasciata*; G, *Sabajenewia aurata vallachica*; H, *Acanthopsis choirorhynchos*; I, *Acanthopsoides graciroides*; J, *Lepidocephalus guntea*; K, *Acanthophthalmus kuhli*; L, *A. anguillaris*. e, epural; h, hypural; hp, hypurapophysis; hs, haemal spine and arch; pc 1, first preural centrum; pc 2, second preural centrum; ph, parhypural; pls, pleurostylar; un, posterior uroneural. Scales indicate 1 mm.

First preural centrum (pc 1) is the last vertebra bearing posterodorsally the pleurostylar and posteriorly the second hypural. In the fishes of the subfamilies Botiinae, Noemacheilinae and Homalopterinae, the bone is ventrally articulated with the parhypural and the first hypural (Figs. 81 A-C, 82 and 83), while

in the fishes of the subfamily Cobitinae, it is fused with both elements (Fig. 81 D-L).

Pleurostylar (pls) is an elongated sheath-like bone which is distally fused with the first preural centrum.   Into the ventral groove of the bone, the third to sixth hypurals are typically inserted (Figs. 81–83).

Last neural spine and arch (ns) supports some procurrent rays composing of the upper part of the caudal fin.   The bone is basally fused with the second preural centrum.

Last haemal spine and arch (hs) supports some procurrent rays   which form the lower part of the caudal fin.   In fishes of the subfamilies Botiinae, Noemacheilinae and Homalopterinae, the bone is basally articulated with the second preural centrum (Figs. 81 A-C, 82 and 83), while in fishes of the subfamily Cobitinae, it is fused with the centrum (Fig. 81 D-L).

Hypural (h) is a triangular flat bone supporting posteriorly the principal caudal rays.   The second hypural is basally fused with the first preural centrum.   The third to sixth hypurals are typically inserted into the posterior groove of the pleurostylar.   In fishes of the   subfamilies   Botiinae,   Noemacheilinae and Homalopterinae, the first hypural is autogenous with the first preural centrum
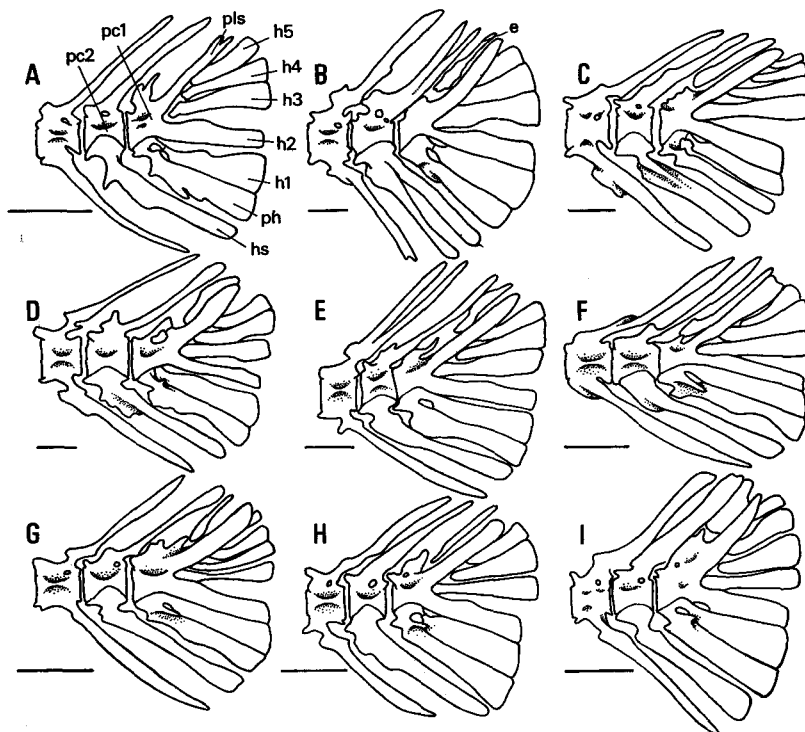
Fig. 82.   Caudal complex in noemacheiline fishes.   A, *Lefua costata*; B, *Noemacheilus barbatulus*; C, *N. stoliczkai*; D, *N. pleurotaenia*; E, *N. botia*; F, *N. masyae*; G, *N. savona*; H, *N. evezardi*; I, *N. tigris*.   For abbreviations, see Fig. 81.   Scales indicate 1 mm.

Table 20. Comparison of several characters of cobitoid caudal complex. ep,

Morphotype		ph and pc 1	pc 2 and its hs	h 1 and pc 1	h 1 and ph
A					fused
B	a				autogenous
	b	autogenous	autogenous	autogenous	fused
	c				autogenous
	d				
C	e				fused
	f	fused	fused	fused	
	g				
	h				
D		autogenous	autogenous	autogenous	autogenous

(Figs. 81 A-C, 82 and 83), while in fishes of the subfamily Cobitinae it is fused with the centrum (Fig. 81 D-L). In some members of the subfamily Noemachei-linae such as *Lefua echigonia*, *L. nikkonis*, *L. costata*, *Noemacheilus toni*, *N. barbatulus*, *N. stoliczkai*, *N. pleurotaenia*, *N. breviceps* and *N. evezardi*, and some members of the subfamily Homalopterinae such as *Hemimyzon formosanum*, *Sinogastromyzon puliensis* and *Annamia normani*, the first hypural is basally

epural; h, hypural; hs, haemal spine; pc, preural centrum; un, posterior uroneural.

ep	un	h	Subfamily and Species
	present	6	Botiinae *Leptobotia curta*
present	absent	5	Noemacheilinae *Noemacheilus toni, N. barbatulus, N.* *pleurotaenia, N. evezardi, N. breviceps* Homalopterinae *Hemimyzon formosanum, Sinogastromyzon* *puliensis, Annamia normani*
			Noemacheilinae *Noemacheilus masyae, N. fowlerianus,* *N. abyssinicus* Homalopterinae *Homaloptera smithi, Crossostoma lacustre*
		6	Noemacheilinae *Noemacheilus stoliczkai*
			Botiinae *Botia macracantha, B. hymenophysa, B.* *modesta, B. dayi* Noemacheilinae *Noemacheilus botia, N. postventralis,* *N. fasciatus, N. pulcher, N. fasciolata,* *N. savona, N. rupecula, N. angorae* *jordanicus, N. tigris, N. pantera,* *Vaillantella euepiptera*
		2	Cobitinae *Misgurnus anguillicaudatus*
		4	Cobitinae *Misgurnus fossilis, M. mizolepis, Cobitis* *taenia taenia, C.taenia striata, C. biwae,* *C. takatsuensis, C. koreensis, C. paludicola,* *Niwaella multifasciata, Acanthopsis* *choirorhynchos, Acanthophthalmus kuhli,* *A. anguillaris, Somileptes gongota*
		3	Cobitinae *Niwaella delicata, Acanthopsoides gracir-* *oides, Sabajenewia aurata vallachica*
		6	Cobitinae *Lepidocephalus guntea*
absent		5	Noemacheilinae *Lefua echigonia, L. costata, L. nikkonis*

autogenous with the parhypural (Figs. 82 A-D, H and 83 B-D), while in other cobitoids examined it is basally fused with the element (Figs. 81, 82 E-G, I and 83 A, E).   In the number of hypurals, the fishes of the superfamily Cobitoidea are classified into five groups.   The first group, having six hypurals, consists of the fishes of the subfamily Botiinae, a cobitine *Lepidocephalus guntea* (Fig. 81 J) and many members of the subfamily Noemacheilinae such as *Noemacheilus postventralis,*

N. stoliczkai, N. pulcher, N. botia, N. fasciatus, N. savona, N. fasciolata, N. rupecula, N. angorae jordanicus, N. tigris, N. pantera and *Vaillantella euepiptera* (Fig. 82 C, E, G, I; Table 20). The second group is characterized in having five hypurals, and includes many members of the subfamily Noemacheilinae such as *Lefua echigonia, L. nikkonis, L. costata, Noemacheilus toni, N. barbatulus, N. pleurotaenia, N. masyae, N. breviceps, N. fowlerianus, N. evezardi* and *N. abyssinicus* (Fig. 82 A, B, D, E, F, H; Table 20), and fishes of the subfamily Homalopterinae (Fig. 83). The third group, bearing four hypurals, is composed of many members of the subfamily Cobitinae such as the genera *Cobitis, Acanthopsis, Acanthophthalmus* and *Somileptes,* and *Misgurnus fossilis, M. mizolepis* and *Niwaella multifasciata* (Fig. 81 E, F, K, L). In a cobitine *Acanthophthalmus kuhli,* the first hypural is wholly fused with the parhypural (Fig. 81 K). The fourth group has three hypurals. It consists of *Niwaella delicata, Sabajenewia aurata vallachica* and *Acanthopsoides graciroides* of the subfamily Cobitinae (Fig. 81 G and I). In this group, the fourth hypural is wholly or partly fused to the fifth (Fig. 81 G and I). In a cobitine *Acanthopsoides graciroides,* the first hypural is wholly fused with the parhypural (Fig. 81 I). The last group has two hypurals, and is represented only by a cobitine *Misgurnus anguillicaudatus* in which the third to fifth are fused to each other to form a large plate (Fig. 81 D).

Parhypural (ph) is a triangular flat bone similar to the hypural in shape and basally has the parhypural foramen for the caudal artery and the hypurapophysis (hp) lying on the dorsal base of the bone. In fishes of the subfamilies Botiinae, Noemacheilinae and Homalopterinae, the hypurapophysis is
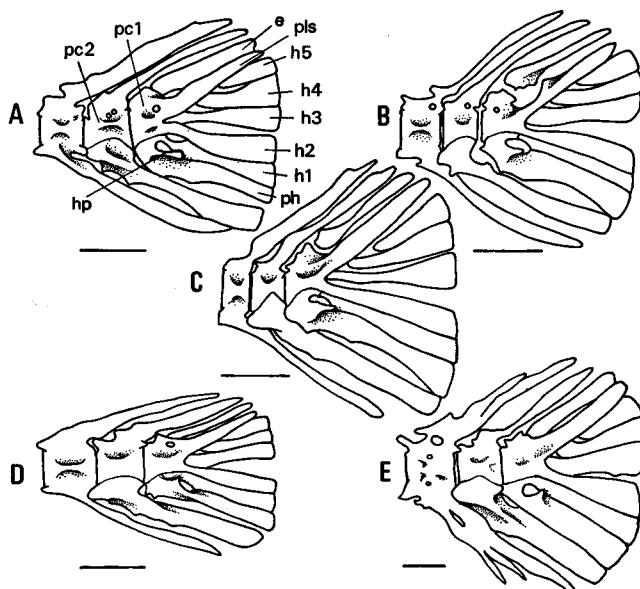
Fig. 83. Caudal complex in homalopterine fishes. A, *Homaloptera smithi*; B, *Hemimyzon formosanum*; C, *Sinogastromyzon puliensis*; D, *Annamia normani*; E, *Crossostoma lacustre*. For abbreviations, see Fig. 81. Scales indicate 1 mm.

well developed (Figs. 81 A-C, 82 and 83), while in the fishes of the subfamily Cobitinae, it is less developed or absent (Fig. 81 D-L). In the fishes of the subfamily Botiinae, Noemacheilinae and Homalopterinae, the bone is articulated with the first preural centrum (Figs. 81 A-C, 82 and 83), while in the fishes of the subfamily Cobitinae, it is fused with the centrum (Fig. 81 D-L).

Uroneurals (un), lying on the lateral side of the proximal part of the pleurostylar, are a pair of small rod-shaped bones (Fig. 81). In a botiine *Leptobotia curta*, the bones are present (Fig. 81 A), while in other cobitoid fishes examined, they are absent.

Epural (e) is a flat elongate bone which is lying between the last neural spine and the pleurostylar. In the fishes of the noemacheiline genus *Lefua*, the bone is absent (Fig. 82 A), while in other cobitoids examined, it is present.

The principal caudal rays include the branched rays plus two unbranched rays of the uppermost and lowermost parts of the fin. In the fishes of the subfamily Botiinae, the principal ray formula is constantly 10 (upper lobe)+9 (lower lobe) =19. In the fishes of the subfamily Cobitinae except *Sabajenewia aurata vallachica*, it is constantly 8+8=16, while 7+7=14 in *S. aurata vallachica*. In the fishes of the subfamilies Noemacheilinae and Homalopterinae, the formula is variable within the range from 11+9=20 to 7+8=15 (Table 21).

The procurrent rays are divided into two kinds of rays, segmented and unsegmented rays. In the fishes of the subfamily Botiinae, three or four segmented rays are laid on each extreme of the fin base, while in other cobitoid fishes examined, many unsegmented rays are present in form of segmented rays.

DISCUSSION

The caudal complex has been considered as one of the most important characters for finding out the fish interrelationships (Gosline, 1961; Nybelin, 1963; Monod, 1968). However, the examinations of the cobitoid caudal complex are still too meager to use for the reconstruction of cobitoid phylogeny.

Among cobitoid fishes examined here, differences are found in the number of hypurals, the relations between the parhypural and the first preural centrum, between the first hypural and the first preural centrum, between the first hypural and the parhypural, and between the last haemal spine and the second preural centrum, and the absence or presence of the epural and the absence or presence of the uroneural (Table 20).

On the basis of the combinations among conditions of the seven characters, the cobitoid caudal complex is divided into four morphotypes (Table 20).

Type A is represented only by *Leptobotia curta*, a member of the subfamily Botiinae. In this type, the parhypural is autogenous with the first preural centrum, the last haemal spine is autogenous with the second preural centrum, the first hypural is autogenous with the first preural centrum and fused with the parhypural, the peural and the uroneural are present, and the number of hypurals is six.

Type B which is distinguished from Type A by the absence of the uroneural includes the fishes of the subfamilies Botiinae except *Leptobotia curta*, Noemacheilinae except the genus *Lefua*, and Homalopterinae. Furthermore, this type is subdivided into five subtypes on the basis of the relation between the first hypural

Table 21. Frequency distribution of principal caudal ray formula in the family Homalopteridae.

Species	Principal ray formula									Total
	11+9=20	10+9=19	9+10=19	10+8=18	9+9=18	9+8=17	8+9=17	8+8=16	7+8=15	
Noemacheilinae										
Lefua echigonia								14		14
L. nikkonis							10			10
L. costata								3	5	8
Noemacheilus toni		1			14					15
N. postventralis					27		1			28
N. barbatulus					4					4
N. stoliczkai					22		3			25
N. pleurotaenia					1					1
N. botia					2					2
N. pulcher		1	1		24					26
N. masyae		1				1				2
N. savona					9		2			11
N. fasciolata		1								1
N. breviceps		20								20
N. fowlerianus		12			2					14
N. rupecula						9		2		11
N. angorae jordanicus		3								3
N. tigris		3								3
N. pantera		2			2					4
N. evezardi				1	1			1		3
N. fasciatus		1								1
Vaillantella euepiptera		1								1
Homalopterinae										
Homaloptera smithi		13					1	1		15
Hemimyzon formosanum		15								15
Sinogastromyzon puliensis		1								1
Annamia normani							5	1		6
Crossostoma lacustre						15				15

and the parhypural, and the number of hypurals. The first subtype, Subtype a, is characterized in having five hypurals and the first hypural separated from the parhypural, and includes the fishes of the subfamily Noemacheilinae such as *Noemacheilus toni*, *N. barbatulus*, *N. pleurotaenia*, *N. evezardi* and *N. breviceps*, and the fishes of the subfamily Homalopterinae such as *Hemimyzon formosanum*, *Sinogastromyzon puliensis* and *Annamia normani*. The second subtype, Subtype b, which is represented by *Noemacheilus fowlerianus*, *N. botia*, *N. masyae* and *N. abyssinicus* of the subfamily Noemacheilinae, *Homaloptera smithi* and *Crossostoma lacustre* of the subfamily Homalopterinae, differs from Subtype a only by the fusion of the first hypural with the parhypural. The third subtype, Subtype c, including a noemacheiline *Noemacheilus stoliczkai*, is different from Subtype a in having six hypurals. The fourth subtype, Subtype d, is distinguished from Subtype a in having the basal fusion between the first hypural and the parhypural. This subtype is composed of the fishes of the subfamily Botiinae except *Leptobotia curta*, and the fishes of the subfamily Noemacheilinae such as *Noemacheilus postventralis*, *N. pulcher*, *N. savona*, *N. fasciolata*, *N. rupecula*, *N. angorae jordanicus*, *N. tigris*, *N. pantera*, *N. fasciatus* and *Vaillantella euepiptera*.

Type C includes the fishes of the subfamily Cobitinae. In this type, the parhypural is fused with the first hypural and the first preural centrum, the first hypural is fused with the first preural centrum, the last haemal spine is fused with the second preural centrum, the epural is present and the uroneural is present. According to the number of hypurals, this type is subdivided into four subtypes. The first subtype, Subtype e, having two hypurals, includes *Misgurnus anguillicaudatus*. The second subtype, Subtype f, having four hypurals, includes the fishes of the genera *Cobitis*, *Acanthopsis*, *Acanthophthalmus* and *Somileptes*, *Niwaella multifasciata*, *Misgurnus fossilis* and *M. mizolepis*. The third subtype, Subtype g, having three hypurals, includes *Niwaella delicata*, *Sabajenewia aurata vallachica* and *Acanthopsoides graciroides*. The fourth subtype, Subtype h, having five hypurals, is represented by *Lepidocephalus guntea*.

Type D, consisting of the fishes of the noemacheiline genus *Lefua*, differs from Subtype a of Type B in lacking the epural.

In order to judge the most primitive cobitoid conditions of these seven characters on the basis of the criterion proposed in the present study (Fig. 84), the conditions of these characters found in other cyprinoid fishes are described below. In group (B) (see Gosline, 1961; Lo and Wu, 1979; Eastman, 1980), there are almost six hypurals or rarely five in *Hypenthelium nigricans* and *Carpiodes carpio* (personal observations), the first hypural is autogenous with the first preural centrum, and usually fused with the parhypural or rarely separated from it in *Hypenthelium nigricans* (personal observations), the parhypural is autogenous with the first preural centrum, the last haemal spine is autogenous with the second preural centrum, and the epural and the uroneural are present. On the other hand, in group (C) (see Ramaswami, 1952b; Gosline, 1961; Monod, 1968; Lundberg and Baskin, 1969; Buhan, 1972; Dixit and Bisht, 1972b; Howes, 1978, 1979, 1980; Wu et al., 1979), there are five or six hypurals, the first hypural is autogenous with the first preural centrum, the parhypural is usually fused with the first hypural with an exception of a cyprinid *Gobiobotia brevibarba* (personal observations), the parhypural is autogenous with the first preural centrum, the last haemal spine is

usually autogenous with the second preural centrum with some exceptions in some American cyprinids (Buhan, 1972), the epural is always present, and the uroneural is often absent.

According to the criterion for the determination of the polarity, the most primitive conditions of these characters in group (A) are determined as follows (Fig. 84): the first hypural is autogenous with the first preural centrum, the parhypural

		A	B	C
1.	Hypurals	2 - 6	5, 6	5, 6
2.	Parhypural and 1st hypural	autogenous fused	autogenous fused	autogenous fused
3.	Parhypural and 1st preural centrum	autogenous fused	autogenous	autogenous fused
4.	1st hypural and 1st preural centrum	autogenous fused	autogenous	autogenous
5.	2nd preural centrum and its haemal spine	autogenous fused	autogenous	autogenous fused
6.	Uroneural	present absent	present	present absent
7.	Epural	present absent	present	present

1. ?
2. ?
3. autogenous
4. autogenous
5. autogenous
6. present
7. present
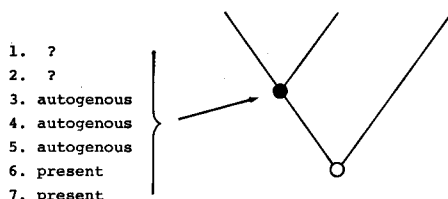
Fig. 84. Character analysis of the cobitoid caudal complex. The most primitive conditions of seven characters in group (A) are shown as the conditions of the common ancestor (●) of groups (A) and (B).

is autogenous with the first preural centrum, the last haemal spine is autogenous with the second preural centrum, the epural and the uroneural are present. However, the most primitive conditions of the number of hypurals and the relation between the first hypural and the parhypural are undeterminable, because the conditions of these characters shared by the three groups are identical (Fig. 84). Thus, the aspects of morphoclines shown in five except these two characters are considered as below. The relations between the first hypural and the first preural centrum, between the parhypural and the first preural centrum, and between the last haemal spine and the second preural centrum are advanced from separate to fused. The epural and the uroneural are advanced from present to absent.

On the basis of these five morphoclines, the relationships among four morphotypes (A, B, C and D) (Table 20) are shown as the evolutionary trend of the cobitoid caudal complex (Fig. 85) (The subdivision of type shown in Table 20 is meaningless here, because their polarities can not be determined).

In the cobitoid caudal complex, the first step of the evolutionary trend is that the uroneural disappears (Fig. 85: A→B). In the next step of the trend, the first hypural and the parhypural are fused with the second preural centrum
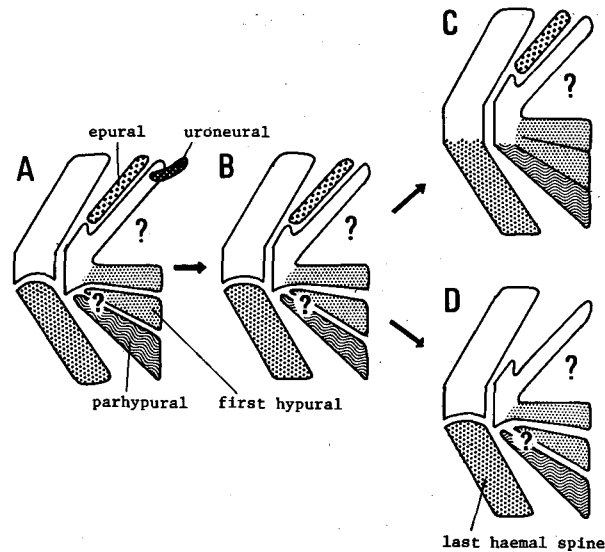
Fig. 85. Evolutionary trends of the cobitoid caudal complex. For explanations, see text.

on the one hand (Fig. 85: B→C), or the epural disappears on the other hand
(Fig. 85: B→D).

Thus, this evolutionary trend displays a progressive reduction in the number
of elements, and hence it well agrees with Gosline's conclusion (1961). However,
the pattern of the disappearance of each element (fusion or loss) has been
rather loosely identified in many cases. Thus, the author attempts to show
it from the ontogenetic view points.

The disappearance of uroneurals consisting of the anterior and posterior sets
has been explained in terms of the fusion with the other caudal elements or between
themselves (Gosline, 1960; Patterson, 1968a). However, the ontogeny of the
caudal complex in two cobitoid fishes lacking the two sets of uroneurals in adult,

Fig. 86. Ontogenetic development of
caudal complex in two cobitoid
fishes, *Misgurnus anguillicaudatus*
(A and B) and *Lefua echigonia* (C
and D). A, 14.7 mm TL; B, 21.3
mm TL; C, 10.6 mm TL; D, 15.9
mm TL. Dotted parts are carti-
laginous, but open parts, ossified.
e, equral; pls, pleurostylar; un 1,
anterior uroneural. Scale indicates
0.2 mm.
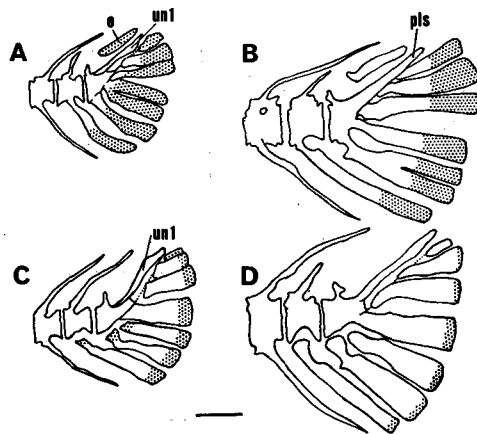
Misgurnus anguillicaudatus and *Lefua echigonia*, shows that the posterior uroneural (un in Fig. 81 A) never occurs during all ontogenetic stages, although the anterior one is fused with the first preural centrum to form the pleurostylar (Fig. 86 B and D). Therefore, contrary to Patterson's (1968a) and Gosline's (1960) conclusions, it is probable that the disappearance of the cobitoid posterior uroneural results from the loss rather than the fusion.

With regard to the number of epurals, it has been considered that there is a progressive reduction in number (Patterson, 1968a). However, there are little reports on the pattern of the disappearance of epurals except for some explanations based on the fusion (Patterson, 1968b; Rosen and Patterson, 1969). From the ontogenetic evidences of the caudal complex, it is presumed that the disappearance of the bone is due to the loss in the superfamily Cobitoidea (Fig. 86 C and D).

VI. Phylogeny of the superfamily Cobitoidea

1. BRANCHING PATTERN OF THE SUPERFAMILY COBITOIDEA

In this section, on the basis of the characters analyzed in the preceding chapter, the branching pattern of species or subspecies examined is reconstructed. In the present study, as stated in the chapter IV, the reconstruction of the branching pattern is made according to the two major principles: 1) the principle of synapomorphy proposed by Hennig (1966) and 2) the principle of parsimony of Nelson (1970).

The conditions of 52 characters already evaluated on 48 species or subspecies examined are shown in Fig. 87. Hennig (1966) states that the greater the number of autapomorphous features that can be demonstrated is, the greater the certainty that the group is monophyletic becomes. Following to this statement, Fig. 88 is demonstrated. In Fig. 88, it is shown that 48 species or subspecies examined here constitute a single large group. The monophyly of this group which will be provisionally called here group (A) is corroborated by four autapomorphous features: the opisthotic is absent (23), the orbitosphenoid has the contact with the supraethmoid-ethmoid complex (24), the basibranchial series is backward shifted relative to the paired elements (26), and the ossified second preethmoid is present (52).

At the branching point a_1, this monophyletic group can be divided into two smaller monophyletic groups (AA) and (AB). Group (AA) is supported by two autapomorphous features: the lateral ethmoid is movable (6) and the articulation between the supraethmoid-ethmoid complex and the frontals is socket-like (7), while group (AB) is based on three autapomorphous features: the tripus is Y-shaped (38), the second descending process forms a part of the gasbladder capsule (39), and the osseous capsule is laterally subdivided (42).

At the branching point a_2, group (AA) is differentiated into two monophyletic groups (AAa) and (AAb) which are considered to be sister groups. The monophyly of group (AAa) is corroborated by two autapomorphous features: the sesamoid bone is present (3), and the parietal is separated from the sphenotic (18). Furthermore, four features, although they occurs as the parallelism in other lineages (Figs. 87 and 88), are considered to be synapomorphy for the group: the presence

of the prepalatine (4), the absence of the preethmoid (5), the absence of the deep subtemporal fossa (12) and the prevomer fusing with the supraethmoid-ethmoid complex (22).   On the other hand, the monophyly of group (AAb) is corroborated by many autapomorphous features such as the absence of the coronomeckelian (2), the orbitosphenoid separated from the pterosphenoid (15), the rod-shaped entopterygoid (29), the reduced cleithrum (32), the parapophysis fused with the ventral side of the centrum (46), the parhypural fused with the first preural centrum (47), the first hypural fused with the first preural centrun (48), and the second preural centrum fused with its haemal spine (49).   The group also shares many derived character states regarded as synapomorphy, although they are found in a part of other lineages (Figs. 87 and 88): the absence of the preethmoid (5), the absence of the deep subtemporal fossa (12), the prevomer fused with the supraethmoid-ethmoid complex (22), four basibranchials (27), the absence of the supratemporal (33), the absence of the postcleithrum (35), three pectoral radials (36), the fourth horizontal process forming the posterior surface of capsule (41) and the absence of the uroneural (50).

At the branching point a_3, group (AB) is differentiated into two smaller groups (ABa) and (ABb).   In Fig. 88, there is no autapomorphous feature showing that the former group (ABa) is monophyletic.   However, three features, which are also found in other lineages, rather loosely support the monophyly of the group: the presence of the prepalatine (4), the absence of the deep subtemporal fossa (12), and the absence of the posterior uroneural (50).   Because of the weakness of evidences supporting the monophyly of the group, there may be a critique to this treatment: group (ABa) is the ancestor of group (ABb) and hence to regard both group as sister groups is cladistically invalid.   In such case, all features that the fishes of group (ABa) share have to be primitive for those of group (ABb).   However, this critique is rejected, since all members examined of group (ABa) share the derived conditions of three characters (4), (12) and (50).   Thus, the monophyly of group (ABa) is retained. On the other hand, the fishes of group (ABb) are considered to constitute a mono-phyletic group because of the common possession of six autapomorphous features: the exoccipital is separated from its fellow (21), the interhyal is absent (25), the cleithrum is enlarged (32), the mesocoracoid is proximally fused with the lateral side of the cleithrum (37), the pelvic bone is enlarged (43) and the enlarged pleural rib is present (45) (Fig. 88).   Furthermore, all members examined of the group commonly possess the derived conditions of two characters: the fourth horizontal process forming a part of capsule (41) and the absence of the uroneural (50), although both features also occur in other lineages.

From this branching pattern, the groups corroborated above are cladistically ranked.   In the present study, in order to minimize the taxonomic confusion (see, Berg, 1940; Ramaswami, 1953), it seems to be reasonable that groups (AAa), (AAb), (ABa) and (ABb) are ranked as the subfamily.   Group (AAa) will be named here as the subfamily Botiinae; (AAb), as the subfamily Cobitinae; (ABa), as the subfamily Noemacheilinae; (ABb), as the subfamily Homalopterinae.   When the rank of these groups is determined, each of two monophyletic sister groups (AA) and (AB) from which these four subfamilies are branched will be necessarily ranked as the family.   Both groups will be called the families Cobitidae (AA) and Homalopteridae (AB).   Then, a large monophyletic group (A) from which two families are bran-
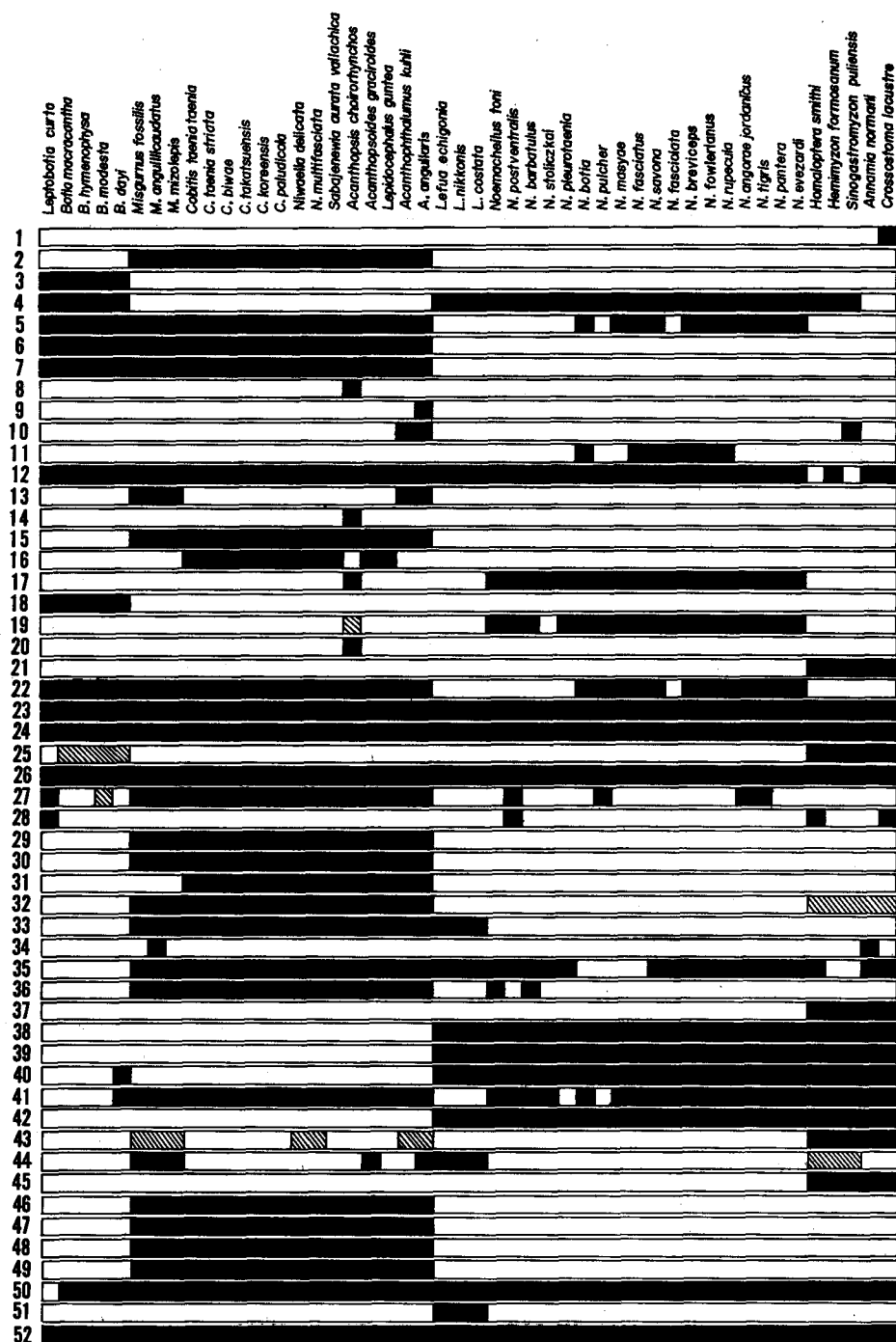
Fig. 87
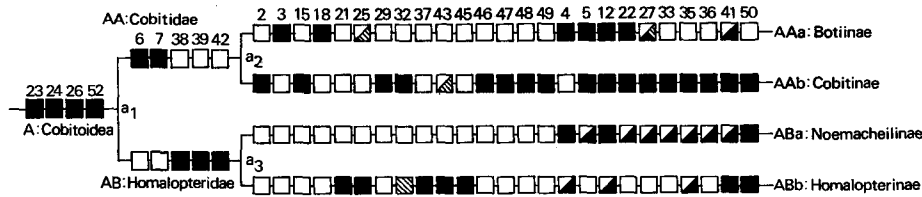
Fig. 88.   Branching pattern of the superfamily Cobitoidea.   For explanations, see text.

ched is considered to be ranked as the superfamily which will be named as the superfamily Cobitoidea.

As a result, new taxonomic treatments derived from the present branching pattern are summarized as follows. (1) The subfamily Noemacheilinae is transferred from the family Cobitidae to the family Homalopteridae. (2) The fishes of the families Homalopteridae and Gastromyzonidae in Hora's sense (1950) are included in a single subfamily, Homalopterinae, of the family Homalopteridae in the present study. (3) The family Homalopteridae in the present study forms the superfamily Cobitoidea with the family Cobitidae, although it has been traditionally believed as the independent family in the suborder Cyprinoidei except cases of Nichols (1938, 1943) who has included the fishes of Hora's families in the family Cobitidae (see, Hensel, 1970).

Fig.87.   The summary of the character conditions of 48 species or subspecies of the superfamily Cobitoidea. Open parts indicate the most primitive conditions of characters; solid black, the most derived condition.   The oblique stripes except a case of the character 25 indicate another condition derived from the most primitive condition. 1. premaxillary; 2, coronomeckelian; 3, sesamoid bone; 4, prepalatine; 5, preethmoid; 6, the movability of lateral ethmoid; 7, the articulation between supraethmoid-ethmoid complex and frontals; 8, frontal; 9, epiotic; 10, fronto-parietal fontanelle; 11, parietal-pterotic bridge; 12, deep subtemporal fossa; 13, the connection between frontal and parasphenoid; 14, the connection between pterosphenoid and pterotic; 15, the connection between orbitosphenoid and pterosphenoid; 16, the connection between pterosphenoid and prootic; 17, the connection between parietal and pterotic; 18, the connection between parietal and sphenotic 19, the connection between sphenotic and epiotic; 20, the connection between sphenotic and supraoccipital; 21, the connection between both exoccipitals; 22, the relation between prevomer and supraethmoid-ethmoid complex; 23, opisthotic; 24, the connection between orbitosphenoid and supraethmoid-ethmoid complex; 25, interhyal; 26, the relation between basibranchial series and paired elements; 27, basibranchials; 28, fourth hypobranchial; 29, the shape of entopterygoid; 30, the shape of opercle; 31, metapterygoid-quadrate fenestra; 32, the shape of cleithrum; 33, supratemporal; 34, posttemporal; 35, postcleithrum; 36, pectoral radials; 37, the relation between mesocoracoid and cleithrum; 38, the shape of tripus; 39, 2nd descending process forming a part of capsule; 40, 2nd horizontal process forming a part of capsule; 41, 4th horizontal process forming the posterior surface of capsule; 42, subdivided capsule; 43, the shape of pelvic bone; 44, pelvic radials; 45, enlarged pleural rib; 46, the relation between parapophysis and centrum; 47, the relation between parhypural and 1st preural centrum; 48, the relation between first hypural and first preural centrum; 49, the relation between second preural centrum and its haemal spine; 50, posterior uroneural; 51, epural; 52, ossified second preethmoid.

In the following sections, the branching patterns of the subfamilies of both families are reconstructed.

A. FAMILY COBITIDAE

a) Subfamily Botiinae

Characters concerned in the branching pattern of the subfamily are summarized in Fig. 89 A. Fig. 89 B is reconstructed from Fig. 89 A.

At the branching point b_1, the subfamily is differentiated into two monophyletic groups. Both groups well agree with the categories of the taxonomic units previously used, the genera *Leptobotia* and *Botia* (Nalbant, 1963). The monophyly of the genus *Leptobotia* is corroborated by two derived features: four basibranchials (27) and the presence of the fourth hypobranchial (28). On the other hand, the genus *Botia* is considered monophyletic because of the common possession of two derived features: the much reduced interhyal (25) and the absence of the uroneural (50).

The interrelationships among *Botia macracantha*, *B. hymenophysa*, *B. modesta* and *B. dayi* will be estimated. Fang (1936) divided the genus *Botia* into three subgenera, *Hymenophysa*, *Botia* and *Sinibotia*. According to his classification, among four species of the genus *Botia* examined here, *B. hymenophysa* and *B. modesta* belong to the subgenus *Hymenophysa*, while *B. macracantha* and *B. dayi* belong to the subgenus *Botia*. However, Taki (1972) pointed out that the relationships of *B. macracantha* to the subgenus *Botia* is problematical. Fang (1936) defined the subgenus *Botia* on the basis of only two species, *Botia macracantha* and *B. almorhae*. However, from his extensive examinations of fishes of the genus *Botia*, Taki (1972) stated that *B. macracantha* is distinguished from other members of the subgenus *Botia* in having the large fontanelle and less-developed gasbladder capsule. Based on these features and the distributional range of *B. macracantha* greatly separated from those of other members of the subgenus, he emphasized that *B. macracantha* occupies the peculiar phylogenetic position different from the subgenus. Thus, he concluded that these evidences seem to justify the erection of a new taxon for *B. macracantha*. In 52 characters examined here, however, there is no derived feature supporting such taxonomic treatment. On the other hand, from the similarity in the fontanelle and the gasbladder capsule, he suggested that *B.*

Fig. 89. Branching pattern of the subfamily Botiinae of the family Cobitidae. A, the summary of character conditions of five species of the subfamily; B, the branching pattern reconstructed from A.
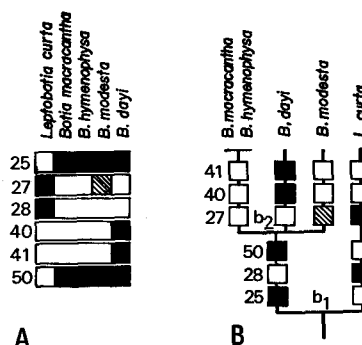
macracantha is closely related to the subgenus *Hymenophysa* than to the subgenus *Botia*, notwithstanding he stated that the similarity of the species to the subgenus *Botia* in the structure of mental lobe cannot be ignored. But, the relationships between *Botia macracantha* and the subgenus *Hymenophysa* can not be estimated.

On the other hand, Taki (1972) classified fishes of the subgenus *Hymenophysa* into two species-groups, *hymenophysa*-group and *modesta*-group. However, there is no synapomorphous feature indicating that the subgenus *Hymenophysa* including both species-groups is monophyletic in 52 characters examined here.

Consequently, the interrelationships among four species of the genus *Botia* cannot be estimated. Therefore, the branching point b_2 is recognized as trichotomy.


b) Subfamily Cobitinae

Characters concerned in the branching pattern of the subfamily are summarized in Fig. 90. Fig. 91 is reconstructed from Fig. 90. The present branching pattern is considered to be the most parsimonious, although parallelisms in three characters occur, the metapterygoid-quadrate fenestra (31), the shape of the pelvic bone (43) and the number of the pelvic radials (44).

At the branching point c_1, two monophyletic groups are differentiated. One of them includes the fishes of the genera *Misgurnus* and *Acanthophthalmus*, while the other consists of the fishes of the genera *Niwaella, Cobitis, Sabajenewia, Lepidocephalus, Acanthopsoides* and *Acanthopsis*. The monophyly of the former group is corroborated by two derived features: the frontal has the contact with the parasphenoid (13) and the pelvic bone is much reduced (43), while the monophyly of the latter is supported by a derived feature, the presence of the metapterygoid-quadrate fenestra (31). However, among three features corroborating both groups, the same derived conditions of two characters, the metapterygoid-quadrate fenestra and the shape of the pelvic bone, occur as parallelism in different lineages of the subfamily.

At the branching point c_2, two groups regarded as sister groups are differentiated. One of them is considered monophyletic based on a derived feature, two pelvic radials (44), although the parallelism for this character occurs in other lineages. On the other hand, the monophyly of the other depends upon two derived features: the fronto-parietal fontanelle is absent (10) and the metapterygoid-quadrate fenestra is present (31). The category of the former group agrees with the genus *Misgurnus*, while that of the latter, with the genus *Acanthophthalmus* in Nalbant's (1963) sense. Myers (1927) established the genus *Cobitophis* for *Acanthophthalmus anguillaris* because of its extremely attenuated anguilliform body. As far as 52 characters examined here are concerned, however, there is no cladistic evidence supporting the erection of *Cobitophis* as the rank of the genus, because both taxa are not sister groups. In this lineage, especially noteworthy may be the phylogenetic position of the genus *Acanthophthalmus* in the subfamily. On the basis of the absence or presence of the epiotic and the subtemporal fossa, Ramaswami (1953) classified the genera of the subfamily Cobitinae into two groups: *Acanthopsis-Lepidocephalichthys-Acanthophthalmus* group and *Cobitis-Somileptes-Misgurnus* group, and concluded that *Acanthophthalmus pangia* is closely related to *Acanthopsis choirorhynchos* and *Lepidocephalichthys guntea* (=*Lepidocephalus guntea* in the

present study). In the former group of Ramaswami's classification, Nalbant (1963) added *Acanthopsoides*, *Paralepidocephalus* and *Eucirrichthys* because of the absence of the epiotic and the subtemporal fossa. Among five examined species regarded to be closely related to *Acanthophthalmus pangia*, however, *Acanthopsis choirorhynchos*, *Lepidocephalus guntea* and *Acanthopsoides graciroides* have the well-developed epiotic in contrast with Ramaswami's and Nalbant's descriptions (Figs. 12 and 13). On the other hand, the fishes of the genera *Paralepidocephalus* and *Eucirrichthys* regarded to lack the epiotic by Nalbant (1963) have never been examined by anybody. Also, the presence or absence of the subtemporal fossa, an important character for Ramaswami's classification, is too indistinct a character to classify the fishes of the subfamily Cobitinae (Figs. 11–13). Thus, the two evidences to justify that the group including *Acanthophthalmus pangia* established by Ramaswami (1953) and Nalbant (1963) is monophyletic become meaningless. To the contrary, the present branching pattern showed that the fishes of the genus *Acanthophthalmus* is closely related to the fishes of the genus *Misgurnus* (Fig. 91). This conclusion is based on two synapomorphous features: the frontal has the contact with the parasphenoid (13), and the pelvic bone is much reduced (43).

At the branching point c_3, two monophyletic groups are differentiated. One of them, corresponding to the generally used genus *Acanthopsis*, is recognized to
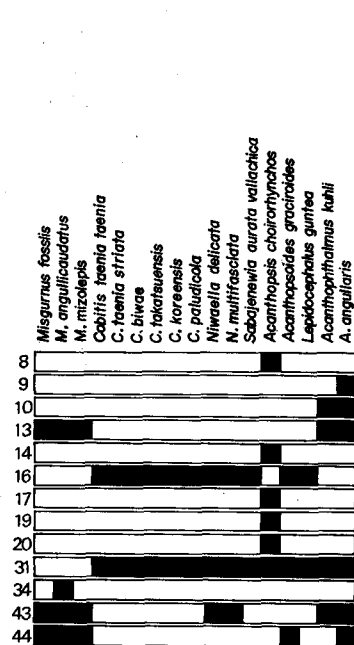
Fig. 90. Summary of character conditions of 17 species or subspecies of the subfamily Cobitinae of the family Cobitidae.
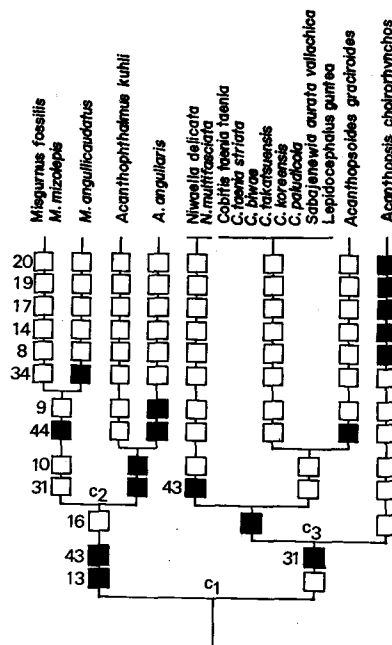
Fig. 91. The most parsimonious branching pattern of the subfamily Cobitinae of the family Cobitidae reconstructed from Fig. 90.

be monophyletic because of the possession of five autapomorphous features: the frontal is fused with its fellow (8), the pterosphenoid has the contact with the pterotic (14), the parietal is separated from the pterotic (17), the sphenotic has the contact with the epiotic (19), and the sphenotic has the contact with the supraoccipital (20). On the other hand, the monophyly of the other is corroborated by an autapomorphous feature: the pterosphenoid is separated from the prootic (16). In this group, the fishes of five generally used genera *Cobitis*, *Sabajenewia*, *Lepidocephalus*, *Niwaella* and *Acanthopsoides* are included. From the cladistic point of view, the monophyly of the group seems to justify to establish a new taxon of the generic rank as a sister group of the genus *Acanthopsis*. However, such systematic treatment should be made after the examinations of several external features by which the genera *Cobitis*, *Sabajenewia*, *Lepidocephalus*, *Niwaella* and *Acanthopsoides* are defined are analyzed.

B. Family Homalopteridae

a) Subfamily Noemacheilinae

Characters concerned in the branching pattern of the subfamily are summarized in Fig. 92. Figs. 93 and 94 are reconstructed from Fig. 92.

At the branching point d_1, two monophyletic groups, constituting sister groups, are differentiated. One of them is considered monophyletic on the basis of four synapomorphous features: the absence of the supratemporal (33), the absence of the postcleithrum (35) (this feature occurs as the parallelism in other lineages), two pelvic radials (44) and the absence of the epural (51). This group corresponds to the generally used genus *Lefua*. On the other hand, the monophyly of the other is corroborated by a synapomorphous feature: the parietal is not connected to the pterotic (17). This group agrees with the category of the genus *Noemacheilus** in

Fig. 92.   Summary of character conditions of 21 species or subspecies of the subfamily Noemacheilinae of the family Homalopteridae.

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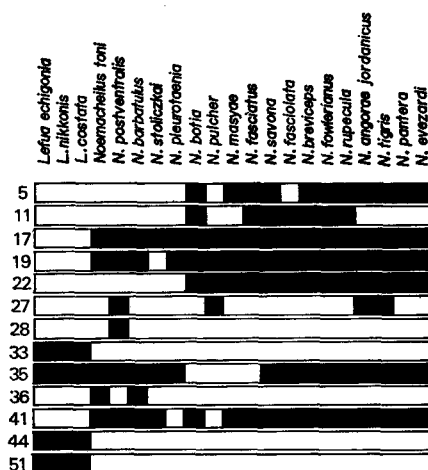
* The present author uses the name *Noemacheilus* instead of *Barbatula* according to Rendahl (1933b) and Berg (1949).

the most general sense.   It is said that this large group consists of more than 100
species or subspecies.   Many authors have tried to divide this genus into several
genera or subgenera (see Banarescu and Nalbant, 1964, 1966, 1968, 1974, 1976).
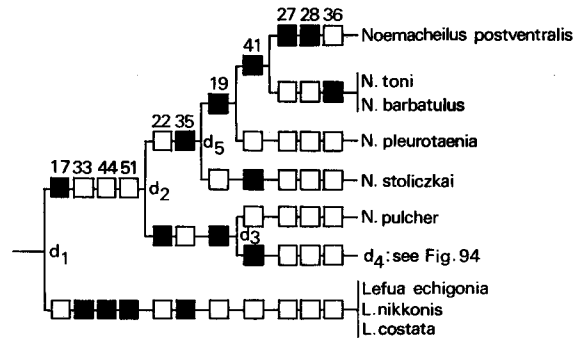
Fig. 93.   The most parsimonious branching pattern of the subfamily Noemacheilinae
      reconstructed from Fig. 92.
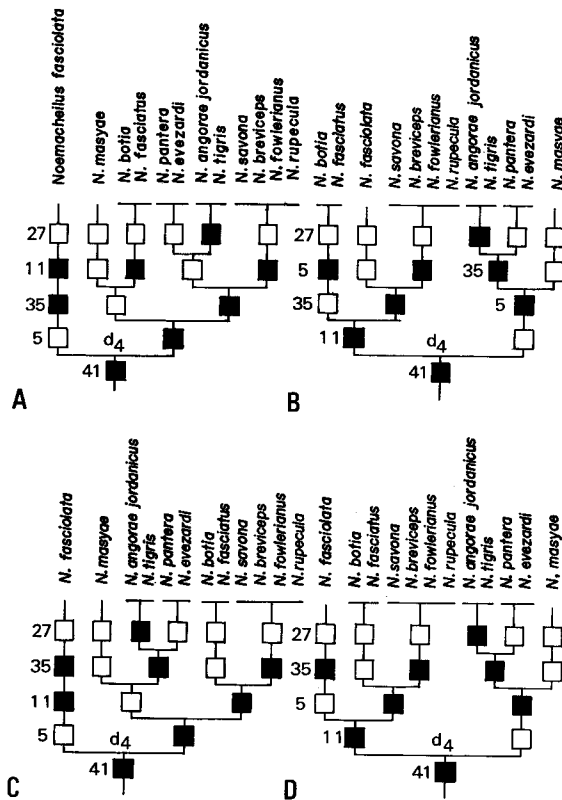
Fig. 94.   Four alternative hypotheses of the most parsimonious branching pattern among
      12 species or subspecies of the subfamily Noemacheilinae.

However, the present branching pattern of the subfamily based on 52 osteological characters cannot provide any evidence to justify such taxonomic subdivision.

Regarding the relationships among *Noemacheilus botia*, *N. fasciolata*, *N. masyae*, *N. fasciatus*, *N. pantera*, *N. angorae jordanicus*, *N. tigris*, *N. savona*, *N. breviceps*, *N. fowlerianus*, *N. rupecula* and *N. evezardi*, four alternative hypotheses (Fig. 94 A-D) are established according to the different combinations among three characters: the presence or absence of the preethmoid (5), the presence or absence of the parietal-pterotic bridge (11), and the presence or absence of the postcleithrum (35) (Fig. 94).   Four hypotheses cannot be rejected by any criterion adopted by the present study, because each of them is considered to be equally the most parsimonious.

The present branching pattern of the subfamily provides some clues to elucidate several phylogenetic problems within the subfamily.

1)   The relationships between *Noemacheilus evezardi* and the fishes of the genus *Lefua*.

Banarescu and Nalbant (1968) proposed the close affinity between *N. evezardi* and the fishes of the genus *Lefua* from the similarity in the length of nasal tube, the shape of body, the structure of lips and the shape and disposition of scales. Among the similarities emphasized by them, the length of nasal tube seems to be the most important evidence for their conclusion.   However, Hora (1935) indicated that in the length of nasal tube there is a continuous gradation between the very short tubes of normal noemacheilines and the very long one of *N. evezardi*.   As shown in Fig. 92, the osteological features of *N. evezardi* is too different from those of the fishes of the genus *Lefua* to justify the close affinity among them.   Thus, it is concluded that the external similarities between them result from the parallelism.

2)   The phylogenetic position of the genus *Vaillantella*.

The genus *Vaillantella* has been traditionally considered as an independent genus of the subfamily Noemacheilinae (Weber and Beaufort, 1916).   However, the phylogenetic position of the genus has been problematical (Nalbant and Banarescu, 1977).   In the present study, it will be descussed comparing eight characters which are peculiar to the subfamilies Botiinae and Noemacheilinae (Table

Table 22.   Comparison of several osteological characters among *Vaillantella*, Botiinae and Noemacheilinae.

Character	*Vaillantella*	Botiinae	Noemacheilinae
3. Sesamoid bone	absent	present	absent
6. Movability of lateral ethmoid	absent	present	absent
7. Articulation between supraethmoid-ethmoid complex and frontals	not socket-like	socket-like	not socket-like
18. Connection between parietal and sphenotic	?	absent	present
38. Tripus	?	triangular	Y-shaped
39. 2nd descending process forming a part of capsule	present	absent	present
40. 2nd horizontal process forming a part of capsule	present	present or absent	present
42. Subdivided capsule	absent	absent	present

22) with those from radiographs of a syntype material (RMNH 7782) of *V. euepiptera* because of the limited materials deposited in museums of the world.

Nalbant and Banarescu (1977) pointed out that the genus *Vaillantella* differs from all other noemacheilines in having the incomplete osseous capsule, and then erected the new subfamily Vaillantellinae for the genus. Furthermore, regarding the interrelationships of the subfamily, they stated that the subfamily is similar to the subfamily Botiinae in having the incomplete ossified capsule while the former is evidently closer to the subfamily Noemacheilinae in lacking the movable lateral ethmoid. Thus, they concluded that the subfamily Vaillantellinae is placed in the intermediate phylogenetic position between the subfamilies Botiinae and Noemacheilinae.
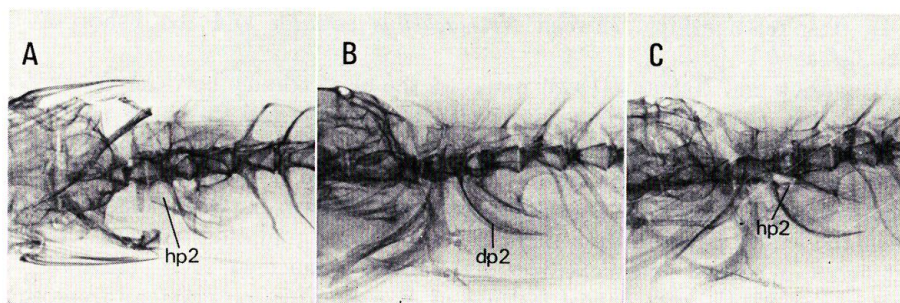
Fig. 95. Three radiographs of the gasbladder capsule of a noemacheiline *Vaillantella euepiptera*. A, ventral view; B, ventrolateral view; C, dorsolateral view. dp, 2, second descending process; hp 2, second horizontal process.

Fig. 96. Comparison of *Vaillantella* with the subfamilies Botiinae and Noemacheilinae in several characters. For explanations, see text.

However, concerning eight observable characters, the genus *Vaillantella* does not share any synapomorphous features with the subfamily Botiinae. The incomplete osseous capsule, which is regarded as the evidence for the close affinity of the genus *Vaillantella* to the subfamily Botiinae, is plesiomorphous feature. On the other hand, the genus shares a synapomorphous feature (Character 39: 2nd descending process forming a part of the capsule) with the subfamily Noemacheilinae (Figs. 95 and 96; Table 22). These facts seem to suggest that there is no distinct difference to be separable the genus *Vaillantella* from all other noemacheilines for the erection of the subfamily Vaillantellinae, and that there is no evidence to justify the close relationships between the genus *Vaillantella* and the subfamily Botiinae in spite of Nalbant and Banarescu's (1977) suggestion. Thus, it is

considered that the establishment of the subfamily Vaillantellinae is questionable. Furthermore, this leads us to a conclusion that the genus *Vaillantella* is recognized to be a member of the subfamily Noemacheilinae and hence the phylogenetic position of the genus suggested by Nalbant and Banarescu (1977) is invalid.

3) The phylogenetic position of *Noemacheilus abyssinicus* within the subfamily.

Noemacheilus abyssinicus which is an outstanding feature of the ichthyofauna of Nile drainage basin is the only known African representative of the subfamily (Boulenger, 1907). In spite of interests of several authors (e.g. Greenwood, 1976), the phylogenetic position of the species within the subfamily is unknown. This may be a result of the rarity of the species. The only known specimen of the species is the holotype. Accordingly, in the present study, the relationships of the species will be found out on the basis of radiographs of the holotype (BMNH 1902. 12.13: 435). Among 16 characters used in the reconstruction of the branching pattern of the subfamily, seven characters are observable from radiographs of the specimen: the prepalatine is present (4), the preethmoid is absent (5), the parietal-pterotic bridge is absent (11), the deep subtemporal fossa is absent (12), the postcleithrum is absent (35), the uroneural is absent (50) and the epural is present (51). Among them, excluding three derived features (4), (12) and (50) which characterizes the subfamily as a whole, remaining two derived ones (5) and (35) are important in order to find out the relationships of the species. Consequently, compared with those of all other members examined here of the subfamily, these two features of the species indicate the close affinity with three West Asian species, *Noemacheilus angorae jordanicus*, *N. pantera* and *N. tigris*, and an Indian species *N. evezardi*.
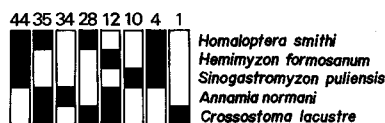
Fig. 97. Summary of the character conditions of five species of the subfamily
Homalopterinae of the family Homalopteridae.

d) Subfamily Homalopterinae

Characters concerned in the branching pattern of the subfamily are summarized in Fig. 97. Fig. 98 is reconstructed from Fig. 97.

At the branching point e_1, two monophyletic groups are differentiated. One of them, consisting of *Homaloptera smithi*, *Hemimyzon formosanum* and *Sinogastromyzon pulinesis*, is considered to be monophyletic because of the common possession of two derived features: the prepalatine is present (4) and the number of pelvic radials is more than three (44). Three alternative relationships among *H. smithi*, *H. formosanum* and *S. puliensis*, which are considered to be equally the most parsimonious, can be reconstructed on the basis of three characters (10), (12) and (35). On the other hand, the monophyly of the other including *Annamia normani* and *Crossostoma lacustre* is corroborated by two synapomorphous features: the
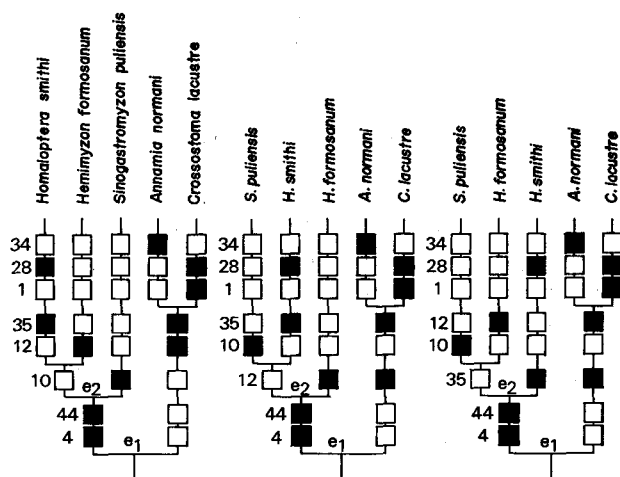
Fig. 98. Three possible branching pattern of the subfamily Homalopterinae reconstructed from Fig. 98.

deep subtemporal fossa is absent (12) and the postcleithrum is absent (35), although both features occur in the former group as the parallelism. The category of both groups well agrees with Hora's (1932) classification of hill stream loaches on the basis of the paired fin rays. This may be justify the subdivision of the subfamily like those made by several authors (Hora, 1932; Ramaswami, 1952c, 1952d; Silas, 1952; Chen, 1980).

In conclusion, the branching pattern of the superfamily Cobitoidea is summarized in Fig. 99. From this branching pattern, the phylogenetic classification of the superfamily may take the following form.

Superfamily Cobitoidea
    Family Cobitidae
        Subfamily Botiinae
        Subfamily Cobitinae
    Family Homalopteridae
        Subfamily Noemacheilinae
        Subfamily Homalopterinae

2. EVOLUTIONARY PROCESS IN THE MODE OF LIFE OF SUPERFAMILY COBITOIDEA

The evolutionary process in the mode of life of a given group provide a basis for finding out the change of the adaptive zone which has brought about the divergence of the group. This process has been generally considered to be necessarily involved in the phylogenetic branching of the group. However, the cladistics has rather neglected inferring this process in the mode of life, and hence has been critisized by its opponents (e.g. Mayr, 1976). Even in the cladistic approach, however, the process can be estimated if the mode of life of the hypothetical ancestors within the branching pattern reconstructed is
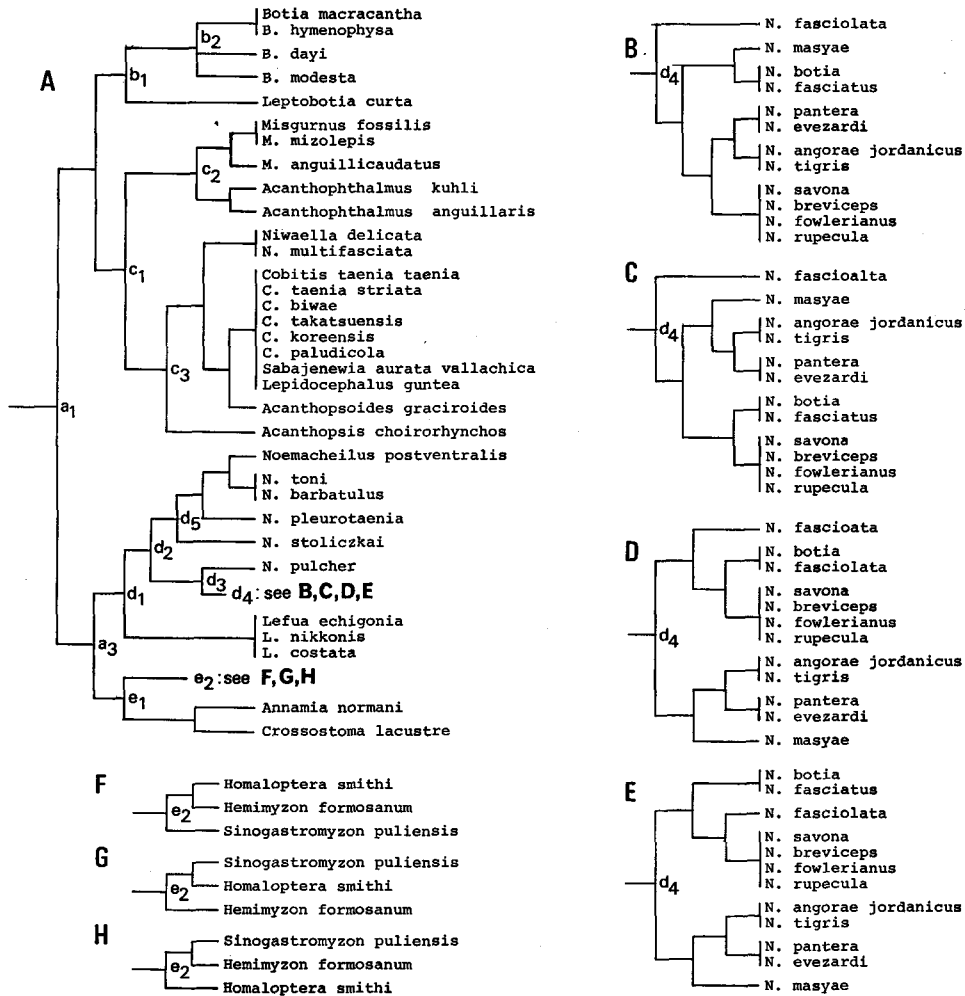
Fig. 99. Branching pattern of the superfamily Cobitoidea.

presumed. Because it is considered that the successive changes in the mode of life of these ancestors represent the process. Especially, synapomorphous features on which the branching pattern is based may provide important clues for inferring the mode of life of the hypothetical ancestors, because it can be assumed that the ancestor of the group having them has already possessed them before the differentiation of its descendants.

In the present study, on the basis of the branching pattern reconstructed in the previous section and the functional aspects of the synapomorphous features, the evolutionary process in the mode of life of the superfamily will be found out from habitat and feeding area at least until subfamilial level.

For presuming the habitat and feeding area of the ancestor of the superfamily

(Fig. 100: branching point a_1), one of four synapomorphous features of the superfamily and an unique unreversed feature may be important: the presence of the ossified second preethmoid (character 52) and the presence of the kinethmoid.

Cyprinoid fishes have developed the pipette-like system of the suction feeding method with the ability to protrude the mouth (Alexander, 1966, 1969; Gosline, 1973). The appearance of the kinethmoid was the greatest contribution to this ability (see pp. 107–108; Alexander, 1966). In his other paper, Alexander (1967) pointed out that the cyprinoid feeding method with such a protrusion mechanism is probably useful for taking food from the bottom. Such a feeding method make it possible to feed from the bottom with the long axis of body as nearly horizontal as possible, since it would seem difficult to maintain an oblique stance of
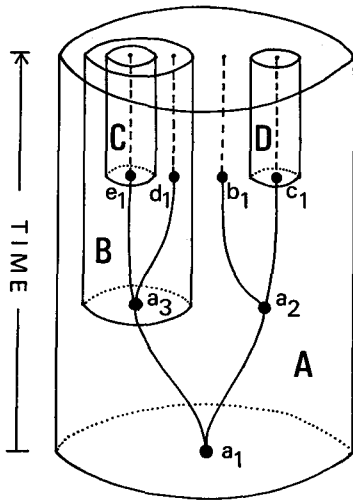
Fig. 100. Evolutionary process shown as the changes between adaptive zones in the superfamily. A, cobitoid zone; B, homalopterid zone; C, homalopterine zone; D, cobitine zone. For explanations, see text.

body in flowing water (Alexander, 1967). From this consideration, it is presumed that the cobitoid ancestor having the kinethmoid was already the bottom feeding fish. On the other hand, the appearance of the ossified second preethmoid seems to have been developed as a mechanism for the downward opening of mouth when the body is situating on the bottom (see, pp. 107–108). In fact, this feature is restricted to the bottom living fish. This fact might suggest that the presence of the bone is closely related to the bottom living habit. Thus, it is highly probable that the cobitoid ancestor was already a bottom living fish.

From the ancestor of the superfamily, the ancestors of the families Cobitidae (Fig. 100: branching point a_2) and Homalopteridae (Fig. 100: branching point a_3) were differentiated. From two autapomorphous features of the former, it is difficult to obtain information about the distinct modification from the cobitoid ancestor to the cobitid ancestor in the habitat and the feeding area. This may suggest that the cobitid ancestor did not escape from the original zone. On the other hand, among three autapomorphous features of the latter, the second descending process forming the gasbladder capsule (39) and the presence of the

subdivided capsule (42) may indicate that the habitat where homalopterid ancestor was available became restricted to the bottom. This consideration is supported by the observation that most of living fishes having the complete gasbladder capsule inhabit on the bottom (Ramaswami, 1955a; Chardon, 1968). In this level of the cobitoid evolution, it is interesting to note that the adaptation to the bottom in homalopterid lineage occurs earlier than in cobitid one.

From the ancestor of the family Cobitidae, two descendants were originated: the ancestors of the subfamilies Botiinae (Fig. 100: branching point b_1) and Cobitinae (Fig. 100: branching point c_1). From synapomorphous features of the subfamily Botiinae, it may be impossible to make clear the occurrence of the change in the habitat and feeding area of the botiine ancestor from those of the cobitid ancestor. In the process of the succeeding diversification within the subfamily, however, there were evolutionary trends of two characters to show the reduction of the interhyal (25) and the formation of the gasbladder capsule (41). The former feature may bring about the minimal change of the basic feeding method adopted by fishes of the subfamily. Because the interhyal seems to have an important role in the lateral swinging of the lateral wall for the feeding suction (see pp. 111–113). On the other hand, the latter seems to indicate that the persistence to the bottom has been increased even in the botiine lineage, although it occurs distinctly later than in other cobitoid lineages.

On the other hand, among synapomorphous features of the subfamily Cobitinae, two features seem to indicate the extension of cobitine available habitat from that of the cobitid ancestor: the reduced cleithrum (32) and the presence of the gasbladder capsule (41). The former shows that the habitat available for the cobitine ancestor was already restricted to the bottom. The latter may be not only an evidence to support this consideration but also an evidence to make possibility of the extension of cobitine habitat. As discussed in the chapter V (p. 137), the reduced cleithrum seems to be closely connected to the swimming method, undulation, adopted by the cobitine fishes. Undulation induces the increase of the efficiency of propeller (Aleev, 1963). As a result, such a swimming method increased the possibility for the movement on or in the bottom confronted by incomparably greater resistance from the surrounding medium than in the movement in the water. Thus, it seems to be suggested that the utilization of the region in the bottom by the cobitine ancestor became possible. This consideration is supported by that the living fishes of the subfamily Cobitinae wriggle into acculations of dead leaves or burrow into the bottom (Inger and Chin, 1962; Nakamura, 1963; Miyadi et al., 1976). This trend is considered to have been increased during the course of the diversification within the subfamily Cobitinae because of the trend toward the reduction in the pelvic bone and the number of pelvic radials which are found in some members of the subfamily (see pp. 154–155).

From the ancestor of the family Homalopteridae, two descendants were differentiated: the ancestor of the subfamilies Noemacheilinae (Fig. 100: branching point d_1) and Homalopterinae (Fig. 100: branching point e_1). In synapomorphous features of the former ancestor, it may be impossible to find evidence indicating the change of the homalopterid original habitat and feeding area. Therefore, in these two aspects, the ancestor of the subfamily may be the

most similar to the ancestor of the family Homalopteridae. On the other hand, the ancestor of the subfamily Homalopterinae may possibly have modified its habitat and feeding area. Among synapomorphous features of homalopterine ancestor, three features seem to have contributed to the formation of sucking disc: the enlarged cleithrum (32), the enlarged pelvic bone (43) and the enlarged pleural rib (45). As pointed out by Hora (1932), the suctorial disc has the function of adhesion. Its formation has been generally considered as an adaptation to the torrential habit (Hora, 1932; Chang, 1945). Thus, it is presumed that the homalopterine ancestor having these three features has already inhabited the torrential region of river. Furthermore, the other synapomorphous feature, the loss of the interhyal, seems to bring about any modification in the feeding method of the homalopterid ancestor, because the loss of the bone decreases the degree of the lateral swinging of lateral wall for the feeding suction (see pp. 111–113).

From these evolutionary process reconstructed on the basis of the successive changes in the feeding area and habitat of hypothetical ancestors, the qualitative changes of the adaptive zones which brought about the divergence of each lineages are deduced.

The basic structure between the adaptive zones found in the cobitoid evolutionary process seems to be that larger zone completely includes some smaller isolated zones in attribute. The largest zone, where the ancestor of the superfamily was, was the cobitoid original zone characterized by the inhabiting near the bottom and the feeding from the bottom. The latter attributes of this zone seem to have been always inherited by all living fishes of the superfamily Cobitoidea, because the original feeding method has been completely maintained during the cobitoid evolution. This seems to suggest that the descendants have not been able to move from the original zone to other independent zones which lacks the attribute for bottom feeding. Thus, the cobitoid divergence is considered to have been accomplished within the limits of the original zone.

From these considerations, the cobitoid divergence in the subfamilial level is presumed (Fig. 100). The ancestor of the family Homalopteridae first transferred from the original zone to the homalopterid zone which was characterized by being better adapted to the fishes' mode of life at the bottom as well as having both attributes of the original zone (Fig. 100: Zone B). The subfamily Noemacheilinae of the family have accomplished the specific diversity in this zone. The ancestor of the other subfamily Homalopterinae of the family entered a new homalopterine zone, and was able to utilize the torrential area of river as its habitat (Fig. 100: Zone C). The living fishes of the subfamily have been diversified in this zone. On the other hand, the ancestor of the family Cobitidae remained in cobitoid original zone (Fig. 100: Zone A). In this zone, the subfamily Botiinae of the family has established the specific diversity. The ancestor of the family Cobitinae transferred from the cobitoid original zone to the new zone which is characterized by utilizing the inside of the bottom (Fig. 100: Zone D).

Consequently, it is considered that the cobitoid divergence in the subfamilial level has resulted from the qualitative changes of the adaptive zones not by the transformation from the original zone to the independent zone located outside of it (see Simpson, 1961) but by the encroachment from the original zone into smaller isolated zone within it.

VII. Zoogeography of the superfamily Cobitoidea

1 DISTRIBUTIONS OF THE GENERA OF THE SUPERFAMILY

The superfamily Cobitoidea is distributed in Eurasia and its adjacent islands and a part of Africa.

1) DISTRIBUTION OF THE FAMILY COBITIDAE

The family Cobitidae is distributed in Eurasia and its adjacent islands and the northwestern part of Africa.

A. Distributions of the genera of the subfamily Botiinae

The subfamily Botiinae, distributing in East Asia and Southeast Asia, comprises two genera: *Leptobotia* and *Botia* (Nalbant, 1963).
(1) *Leptobotia* (Fig. 101)
Fishes of this genus are found in Amur drainage from Blagoveschensk to Liman; Ussuri; Sungari (Berg, 1949; Nicholsky, 1956), Liao drainage (Mori, 1928), Central
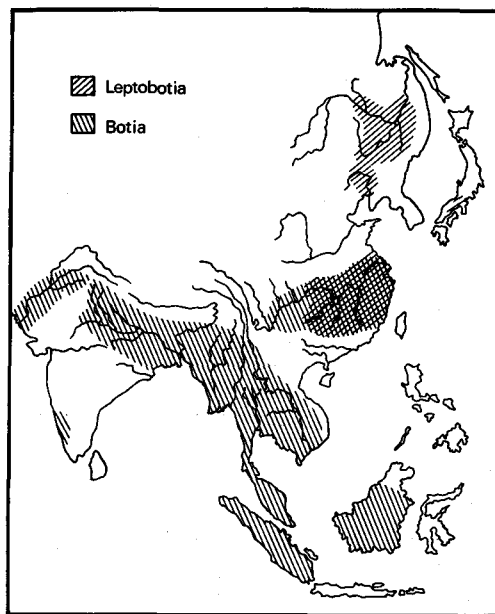
Fig. 101. Distributions of the genera *Leptobotia* and *Botia* of the subfamily
    Botiinae of the family Cobitidae.

Japan (Nakamura, 1963), Fukien (Fang, 1936; Nichols, 1943) and Chan drainage (Rendahl, 1932; Nichols, 1943; Anonymous, 1976).
For the zoogeographical analysis, a Japanese species *Leptobotia curta* is
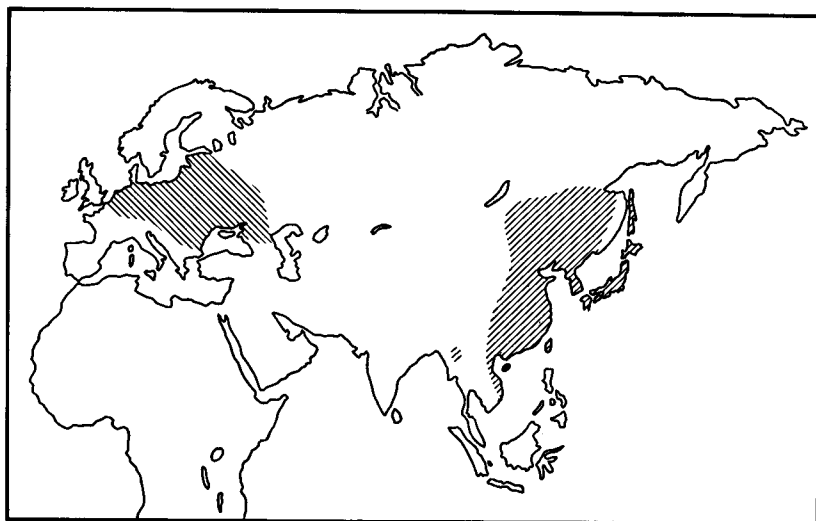
Fig. 102. Distribution of the genus *Misgurnus*, the subfamily Cobitinae.

examined.

(2) *Botia* (Fig. 102)

Fishes of this genus are known from Sumatra and Borneo (Weber and Beaufort, 1916), Mekong and Menam drainages (Smith, 1945; Kawamoto et al., 1972; Taki, 1974), Burma (Rendahl, 1948), Ganges-Brahmaputra drainage (Banarescu and Nalbant, 1968; Rahman, 1974), Indus drainage (Mirza, 1975), and South China (Rendahl, 1932; Fang, 1936; Nichols, 1943; Anonymous, 1976).

For the zoogeographical analysis, four species of the genus are examined: *Botia macracantha*, *B. hymenophysa*, *B. modesta* and *B. dayi*.

B. Distribution of the genera of the subfamily Cobitinae

The subfamily Cobitinae is distributed in Eurasia and its adjacent islands and Morocco of Africa, and comprises 13 genera: *Misgurnus*, *Cobitis*, *Sabajenewia*, *Niwaella*, *Somileptes*, *Enobarichthys*, *Acanthopsis*, *Acanthopsoides*, *Lepidocephalus*, *Paralepidocephalus*, *Acanthophthalmus*, *Neoeucirrhichthys* and *Eucirrhichthys* (Nalbant, 1963; Banarescu and Nalbant, 1968).

(1) *Misgurnus* (Fig. 102)

Fishes of this genus are discontinuously distributed in Europe and East Asia. The detail locality of this genus is as follows: Denmark; Loire drainage; rivers falling into North Sea and Baltic Sea from Scheldt to Neva; Pslov drainage; Il' men; Vuoksa; rivers of Black Sea from Danube to Don; Lower reaches of Kuban River, Volga drainage (Berg, 1949; Spillmann, 1961; Banarescu, 1964), Amur drainage (Berg, 1949; Nicholsky, 1956; Dulma, 1973), North China (Mori, 1934; Nichols, 1943; Berg, 1949), Sakhalin (Sato, 1942; Berg, 1949), Korea (Uchida, 1939; Choi et al., 1980; Jeon, 1980), Japan (Nakamura, 1963), Taiwan (Chen, 1969), Hainan (Nichols and Pope, 1927), South China (Rendahl, 1932; Nichols, 1943; Anonymous, 1976), Tonkin, Vietnam (Rendahl, 1944; Orsi, 1974),

and Irawadi drainage (Rendahl, 1943).

For the zoogeographical analysis, three species of this genus are examined: *Misgurnus fossilis*, *M. anguillicaudatus* and *M. mizolepis*. The first species is used as an European representative, and the latter two are used as East Asian representatives.

(2)   *Cobitis* (Fig. 103)

This genus is distributed in the large part of Eurasia and northwestern Africa, and shows the widest distributional range of all cobitine genera.   The detail distribution of this genus is described as follows: Europe east to Portugal, Siberia west to Lena drainage (Berg, 1949; Spillmann, 1961; Bacescu, 1961, 1962; Banarescu, 1964; Zanandrea et al., 1965; Bacescu and Mayer, 1969), Morocco (Pellegrin, 1929), Turkey (Banarescu and Nalbant, 1964), Greek (Stephanidis, 1974), Syria, Lebanon
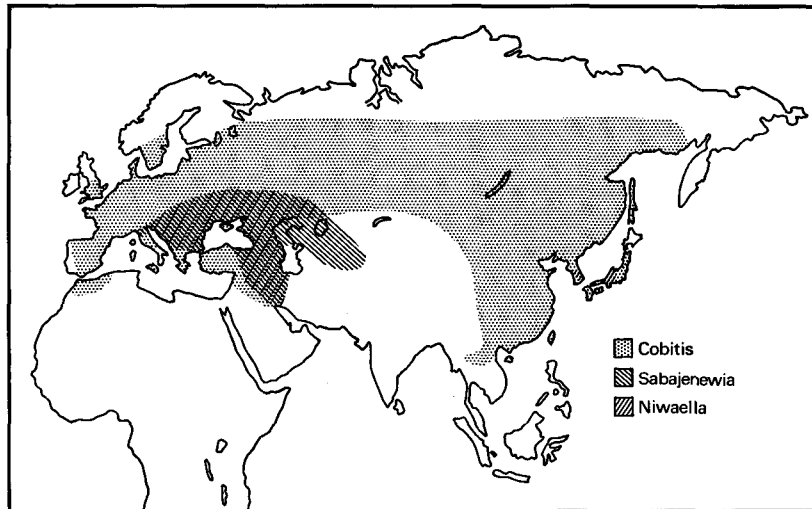
Fig. 103.   Distributions of the genera *Cobitis*, *Sabajenewia* and *Niwaella*, the subfamily
      Cobitinae.

(Berg, 1949), Iran (Kähsbauer, 1963; Banarescu and Nalbant, 1966), Iraq (Al-Nasiri and Hoda, 1975), Mongolia (Dulma, 1973; Nalbant et al., 1970), Amur drainage including Sungari and Ussuri (Berg, 1949; Nicholsky, 1956), Sakhalin (Sato, 1942; Berg, 1949), Japan excluding Hokkaido (Nakamura, 1963), Korea (Uchida, 1939; Choi et al., 1980; Jeon, 1980), Taiwan (Chen, 1969), Hainan (Nichols and Pope, 1927), South China (Rendahl, 1932; Nichols, 1943; Anonymous, 1976), North China (Mori, 1934; Berg, 1949), and Meping of North Thailand (Smith, 1945; Nalbant, 1963).

For the zoogeographical analysis, six species or subspecies of this genus are examined: *Cobitis taenia taenia*, *C. taenia striata*, *C. biwae*, *C. takatsuensis*, *C. koreensis* and *C. paludicola*.   *Cobitis taenia taenia* has the widest distributional range of all species of *Cobitis*, though it shows a disjunct distribution between Europe and East Asia.   *Cobitis paludicola* is used as a representative of European

species, while other species and subspecies are examined as representatives of East Asian members.

(3) *Sabajenewia* (Fig. 103)

The distribution of this genus is restricted in southern East Europe, Black Sea-Caspian Sea-Aral Sea region, and West Asia. The detail localities of this genus are as follows: North Italy (Bacescu, 1962; Zanandrea et al., 1965), Balkan Peninsula (Nalbant, 1963; Stephanidis, 1974), Danube drainage (Banarescu, 1964; Banarescu et al., 1972), Don drainage (Nalbant, 1963), eastern tributaries of Black Sea and Caspian Sea (Berg, 1949; Nalbant, 1963), tributaries of Aral Sea (Nalbant, 1963), Syr and Amu drainages (Berg, 1949), and Euphrate drainage and West Iran (Banarescu and Nalbant, 1966).

The zoogeographical analysis is made on the basis of a subspecies *Sabajenewia aurata vallachica*.

(4) *Niwaella* (Fig. 103)

The distribution of this genus including only two species is restricted in central Japan and southeastern Korea. *Niwaella delicata* is in central Japan (Niwa, 1976) and *N. multifasciata* is in southeastern Korea (Sawada and Kim, 1977).

The zoogeographical analysis is made on the basis of both species.

(5) *Somileptes*

The distribution of this monotypic genus is restricted to Assam of northeastern India (Banarescu and Nalbant, 1974; Jayaram, 1974).

The genus is excluded from the zoogeographical analysis because of the lack of material examined.

(6) *Enobarichthys*

This monotypic genus is known from Madras of southeastern India (Day, 1875). This genus is excluded from the zoogeographical analysis because of the
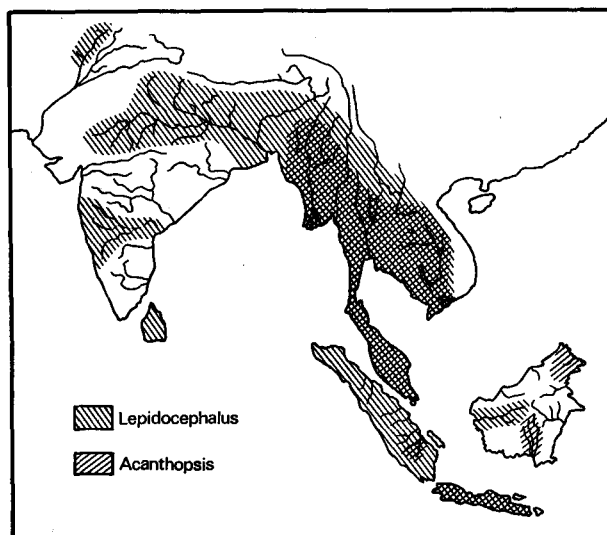
Fig. 104. Distributions of the genera *Lepidocephalus* and *Acanthopsis*, the subfamily Cobitinae.

absence of material at hand.
(7)   *Acanthopsis* (Fig. 104)
    This genus consists of a single species *A. choirorhynchos* which is distributed in
Borneo (Weber and Beaufort, 1916; Inger and Chin, 1962), southeastern Sumatra
and Java (Weber and Beaufort, 1916), Malay Peninsula (Smith, 1945), Mekong and
Menam drainages (Smith, 1945; Kawamoto et al., 1972; Taki, 1974), and
Irawadi-Chindwin drainage (Rendahl, 1948).
    A. choirorhynchos is examined for the zoogeographical analysis.
(8)   *Acanthopsoides* (Fig. 105)
    This monotypic genus are known from Mekong drainage (Smith, 1945; Taki,
1974) and Menam drainage (Fowler, 1934; Smith, 1945).
    A. graciroides is used for the zoogeographical analysis.
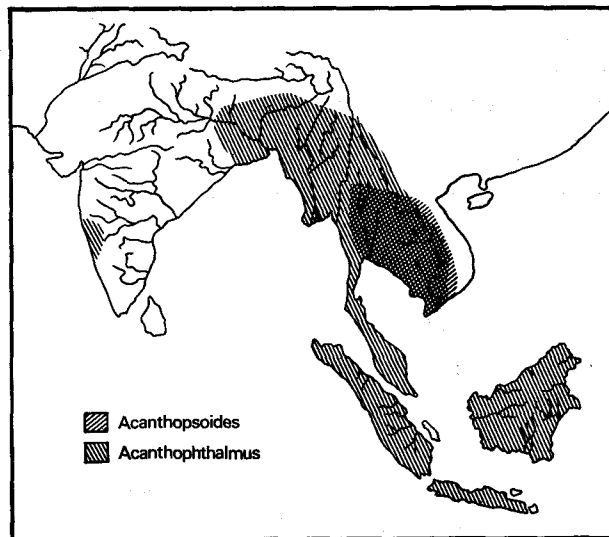
Fig. 105.   Distributions of the genera *Acanthopsoides* and *Acanthophthalmus*, the subfamily
        Cobitinae.

(9)   *Lepidocephalus* (Fig. 104)
    Fishes of this genus are distributed in Southeast Asia and Indian Peninsula.
The detail distribution of this genus is as follows: southwestern Borneo, Java,
Sumatra (Weber and Beaufort, 1916), Malay Peninsula (Weber and Beaufort, 1916;
Smith, 1945), Mekong drainage (Taki, 1974), Menam drainage (Smith, 1945),
Salween drainage (Rendahl, 1948), Chindwin-Irawadi drainage (Rendahl, 1948),
Brahmaputra-Ganges drainage (Day, 1875; Banarescu and Nalbant, 1968), Indus
drainage (Mirza, 1975), Kistna drainage (Banarescu and Nalbant, 1968), and
southwestern India and Ceylon (Day, 1875; Munro, 1955).
    For the zoogeographical analysis, *L. guntea* which has the widest distributional
range of all species of the genus is used.
(10)   *Paralepidocephalus*
    This monotypic genus is known from Shiping of Yunnan, South China (Tchang,

1935). This genus is excluded from the zoogeographical analysis because of the absence of material examined.

(11) *Acanthophthalmus* (Fig. 105)

This genus is distributed in Southeast Asia and Indian Peninsula, and thus mostly overlaps the genus *Lepidocephalus* in distribution. The detail localities of this genus are as follows: Borneo (Weber and Beaufort, 1916; Inger and Chin, 1962), Java (Weber and Beaufort, 1916), Sumatra (Weber and Beaufort, 1916), Malay Peninsula (Weber and Beaufort, 1916), Singapore (Alfred, 1966), Mekong and Menam drainages (Smith, 1945), Salween drainage (Rendahl, 1948), Irawadi-Chindwin drainage (Rendahl, 1948), Ganges-Brahmaputra drainage (Hamilton, 1822; Rahman, 1974), and Goa of southwestern India (Tilak, 1972).

The zoogeographical analysis is made based on two species, *A. kuhli* and *A. anguillaris*.

(12) *Neoeucirrhichthys*

Fishes of this genus are known from Janali River of Brahmaputra drainage at Ramiora, Goalpara district (Banarescu and Nalbant, 1968).

This genus is excluded from the zoogeographical analysis because of the lack of material examined.

(13) *Eucirrhichthys*

Fishes of the genus are known from Sarawak of northwestern Borneo (Weber and Baeufort, 1916). This genus is excluded from the zoogeographical analysis due to the lack of material at hand.

2) DISTRIBUTION OF THE FAMILY HOMALOPTERIDAE

The family is distributed in Eurasia and its adjacent islands and the north-eastern part of Africa.

A. Distributions of the genera of the subfamily Noemacheilinae

The subfamily Noemacheilinae, consisting of three genera, *Lefua*, *Noemacheilus* and *Vaillantella* (see Banarescu and Nalbant, 1968), is distributed in Eurasia and its adjacent islands and Blue Nile of Africa.

(1) *Lefua* (Fig. 106)

Fishes of this genus are known from Amur drainage including Sungari and Ussuri (Berg, 1949; Nicholsky, 1956), Liao drainage (Mori, 1934), Japan (Nakamura, 1963), Korea (Uchida, 1939; Choi et al., 1980; Jeon, 1980), and Shanhai of China (Nichols, 1943).

For the zoogeographical analysis, three species of the genus, *Lefua echigonia*, *L. nikkonis* and *L. costata*, are examined.

(1) *Noemacheilus* (Fig. 106)

This genus, comprizing more than 100 nominal species, has the widest distributional range of all cobitoid genera as well as all noemacheiline genera. Banarescu and Nalbant (1964, 1966, 1968, 1974, 1976) has attempted the subdivision of the genus into several separate genera and/or subgenera. In the present study, as stated previously, however, the present author will deal with the genus *Noemacheilus* as an only valid genus.

Fishes of this genus are known from all Eurasia except South Spain, South
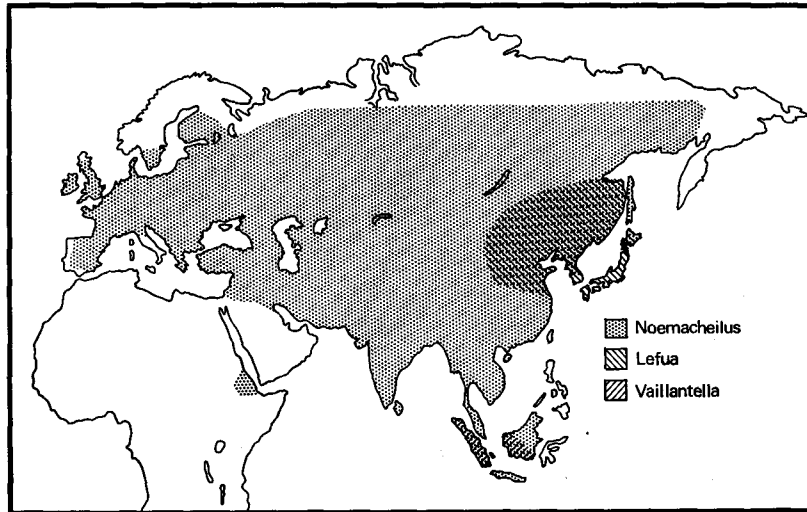
Fig. 106. Distributions of the genera *Lefua*, *Noemacheilus* and *Vaillantella*, the subfamily Noemacheilinae.

and Central Italy, northern part of Scotland, Norway, Sweden north of 57°N and east of Kolyma River (Hora, 1922a, 1922b; Rendahl, 1932, 1933, 1948; Mori, 1934, 1936; Uchida, 1939; Nichols, 1943; Smith, 1945; Berg, 1949; Mori et al., 1951; Nicholsky, 1956; Dewitt, 1960; Spillmann, 1961; Tchang et al., 1963; Banarescu, 1964; Banarescu and Nalbant, 1964, 1966a, 1966b, 1968; Alfred, 1966; Dulma, 1973; Rahman, 1974; Taki, 1974; Mirza, 1975; Choi et al., 1980; Jeon, 1980). Furthermore, following localities are known: Sakhalin (Sato, 1942), Hokkaido of Japan (Nakamura, 1963), Hainan (Nichols and Pope, 1927), Borneo (Weber and Beaufort, 1916; Inger and Chin, 1962), Sumatra and Java (Weber and Beaufort, 1916), Ceylon (Munro, 1955), Blue Nile of East Africa (Boulenger, 1907).

For the zoogeographical analysis, 18 species or subspecies of this genus are examined. *Noemacheilus toni* and *N. postventralis* are as Siberian and Northeast Asian representatives, *N. barbatulus* as European representative, *N. stoliczkai* as High Asian representative, *N. pleurotaenia*, *N. pulcher*, *N. fasciolata* as South Chinese representatives, *N. botia*, *N. masyae*, *N. savona*, *N. fowlerianus*, *N. breviceps*, *N. rupecula*, *N. evezardi* and *N. fasciatus* as South Asian and Southeast Asian representatives, and *N. angorae jordanicus*, *N. tigris* and *N. pantera* as West Asian representatives.

(3) *Vaillantella* (Fig. 107)

The distribution of this genus, consisting of only three species, is restricted in southern part of Malayan Peninsula, northeastern slope of Sumatra and western slope of Borneo (Weber and Beaufort, 1916; Tweedie, 1956; Nalbant and Banarescu, 1977).

This genus is excluded from the zoogeographical analysis because of the absence of available specimen.

B. Distributions of the genera of the subfamily Homalopterinae
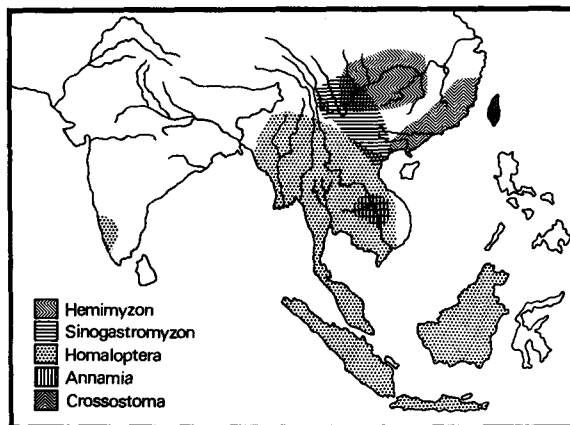
Fig. 107. Distributions of the genera *Hemimyzon, Sinogastromyzon, Homaloptera, Annamia*
   and *Crossostoma,* the subfamily Homalopterinae.

    The subfamily Homalopterinae which is distributed in South Asia, Southeast
Asia and southern East Asia, consists of 26 genera (Silas, 1952; Chen, 1978).   In
the present study, five genera of them are used for the zoogeographical analysis:
Hemimyzon, Sinogastromyzon, Homaloptera, Annamia and *Crossostoma.*
(1) *Balitoropsis*
    Fishes of this genus are known from Kao Chong, Trang Province of Thailand
(Smith, 1945) and Lanchen River, Yongping Xian of China (Chen, 1978).
(2) *Balitora*
    The distribution of this genus is restricted in India and Burma (Silas, 1952).
(3) *Sinohomaloptera*
  Fishes of the genus are found in Cheng Kon Tsuen of Hainan, Kwangsi, and
Yunnan (Silas, 1952; Chen, 1978).
(4) *Lepturichthys*
    The distribution of this genus is restricted in the upper part of Chan drainage,
Min River, Szechwan, Hupeh, Tungtin Lake, and Hunan (Silas, 1952; Anonymous,
1976; Chen, 1978).
(5) *Hemimyzon* (Fig. 107)
    Fishes of the genus are distributed in Chan drainage and Taiwan (Silas, 1952;
Liang, 1974; Anonymous, 1976; Chen, 1978).   In the present study, *H. formosanum*
is used for the zoogeographical analysis.
(6) *Sinogastromyzon* (Fig. 107)
    Fishes of this genus are known from Kwangsi, Kweichow, Anning River near
Taihoechang of Szechwan, Taiwan, and Tonkin of Vietnam (Silas, 1952; Liang,
1974; Anonymous, 1976; Chen, 1978).   In the present study, *S. puliensis* is used
for the zoogeographical analysis.
(7) *Metahomaloptera*
    Fishes of this genus are distributed in the upper part of Chan drainage (Chen,
1978).
(8) *Homaloptera* (Fig. 107)

The distributional range of this genus is the widest among those of all other homalopterine genera. The detail distribution of the genus is as follows: Annamalai Hills of India (Silas, 1952), Mekong and Menam drainages (Smith, 1945; Taki, 1974), Burma (Silas, 1952), Tonkin of Vietnam (Silas, 1952), Malay Penincula (Silas, 1952), and Sumatra, Java and Borneo (Weber and Beaufort, 1916; Hora, 1932).

H. smithi is used for the zoogeographical analysis.

(9) Bhavania

The distribution of this genus is restricted in hill ranges of Msyore, Nilgiris and Travacore of Indian Peninsula (Silas, 1952).

(10) Neohomaloptera

The distribution of the genus is restricted in Johore and Malay Peninsula (Silas, 1952).

(11) Travancoria

This genus is known from only hill ranges of northern Travancore, Annamalai Hills, and Western Ghats of South India (Silas, 1952).

(12) Pseudohomaloptera

The fishes of the genus are found in Bo River of Borneo (Silas, 1952).

(13) Glaniopsis

The distribution of this genus is restricted in Borneo (Weber and Beaufort, 1916; Silas, 1952; Inger and Chin, 1962).

(14) Annamia (Fig. 107)

Fishes of the genus are known from Kontum of Vietnam (Hora, 1932) and Houei Nhang River of Laos (Taki, 1974).   In the present study, A. normani is used for the zoogeographical analysis.

(15) Crossostoma (Fig. 107)

Fishes of this genus are distributed in Fukien, Kwantung of China (Nichols, 1943; Silas, 1952) and Taiwan (Chen, 1969).   In the present study, C. lacustre is used for the zoogeographical analysis.

(16) Liniparhomaloptera

The distribution of this genus is restricted in Poh-lo district of Kwangtung, and Hong Kong (Nichols, 1943; Silas, 1952).

(17) Vanmanenia

Fishes of the genus are distributed in Fukien and Chekiang of China (Silas, 1952).

(18) Praeformosania

The distribution of this genus is restricted in south Kweinchow and north-western Kwangsi of China (Nichols, 1943; Silas, 1952).

(19) Sewellia

The fishes of this genus is known from only Cochin China (Hora, 1932).

(20) Paraprotomyzon

This genus is known from only eastern Szechwan of China (Silas, 1952).

(21) Pseudogastromyzon

Fishes of this genus are distributed in Kwantung, Fukien, South Chekiang of China, and Hong Kong (Nichols, 1943; Silas, 1952).

(22) Beaufortia

Fishes of this genus are known from Szechwan, Kweichow, northwestern and

southwestern Kwangsi, and Hainan of China (Nichols, 1943; Silas, 1952).

(23) *Protomyzon*

The distribution of this genus is restricted in Borneo (Weber and Beaufort, 1916; Hora, 1932; Silas, 1952; Inger and Chin, 1962).

(24) *Progastromyzon*

The genus is known from Borneo (Silas, 1952; Inger and Chin, 1962).

(25) *Neogastromyzon*

The genus is found in Howong River of Borneo (Hora, 1932; Silas, 1952).

(26) *Gastromyzon*

Fishes of this genus are known from Borneo (Silas, 1952; Inger and Chin, 1962).

2. CENTER OF ORIGIN AND PHYLOGENETIC DISPERSAL ROUTE OF THE SUPERFAMILY

The center of origin and phylogenetic dispersal route of the superfamily are deduced on the basis of the branching pattern of 48 species or subspecies reconstructed in the previous chapter. According to the previous section, the species or subspecies and genera examined here are reasonably classified into several patterns in distribution. In the present study, from these distributional patterns, six geographical regions which will be defined below are established (Fig. 108). On the basis of these regions, the center of origin of the superfamily will be identified as one or more of six regions, while the phylogenetic dispersal route will be reconstructed as the relationships among these regions. Boundaries of these regions that will be defined here well agree with those of the zoogeographical regions based on the distributional patterns of freshwater fishes defined by several authors (e.g. Mori, 1936; Darlington, 1957; Banarescu, 1970; Mirza, 1975).
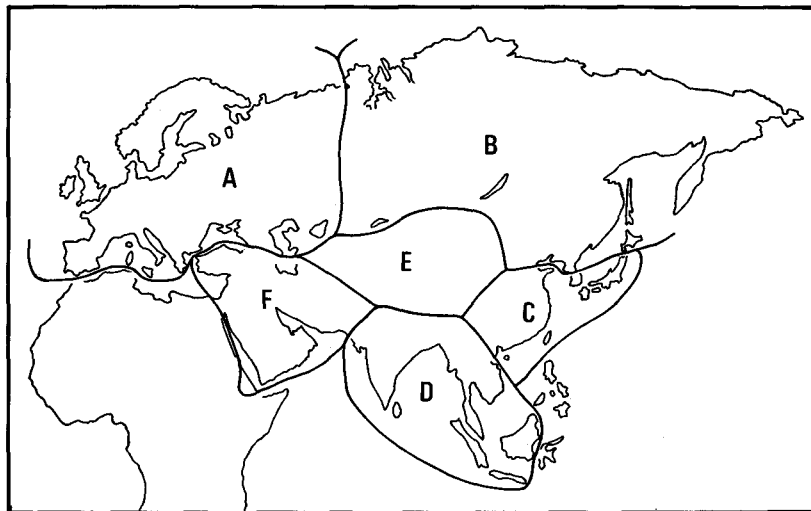
Fig. 108. Zoogeographical regions constructed on the basis of the distributional patterns of cobitoid fishes examined. A, Europe; B, Siberia and Northeast Asia; C, South China; D, Southeast Asia and South Asia; E, High Asia; F, West Asia.

"Europe" (Region A) is defined as the area demarcated from "Siberia and Northeast Asia" by the Ural Range, and from "West Asia" by Kavkas Range and Bosporous Channel-Marmara Sea, and includes the basins of the Caspean and Aral seas except the upper reaches of Syr and Amu drainages. Cobitoid species represented this region are shown below.

Subfamily Cobitinae

Misgurnus fossilis, Cobitis paludicola and *Sabajenewia aurata vallachica*

Subfamily Noemacheilinae

Noemacheilus barbatulus

"Siberia and Northeast Asia" (Region B) is defined as the area included Siberia, North China north of Shansi Province, North Korea, Sakhalin and Hokkaido of Japan, and bordered "High Asia" in Mongolia, and Hopeh and Shansi of China.

Subfamily Noemacheilinae

Noemacheilus toni, N. postventralis, Lefua nikkonis

"South China" (Region C) is defined as the area demarcated from "South Asia and Southeast Asia" by the watershed between Mekong and Song Koi drainages, and bordered "High Asia" in Yunnan, Szechwan and Shensi of China.

Subfamily Botiinae

Leptobotia curta

Subfamily Cobitinae

Cobitis taenia striata, C. biwae, C. takatsuensis, C. koreensis, Niwaella delicata, N. multifasciata

Subfamily Noemacheilinae

Lefua echigonia, Noemacheilus pleurotaenia, N. pulcher, N. fasciolata

Subfamily Homalopterinae

Hemimyzon formosanum, Sinogastromyzon puliensis, Crossostoma lacustre

"South Asia and Southeast Asia" (Region D) is defined as the area demarcated from "West Asia" by the Central Brahui Ranges, Kharan-Makran Ranges and the adjacent ranges in Iran, and from "High Asia" by the Himalayas and Hindu Kush.

Subfamily Botiinae

Botia macracantha, B. hymenophysa, B. modesta, B. dayi

Subfamily Cobitinae

Acanthopsis choirorhynchos, Acanthopsoides graciroides, Acanthophthalmus kuhli, A. anguillaris, Lepidocephalus guntea

Subfamily Noemacheilinae

Noemacheilus botia, N. masyae, N. fasciatus, N. savona, N. breviceps, N. fowlerianus, N. rupecula, N. evezardi

Subfamily Homalopterinae

Homaloptera smithi, Annamia normani

"High Asia" (Region E) is defined as the area surrounded by other five regions.

Subfamily Noemacheilinae

Noemacheilus stoliczkai

"West Asia (Region F) is defined as the area demarcated from "High Asia" by northeastern parts of Afghanistan and Pakistan.

Subfamily Noemacheilinae

Noemacheilus angorae jordanicus, N. tigris, N. pantera

All other species examined are distributed through two or more regions: *Misgurnus anguillicaudatus*, Regions B, C and D; *Misgurnus mizolepis*, Regions B and C; *Cobitis taenia taenia*, Regions A, B and C; *Lefua costata*, Regions B and C.

Thus, Fig. 109 is given by applying these regions to the branching pattern of the superfamily. From this scheme, it is deduced that the ancestor of the superfamily represented as the branching point a_1 originated in South China (Region C) and/or South Asia and Southeast Asia (Region D). Furthermore, the families Cobitidae and Homalopteridae of the superfamily are considered to be differentiated in different regions: the family Cobitidae in South Asia and Southeast Asia (Region D) (Fig. 109: branching point a_2), while the family Homalopteridae in South China (Region C) (Fig. 109: branching point a_3).

Regarding the four subfamilies of the two families, the center of origin and the direction of dispersal will be judged as below.

1) The family Cobitidae

(1) the subfamily Botiinae

The ancestor of the subfamily (Fig. 109: branching point b_1) is considered to be differentiated in South China (Region C) and/or South Asia and Southeast Asia (Region D). However, the direction of dispersal cannot be estimated in the present study.

(2) the subfamily Cobitinae

The ancestor of the subfamily (Fig. 109: branching point c_1) seems to have been originated in South Asia and Southeast Asia (Region D). From Fig. 109, the direction of dispersal from South Asia and Southeast Asia (Region D) to Europe (Region A) through South China (Region C) and Siberia and Northeast Asia (Region B) is deduced. *Misgurnus anguillicaudatus* has been exceptionally found in North Burma, separating from its main distributional range (Fig. 102) (Rendahl, 1943). The present zoogeographical analysis indicates that the occurrence of this species in North Burma is probably the second dispersion from South China (Region C) (Fig. 109).

2) The family Homalopteridae

(1) the subfamily Noemacheilinae

The center of origin of the subfamily is reasonably identified with South China (Region C). Then, the subfamily seems to have been phylogenetically dispersed in two directions, although several species have been originated in the original locality of the subfamily. One of them is the dispersal toward Siberia and Northeast Asia (Region B) and following it the extension of the distributional range to High Asia (Region E) or Europe (Region A). This is displayed by five species, *Noemacheilus pleurotaenia, N. stoliczkai, N. postventralis, N. toni* and *N. barbatulus*. On the other hand, the other dispersal history is displayed by thirteen species or subspecies, *Noemacheilus pulcher, N. fasciolata, N. masyae, N. botia, N. fasciatus, N. pantera, N. evezardi, N. angorae jordanicus, N. tigris, N. savona, N. breviceps, N. fowlerianus* and *N. rupecula*. On the phylogenetic relationships among them, four alternative hypotheses are reconstructed (Figs. 109 and 110). However, the

Region | Species or Subspecies

(D)   Botia macracantha
(D)   B. hymenophysa
(D)   B. dayi
(D)   B. modesta
(C)   Leptobotia curta

(A)   Misgurnus fossilis
(B) (C)   M. mizolepis
(B) (C) (D)   M. anguillicaudatus
(D)   Acanthophthalmus kuhli
(D)   A. anguillaris
(C)   Niwaella delicata
(C)   N. multifasciata
(A) (B) (C)   Cobitis taenia taenia
(C)   C. taenia striata
(C)   C. biwae
(C)   C. takatsuensis
(C)   C. koreensis
(A)   C. paludicola
(A)   Sabajenewia aurata vallachica
(D)   Lepidocephalus guntea
(D)   Acanthopsoides graciroides
(D)   Acanthopsis choirorhynchos

(B)   Noemacheilus postventralis
(B)   N. toni
(A)   N. barbatulus
(C)   N. pleurotaenia
(E)   N. stoliczkai
(C)   N. pulcher

(C)   Lefua echigonia
(B)   L. nikkonis
(B) (C)   L. costata

Tree node labels: b2 (D); b1 (C),(D); a2 (D); (B),(C),(D); c2 (A),(B),(C); (B),(C); c1 (D); c3 (D); (C),(D); (A),(B),(C),(D); (A),(B),(C),(D); a1 (C),(D); d5 (B),(C); (A),(B); d2 (B),(C),(E); d1 (C); (C) or (C),(D); d3 see Fig.110; a3 (C); (B),(C); e1 see Fig. 111; (C) or (C),(D)

Fig. 109.   Center of origin and phylogenetic dispersal route of the superfamily Cobitoidea.

dispersal histories deduced from these hypotheses are identical.   In this history, the direction of dispersal was from South China (Region C) to West Asia (Region F) through South Asia and Southeast Asia (Region D).
(2)   the subfamily Homalopterinae
    The ancestor of the subfamily is reasonably considered to have been differentiated in South China (Region C) except the case of the third hypothesis of the branching pattern (Fig. 111 C).   If two other hypotheses of the branching pattern (Fig. 111 A and B) are adopted, it is considered that the dispersal toward South Asia and Southeast Asia (Region D) occurred.   On the other hand, in the case of the third hypothesis of the branching pattern, the direction of dispersal is undeterminable.
    In conclusion, the dispersal route of the superfamily will be summarized from the directions of dispersal in above four subfamilies.   As stated above, the ancestor of the superfamily originated in South China and/or South Asia and Southeast Asia.   Following this creation, the ancestors of the families Cobitidae and Homalopteridae were differentiated in South Asia-Southeast Asia and South China respectively.   From its original distributional range, the former has

A

```
            d₃                          (C)   N. pulcher
        (C)                             (C)   N. fasciolata
              d₄                        (D)   N. masyae
          (C),(D)      (D)              (D)   N. botia
                                        (D)   N. fasciatus
                  (D)                   (F)   N. pantera
                              (D),(F)   (D)   N. evezardi
                         (F)            (F)   N. tigris
                                 (F)    (F)   N. angorae jordanicus
                    (D),(F)             (D)   N. savona
                                        (D)   N. breviceps
                              (D)       (D)   N. fowlerianus
                                        (D)   N. rupecula
```

B

```
            d₃                          (C)   N. pulcher
        (C)                             (C)   N. fasciolata
              d₄                        (D)   N. masyae
          (C),(D)   (D),(F)             (F)   N. angorae jordanicus
                                 (F)    (F)   N. tigris
                         (F)            (F)   N. pantera
                              (D),(F)   (D)   N. evezardi
                  (D)                   (D)   N. botia
                                 (D)    (D)   N. fasciatus
                         (D)            (D)   N. savona
                                        (D)   N. breviceps
                              (D)       (D)   N. fowlerianus
                                        (D)   N. rupecula
```

C

```
            d₃                          (C)   N. pulcher
        (C),(D)            (C),(D)       (C)   N. fasiolata
                                 (D)    (D)   N. botia
                                        (D)   N. fasciatus
                  (D)                   (D)   N. savona
              d₄                        (D)   N. breviceps
          (D)                 (D)       (D)   N. fowlerianus
                                        (D)   N. rupecula
                         (F)            (F)   N. angorae jordanicus
                                 (F)    (F)   N. tigris
                  (D),(F)               (F)   N. pantera
                              (D),(F)   (D)   N. evezardi
                                        (D)   N. masyae
```

D

```
            d₃                          (C)   N. pulcher
        (C),(D)          (D)            (D)   N. botia
                                 (D)    (D)   N. fasciatus
                  (D)                   (C)   N. fasciolata
                      (C),(D)           (D)   N. savona
              d₄                        (D)   N. breviceps
          (D)                 (D)       (D)   N. fowlerianus
                                        (D)   N. rupecula
                         (F)            (F)   N. angorae jordanicus
                                 (F)    (F)   N. tigris
                  (D),(F)               (F)   N. pantera
                              (D),(F)   (D)   N. evezardi
                                        (D)   N. masyae
```

Fig. 110

dispersed in one direction: toward Europe (Region A) through Siberia and North-east Asia (Region B) (Fig. 112).   On the other hand, from its ancestral range, the latter has dispersed in two directions: toward West Asia (Region F) and toward

Fig. 111.   Three alternative hypotheses of the center of origin and dispersal route of the subfamily Homalopterinae.

Fig. 112.   Center of origin and phylogenetic dispersal route of the superfamily Cobitoidea. Arrows indicate the direction of dispersal.

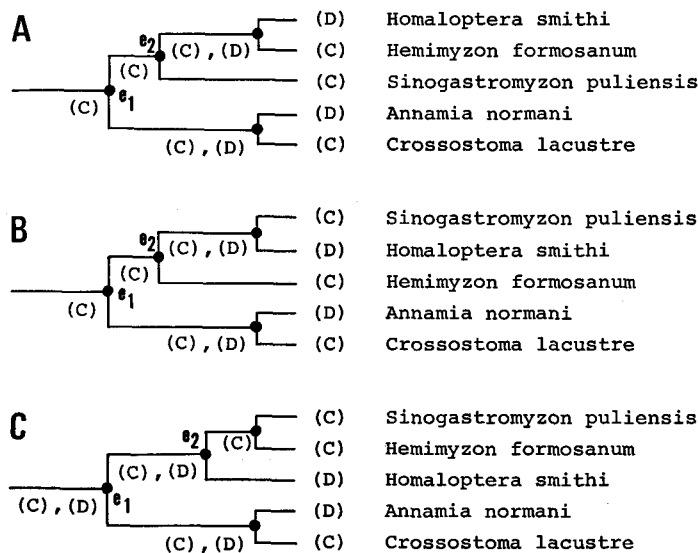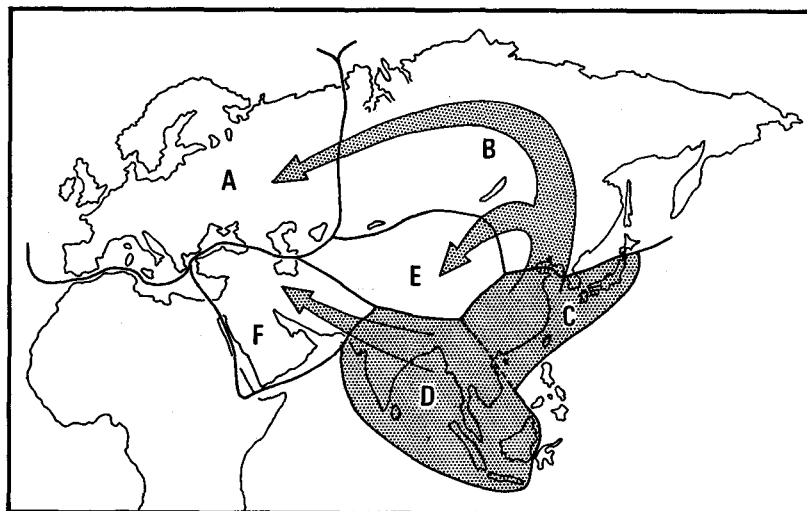Fig. 110.   Four alternative hypotheses of the center of origin and the dispersal route of thirteen species or subspecies of the subfamily Noemacheilinae.

Europe (Region A) and High Asia (Region E) through Siberia and Northeast Asia (Region B) (Fig. 112). In addition to this conclusion, noteworthy for the cobitoid dispersal route is that the possibility of the phylogenetic dispersal route between West Asia (Region F) and Europe (Region A) has hardly occurred, although some species of the cobitine genera *Cobitis* and *Sabajenewia* are commonly distributed in both regions.

VIII. Summary

The present study was intended to elucidate the phylogeny and zoogeographical history of the superfamily Cobitoidea. The former is established by reconstructing the branching pattern of the superfamily and deducing the evolutionary process of the superfamily. The latter is accomplished by estimating the center of origin and phylogenetic dispersal route of the superfamily. The specimens of 48 species or subspecies of 17 genera collected from inland waters of Eurasia and its adjacent islands were used for the establishment of the above purposes. Eleven skeletal parts of each specimen were examined: mandibular arch, cranium, hyoid arch, branchial apparatus, suspensorium, pectoral girdle and fin, Weberian apparatus and gasbladder capsule, pelvic girdle and fin, dorsal and anal fins, vertebrae and their accessary bones, and caudal complex and fin. Fifty-two characters of their parts were selected and adopted to reconstruct the branching pattern of the superfamily, because they are conservative.

For reconstructing the phylogenetic relationships of the superfamily, the principle of synapomorphy proposed by Hennig (1966) and the principle of parsimony of Nelson (1970) are used. The polarity of each morphocline of characters was determined according to new criterion: when each morphocline found in a give group and its closest related group has two or more character states, if the character state between the given morphoclines is identical, the state is the most primitive.

The conclusion of the present are summarized as follows.

1. PHYLOGENY OF THE SUPERFAMILY

(1) Branching pattern

(a) The superfamily Cobitoidea is considered to be a monophyletic group because it has four kinds of synapomorphy: the opisthotic is absent, the orbitosphenoid has the contact with the supraethmoid-ethmoid complex, the basibranchial series is shifted backward relative to the paired elements, and the ossified second preethmoid is present.

(b) Two families Cobitidae and Homalopteridae are recognized in the superfamily. The monophyly of the former is supported by two autapomorphous features: the movable lateral ethmoid and the socket-like articulation between the frontals and the supraethmoid-ethmoid complex. The monophyly of the family Homalopteridae is corroborated by three autapomorphous features: the Y-shaped tripus, the second descending process forming a part of the gasbladder capsule, and the laterally subdivided osseous capsule.

(c) The family Cobitidae is composed of two subfamilies Botiinae and Cobitinae. The subfamily Noemacheilinae, which has been regarded as one of

subfamilies of the family Cobitidae, is transferred from this family to the family Homalopteridae.

(d) The family Homalopteridae consists of two subfamilies Noemacheilinae and Homalopterinae. The fishes of the families Homalopteridae and Gastromyzonidae in Hora's sense (1950) are included in a subfamily, Homalopterinae, of the family.

(e) The monophyly of the subfamily Botiinae is corroborated by two features: the presence of the sesamoid bone and the parietal separated from the sphenotic. In this subfamily, two genera *Leptobotia* and *Botia* were recognized. There is no synapomorphy to support the erection of new taxon and the subdivision of the genus *Botia*.

(f) The subfamily Cobitinae is considered monophyletic because of the absence of the coronomeckelian, the orbitosphenoid separated from the pterosphenoid, the rod-shaped entopterygoid, the reduced cleithrum, the parapophysis fused with the ventral side of the centrum, and the second preural centrum fused with its haemal spine. The subfamily is divided into two large lineages: *Misgurnus-Acanthophthalmus* group and *Cobitis-Niwaella-Sabajenewia-Lepidocephalus-Acanthopsoides-Acanthopsis* group.

(g) The subfamily Noemacheilinae is considered to be monophyletic because of the presence of the prepalatine and the absence of the deep subtemporal fossa. In this subfamily, three genera were recognized: *Lefua, Noemacheilus* and provisionally *Vaillantella*. There is no cladistic evidence to support the subdivision of the large genus *Noemacheilus*. The close affinity between *Noemacheilus evezardi* and the fishes of the genus *Lefua* emphasized by Banarescu and Nalbant (1968) was not recognized.

(h) The monophyly of the subfamily Homalopterinae is supported by following synapomorphous features: the exoccipital separated from its fellow, the absence of the interhyal, the enlarged cleithrum, the mesocoracoid fused with the cleithrum, the enlarged pelvic bone, and the enlarged pleural rib.

(2) Evolutionary process

The evolutionary process inferred from the branching pattern was discussed from the view points of the feeding area and the habitat of the superfamily.

The ancestor of the superfamily was originally in the largest zone characterized by habitation near the bottom and feeding from the bottom. Though the ancestor of the cobitids was remained in this original zone, the homalopterid ancestor invaded into a smaller zone by adapting better to the bottom. In the family Cobitidae, botiines have been accomplished the specific diversity in the original zone, while the cobitines has diversified after encroaching to smaller zone characterized by utilizing the area under the bottom. In the family Homalopteridae, the ancestor of the Homalopterinae entered from the homalopterid zone to smaller zone by utilizing the torrential area of a river, though the noemacheiline ancestor remained in the homalopterid zone.

The feature of structure between the adaptive zones in the cobitoid evolution was that the larger zone completely included some smaller isolated zones in attribute. The evolutionary process which brought about the divergence of each lineage was the qualitative changes of the adaptive zones.

2. ZOOGEOGRAPHY OF THE SUPERFAMILY

The center of origin and the phylogenetic dispersal route of the superfamily were found out from the branching pattern into which the distributional patterns of species or subspecies examined are applied. The center of origin of the superfamily is considered to be South Asia and/or Southeast Asia-South Asia. The ancestors of the families Cobitidae and Homalopteridae were differentiated in Southeast Asia-South Asia and South China respectively. The family Cobitidae has phylogenetically dispersed from its ancestral distributional range toward Europe through Siberia and Northeast Asia. On the other hand, the family Homalopteridae has dispersed by two routes. One of them is toward West Asia, while the other is toward Europe or High Asia through Northeast Asia and Siberia. Regarding the phylogenetic dispersal route of the superfamily, the exchange between West Asia and Europe is hardly present.

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