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ADAPTIVE RADIATION IN THE MASTACEMBELOID FISHES

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ABSTRACT

The modifications of various characters such as body, head, scales, spines snout, jaws, pectoral girdle, caudal fin skeleton, vertebrae and alimentary canal have been traced in the three families of mastacembeloid fishes namely, Mastacembelidae, Pillaiidae and Chaudhuriidae. It is concluded that all these families constitute a homogeneous group and have evolved from some perciform fish, sharing most of the characters of Mastacembelidae (spring eels) in adaptation to different modes of living. Pillaiidae forms a link between Mastacembelidae and Chaudhuriidae, the latter, the extremely specialised fish, probably evolved through stages resembling Pillaiidae.

INTRODUCTION

Though appreciating the basic common characters between Mastacembelidae (Spiny eels) and Chaudhuriidae, Berg (1940) recognised two separate orders Mastacembeliformes and Chaudhuriiformes, respectively. Greenwood, Rosen, Weitzman and Myers (1966), however, grouped these families under the suborder Mastacembeloidei of the order perciformes. Yazdani (1976) created the family Pillaiidae for the genus *Pillaia* Yazdani and placed it under the suborder Mastacembeloidei.

The mastacembeloid fishes offer an exceptional opportunity for studying the adaptive radiation. They form a homogeneous group which is characterised by their eel-like body, non-protractile upper jaw, absence of pelvic girdle and fin, pectoral girdle attached to the vertebral column, short pectoral fin, elongated skull which gradually narrows anteriorly, large nasals, frontal and infraorbitals, small lateral ethmoid, and swim-bladder without an open duct. Among them, Mastacembelidae contains two genera, *Mastacembelus* and *Macrognathus* and Chaudhuriidae and Pillaiidae each contains single genus, *Chaudhuria* and *Pillaia*, respectively. Mastacembelidae occurs both in the Oriental and Ethiopian regions whereas Chaudhuriidae is restricted in distribution to the Inlé Lake, Upper Burma at an altitude of 3,000 ft. (See Annandale, 1918), and Pillaiidae to the Khasi Hills at an altitude of 3,500 ft. (See Yazdani, 1972, 1976) and plains of Assam in India (See Talwar, Yazdani and Kundu, 1977).

Both Pillaiidae and Chaudhuriidae can be distinguished from Mastacembelidae by the absence of spines before dorsal and anal fins, absence of scales and fleshy rostral appendage, and caudal fin lacking branched rays. Pill-

aiidae can be further distinguished from Chaudhuriidae by the caudal having 8-12 rays, which is united with the dorsal and anal and presence of a very indistinct fleshy rostral process.

Material and Method

The morphology of the following species has been studied. The classification of species followed is that of Greenwood, Rosen Weitzman & Myers (1966).

Mastacembelidae	*Mastacembelus armatus* Lacépède
Pillaiidae	*Pillaia indica* Yazdani *Pillaia khajuriai* Talwar, Yazdani and Kundu.
Chaudhuriidae	*Chaudhuria caudata* Annandale

The various characters of *M. armatus* and *P. indica* have been studied by dissecting specimens as well as by examining alizarin preparations. The type-specimens of *C. caudata* and *P. khajuriai* which is the only material of these species available at the Zoological Survey of India, Calcutta, have been examined. For comparison with the members of other families, informations about various characters of *Chaudhuria caudata*, the only known species of the Chaudhuriidae, have been taken from published work.

The main outlines of most of the figures have been drawn free hand.

Natural History

A brief account of the natural history of mastacembeloid fishes is given below :

The spiny eels (*Mastacembelidae*) : The spiny eels occur in plains as well as at high altitudes, in running and still waters, clear or muddy, usually hiding in crevices of rocks or among vegetation near the bank.

Sundar Raj (1916, p. 289) and Job (1941, p. 130) have observed that in an aquarium *Macrognathus aculeatus* and *Mastacembelus pancalus* both lie buried in the mud or sand during the day, while at night they swim about freely. Job (*op. cit*) says the following about the burrowing habits of *M. pancalus* : "The fish glides about the bottom nosing the substratum with its mobile, trilobed sensitive snout and selecting a suitable spot, wriggles itself into the substratum by a brisk side to side and forward movement until most of the body and tail are concealed. sometimes the tail sticks out as also the tip of the head". Deraniyagala (1932, p. 269) has made the following observations regarding the use of spines by *Mastacembelus armatus* for defensive purpose : "When held in the hand the fish wriggles backward and its short dorsal spines act like the teeth of saw inflicting a nasty slash in the palm of the inexperienced fishermen".

The food and feeding behaviour of these fishes is not properly known. However, the gut contents of some of these fishes have been found to contain eggs and fry of other fishes (Hamid Khan, 1934, p. 268), crustaceans, larvae of insects, coleopterans (Job, 1941, p. 131). These food items clearly suggest that the spiny eels are carnivorous.

These fishes grow to a large size. *Mastacembelus armatus* is said to grow to 3 ft. (Job, 1941).

The Indian eel-like fish (*Pillaiidae*) : I have observed the habits of *Pillaia indica* both in an aquarium and in its natural habitat. This little fish is very inactive and mostly spends its time lying at the bottom either buried in mud or clinging to some submerge vege-

tation along the edges of streams which have over-hanging vegetation (Fig. 1). It appears to have a very narrow range of habitat preference, and even in the same stream it occurs only in certain areas near the edge where the bottom contains a very fine mud. It is only found in those areas of the stream where the water is moving very slowly. Its ecological niche is so restricted that no other fish has generally been collected with it. It avoids light and tries to hide into the mud. It has been reported by *Khasi* people that this fish is also found in the paddy field (adjoining the streams) during the rainy season. Its swimming and crawling movements resemble those of the anguilliform fishes. It appears to be a hardy fish as I was able to bring by train a live specimen to Poona from the Khasi Hill, keeping it in a big jar containing water, a little mud at the bottom and a few aquatic plants.

P. indica does not seem to search for its food. It catches the moving food and gulps it while entangling itself to some submerged vegetation in the stream. The gut contents of this fish have been found to contain parts of mayfly (Ephemeroptera) naiads, parts of other insects and spores. This suggests that *P. indica* is also a carnivorous fish.

Pillaia khajuriai, the only other species in the family Pillaiidae, has been found to occur in the paddy fields of Garo Hills (Meghalaya) and in the Kaziranga Wild Life Sanctuary (Assam) which is situated on the southern bank of R. Brahmaputra, very close to Mikir Hills. The close resemblance

Fig. 1. A sketch of the habitat of *Pillaia indica* showing its way of life.

of *P. khajuriai* with *P. indica* suggests that it perhaps shares the habits of the latter.

Both *P. indica* and *P. khajuriai* do not grow to a large size : the mature specimens of *P. indica* range between 37—77 mm. in length, whereas the specimens of *P khajuriai*, so far available. vary in length from 57.0 86 mm.

The Burmese eel-like fish (Chaudhuriidae) : *Chaudhuria caudata* appears to be a high altitude species, for, it is so far restricted in distribution to Inlé Lake and a stream in Upper Burma. Its habits are unknown. However, Annandale (1918) stated that these fish were obtained in fishing baskets filled with peat and weeds and sunk in the Inlé Lake and also from dense vegetation at the edge of floating islands. This clearly suggests that *C. caudata* is a bottom dweller and perhaps hides under vegetation etc. Annandale (*op. cit*) also found that the stomach of a specimen of *C. caudata* was full of young crustaceans. This suggests that it is a carnivorous fish and perhaps moves around in search for food. The occurrence of *C. caudata* in the floating islands as well as at the bottom of the lake (see Annandale *op. cit*) clearly indicates that it is an active fish which swims around in search for food etc.

C. caudata does not grow to a large size : the largest mature specimen known so far is 52.0 mm. in total length (Annandale, *op. cit.*).

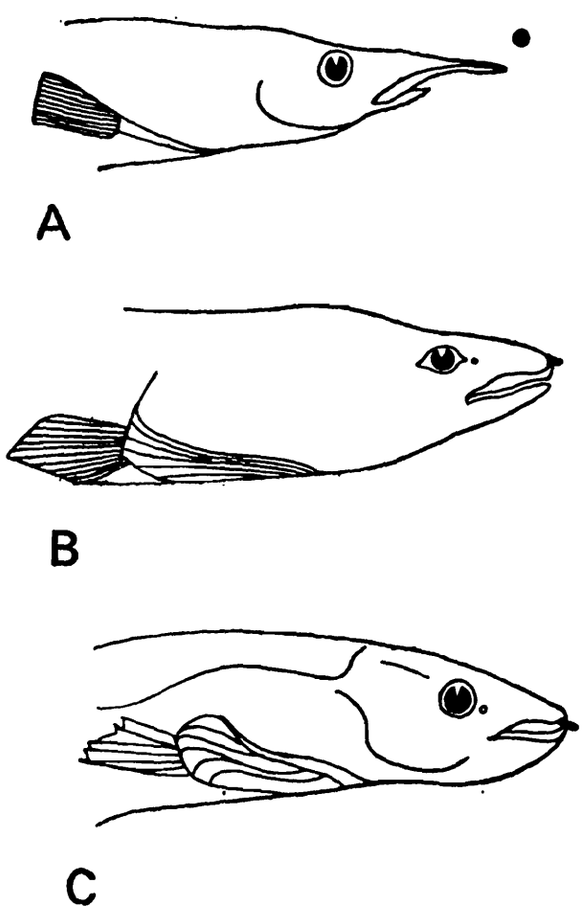

Fig. 2. Outline drawings (semidiagrammatic) of heads in A—Mastacembelidae, B—Pillaiidae, C—Chaudhuriidae.

Morphological Characters

The morphological characters showing various modifications in different groups of mastacembeloid fishes will now be described.

Body : In all the mastacembeloid fishes the body is eel-like, elongated (Fig. 6). In Mastacembelidae and Chaudhuriidae, the body is compressed whereas in Pillaiidae it is subcylindrical. The dorsal and anal fins are united with the caudal in Pillaiidae and some members of Mastacembelidae whereas in Chaudhuriidae the caudal fin is united to the dorsal and anal by a low membrane and gives it a characteristic appearance of a broom.

The body is covered with minute scales in Mastacembelidae but in Pillaiidae & Chaudhuriidae it is completely naked. Similarly, there are free spines before long dorsal and anal fins in Mastacembelidae but no such spines occur in other families.

Head : In *Pillaia indica* the head shows a characteristic depression, especially in the

preorbital region ; in *P. Khajuriai*, however, the head is rather conical and less depressed. In other families the head is somewhat conical, more so in Mastacembelidae owing to the rostral appendage (Fig. 2).

The eyes are almost dorsally placed in *P. indica* but in *P. Khajuriai* and other families (Mastacembelidae and Chaudhuriidae) they are situated laterally.

The mouth is subterminal in Mastacembelidae but terminal in Pillaiidae and Chaudhuriidae. (Fig. 2)

Snout : In Mastacembelidae, the snout is elongated and provided with a well-developed fleshy rostral appendage. It is supported by a cartilaginous rod, ending in a sensitive tip flanked by the tubular anterior nostrils. In Pillaiidae and Choudhuriidae the snout is short but in the former a very indistinct fleshy rostral process bearing the tubular anterior nostrils exists whereas in Chaudhuriidae, there is no trace of such a process.

Jaws : The upper jaw is non-protractile in all the mastacembeloid fishes. In Mastacembelidae, the upper jaw consists of two bones *viz.* a premaxilla bearing teeth and a toothless maxilla, as is found in all the perciform fishes (see Greenwood *et. al.*, 1966). In Pillaiidae (*P. indica*), however, the upper jaw consists of a single hockey-stick shaped bone bearing

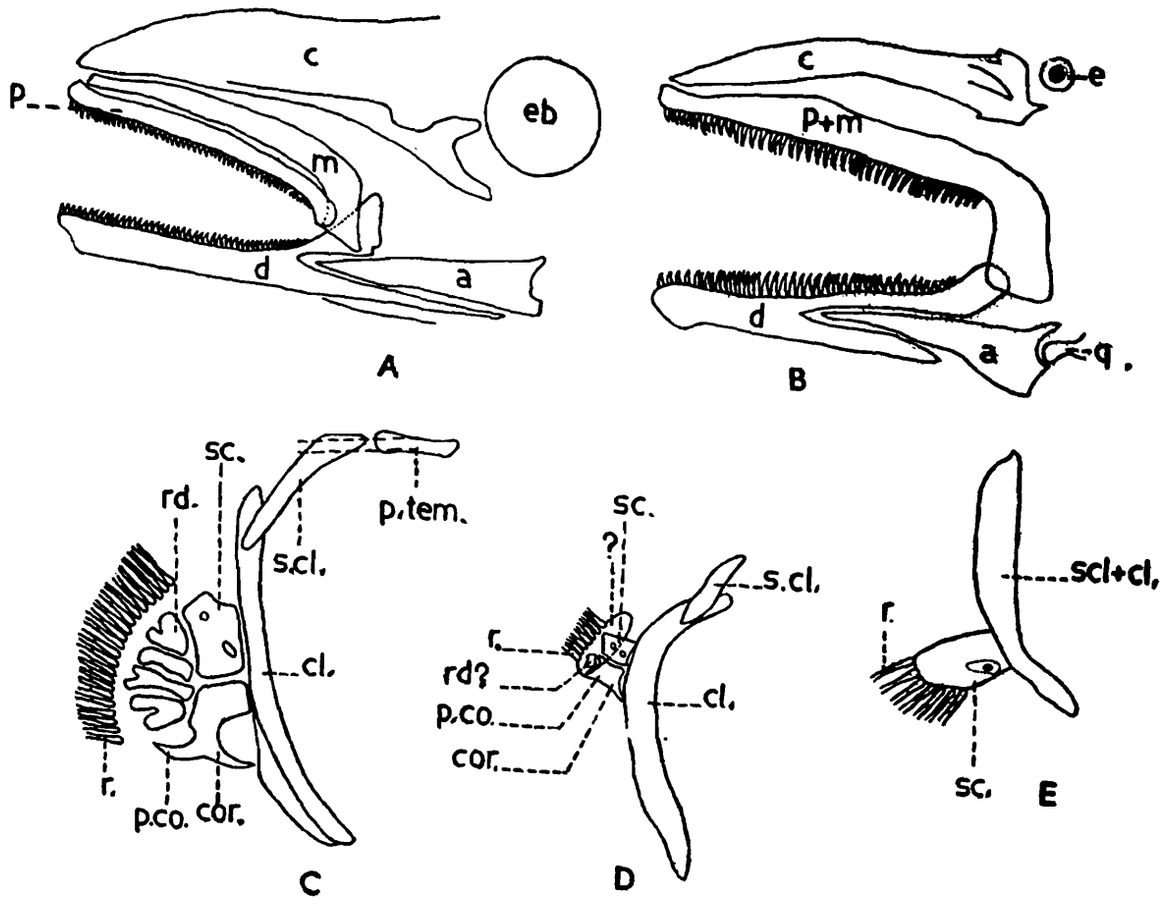

Fig. 2. Outline drawings (semidiagrammatic) (A—B) The jaw bones of, A—*Mastacembelus armatus*, B—*Pillaia indica*. (C—E) Pectoral girdles of C—*Mastacembelus armatus*, D—*Pillaia indica*, E—*Chaudhuria caudata* (Adopted from Annandale & Hora, 1923.)

teeth (Fig. 3 B), corresponding to the premaxilla of perciform fishes. But the jaw muscles, adductor mandibulae (A_1) inserts directly on the posterior ventral face of this bone. As in the perciform fishes this muscle inserts on the posterior ventral face of the maxilla, it appears quite probable that in *P. indica* the posterior half of the single upper jaw bone represents the maxilla. This view also finds support by the fact that premaxilla and maxilla of *Mastacembelus armatus* (Fig. 3 A) together give a hockey-stick shape rather comparable to the upper jaw bone of *P. indica.*

No proper account of the upper jaw of *Chaudhuria caudata* (Chaudhuriidae) is available. However, the tooth-bearing upper jaw bone in *C. caudata* which Annandale (1918) called "maxillary" appears to correspond to the upper jaw bone of *P. indica.* It seems probable that in *C. caudata* also the upper jaw consists of a single bone bearing teeth which represents both premaxilla and maxilla.

In all the three families, both the upper and lower jaws bear sharp conical, inwardly curved teeth.

Pectoral girdle : In Mastacembelidae, the pectoral girdle consists of a supracleithrum, attached by ligaments to the vertebra column, hypercoracoid with perforation, hypocoracoid with a strong post coracoid process ; four radials, two on the hyper and two on the hypocoracoid (Fig. 3 C), no mesocoracoid ; and no post-temporal but the lateral line canal is ossified in this region and posses through the supracleithrum. The pectoral fin contains 17—27 rays.

In Pillaiidae, the supracleithrum is attached

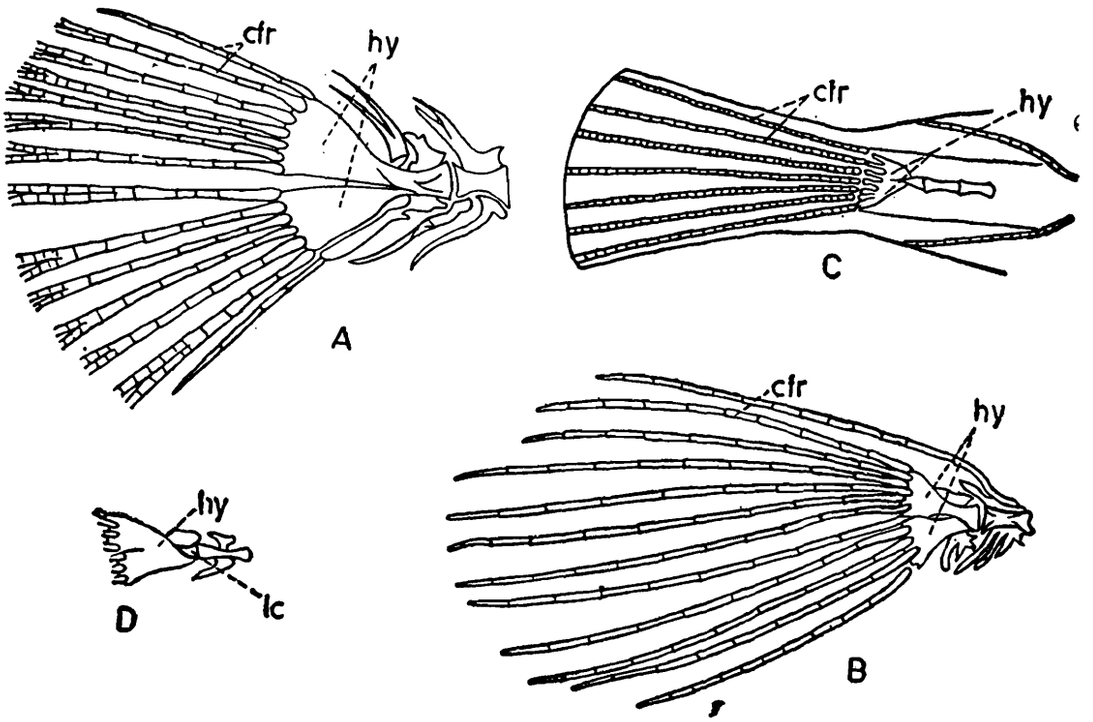

Fig. 4. Outline drawings of caudal fin skeleton of A—*Mastacembelus armatus*, B—*Pillaia indica*, C—Tail of *Chaudhuria caudata* (Adopted from Fig. 1 of Annandale, 1918 ; the hypural bones are represented diagrammatically and the dorsal and ventral elements of the vertebrae are omitted), D—Caudal fin skeleton of *Chaudhuria* (*After* White, 1918.)

to the vertebral column, cleithrum is present but post-temporal bone, including its lateral line component, is absent ; hypercoraiod with perforation, hypocoracoid with a post-coracoid process and a small differentiated bone, which might represent one of the radials, is present. In addition, a roughly oval, flat bone lying median to hyper & hypocoracoids is undetermined (Fig. 3 D). is attached to the vertebral column. Hypo- and hypercoracoids are not distinguishable but a large, conspicuous perforation in this region indicates the presence of hyper coracoid. The radials are not differentiated. The pectoral fin contains only 6 rays.

Caudal fin skeleton : In Mastacembelidae the caudal fin is homocercal, short, either

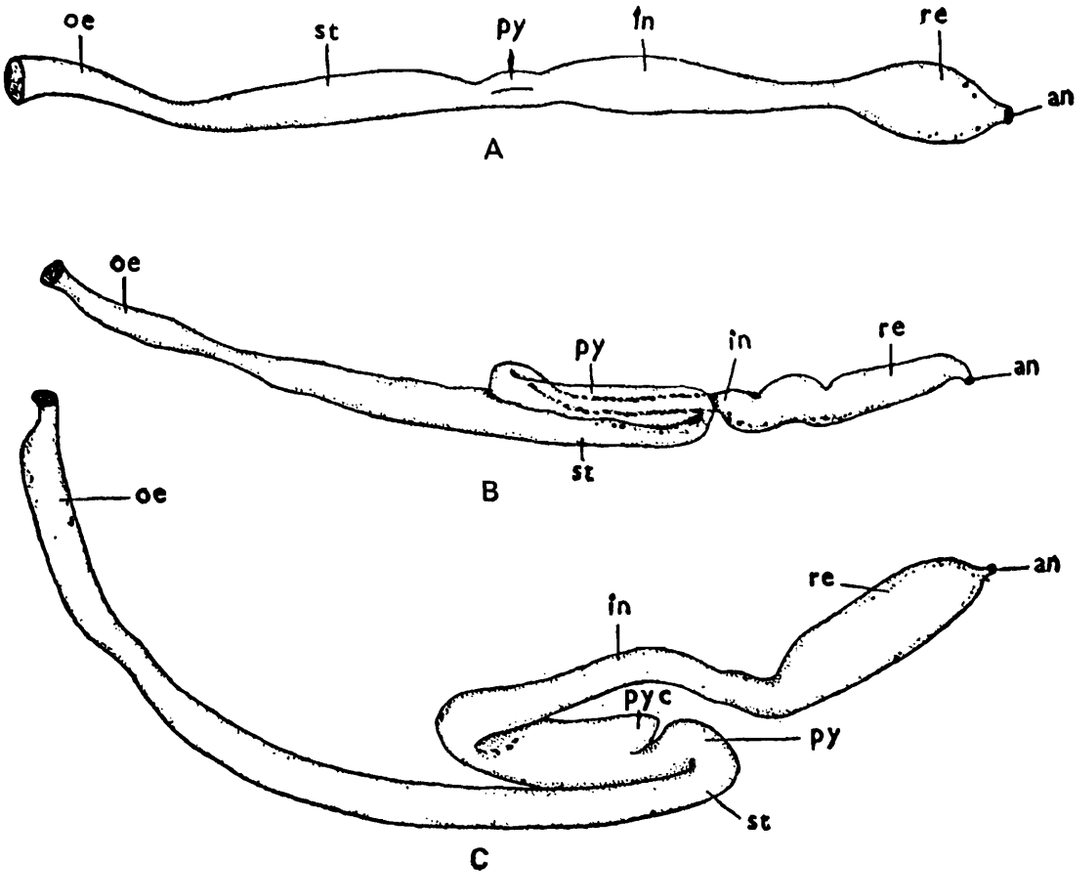

Fig. 5. Outline drawings of alimentary canals of [A—*Chaudhuria caudata* (*After* Annandale, and Hora 1923, enlarged), B—*Pillaia indica*, C—*Mastacembelus armatus*.

The pectoral fin contains 7—9 rays in *Pillaia indica* and 19-20 rays in *P. khajuriai.*

Annandale & Hora (1923) have given a brief account of the pectoral girdle of *Chaudhuria caudata* ; their illustration of this bone is reproduced in Fig. 3 E. The pectoral girdle lacks post-temporal, and the supracleithrum which is completely fused with the cleithrum, confluent with the dorsal and anal or narrowly separated. Five to seven hypurals bearing 15 or more branched rays are present (Fig. 4 A).

In Pillaiidae the caudal fin is homocercal, short, confluent with the dorsal and anal. Two large hypurals which are united at their bases and fused with the last centrum, bear 8—10 unbranched rays (Fig. 4 B).

In Chaudhuriidae (See Annandale 1918, White-house, 1918) the caudal fin is homocercal, fairly long and separated by the dorsal and anal. Two large hypurals which are united at their bases and firmly attached to or fused with the last centrum bear 7 unbranched rays (Fig. 4 C. D)

Vertebrae. In Mastacembelidae, the number of vertebrae varies from 85-96 (37-39 precaudal, and 47-48 caudal) (Sufi 1956) and in Pillaiidae and Chaudhuriidae it is 62 (26 pre-caudal and 36 caudal) and 70, respectively. Thr first few vertebrae in all these fishes possess flattened neural spine : in Mastacembelidae the first 4 to 8 vertebrae, in Pillaiidae first 3 or 4 vertebrae and in Chaudhuriidae at least first two vertebrae bear flattened neural spine.

Alimentary canal : In Mastacembelidae, the oesophagus is narrow and tubular. The stomach is bent a little in front of the pyloric end in a V- or U-shaped fashion ; the tubular cardiac portion of the stomach widens out behind and particularly at the bend it consists of the long anterior limb, the bend and the short posterior limb, ending in the pylorus. There are two lateral pyloric caeca. The intestine is long, narrow and bent like a 'U'. It consists of a short limb, the bend and a long second limb. The second limb is directed forwards and ends in the rectum. The rectum is elongated, fusiform and is much wider than the intestine (Fig. 5C).

In Pillaiidae, the oesophagus is narrow and tubular ; it narrows behind and passess gradually into the stomach. The stomach is long and tubular and is bent on itself in front of the pyloric end in a narrow U-shaped fashion (Fig. 5B). It, therefore, consists of a long anterior limb, the bend and the short posterior limb, ending in the pylorus. There are no pyloric caeca. The intestine is narrow, tubular and bent like a 'U' running posteriorly almost under the bend of the stomach. It, therefore, consists of a short limb, the bend a long second limb. The second limb is

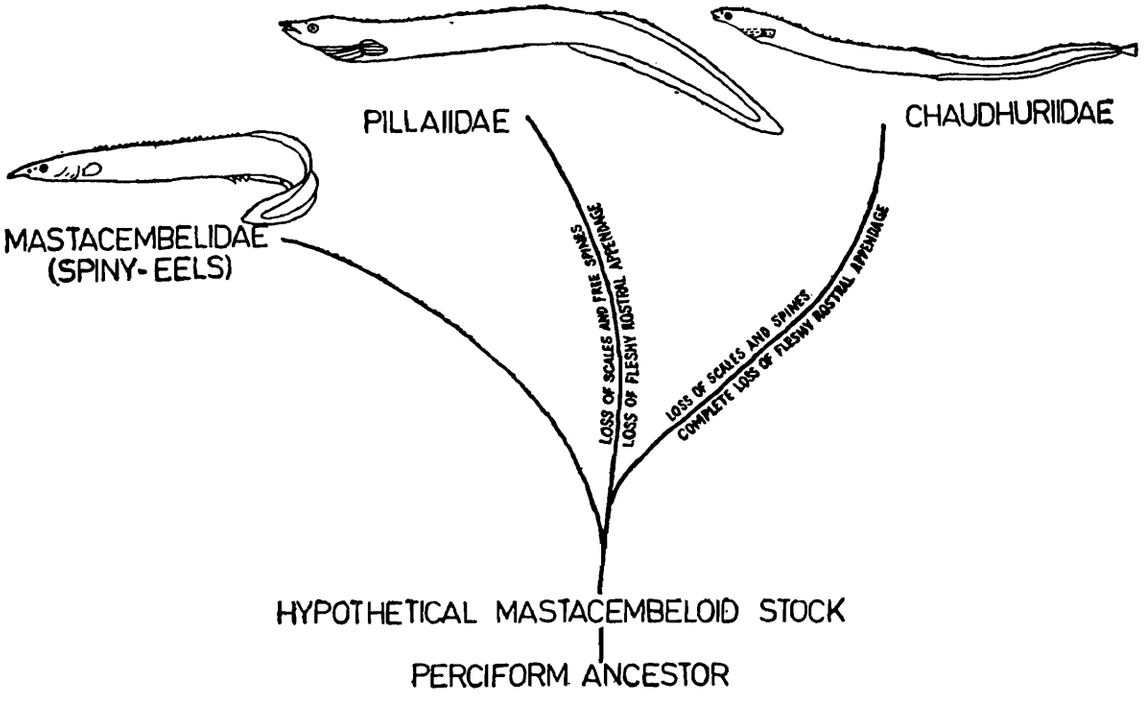

Fig. 6. Diagram showing my conception of the evolutionaryrelationships of Mastacembeloid fishes.

a narrow tube which ends in the rectum. The rectum is wide in front and narrow, tapering behind. It has two annular constriction in its front half.

The account of alimentary canal of *Chaudhuria caudata* have been given by Annandale & Hora (1923) and Mitra & Ghosh (1931). In Chaudhuriidae, the alimentary canal is almost straight, the oesophagus is more or less funnel-shaped and is imperceptibly continuous with the stomach. The stomach is long, straight, tubular and somewhat tapering. The pyloric portion of the stomach is externally demarcated from the cardiac portion by a faint oblique groove. There are no pyloric caeca. The intestine is wide, tubular and runs straight to the rectum which is somewhat club-shaped, wide in front, narrow and tapering behind. It is separated from the intestine by a distinct annular constriction (Fig. 5A).

Discussion

The various morphological characters of mastacembeloid fishes will now be discussed in relation to their habits and habitats.

The eel-like, elongated body in mastacembeloid fishes is well suited for hiding in crevices, and for concealing in mud or sand or under some vegetation. Both Chaudhuriidae and Pillaiidae appear to rely on concealment alone for escaping enemies, whereas in Mastacembelidae the protection from enemies appears to be achieved both by way of concealment and by use of spines as an organ of defence. The compressed body with scales and spines in Mastacembelidae is equipped well for exploiting various types of habitat and this has perhaps resulted in their wider distribution. The members of Pillaiidae which have subcyclindrical, naked body, have only succeeded in exploiting narrow range of ecological niches where they can easily borrow in mud or hide under vegetation to capture the live prey. These fishes have specialised to burrow in fine mud, coming out and hiding under vegetation for food etc. The streams and paddy fields wherefrom *Pillaia* spp. have been recorded do not have many predators. This factor seems to have prevented these fishes from exploiting new niches where they might face greater danger of predation. Probably, this is one of the important reasons why members of Pillaiidae are restricted in distribution to a small area in the north-eastern part of India, although they are capable of living in plains as well as at high altitudes. In Chaudhuriidae, the body is rather compressed and lacks scales and spines. The naked body is better suited for hiding under dense vegetation *etc.* rather than in crevices in rock, or in mud or sand. These fishes appear to have specialized for living at high altitudes where predators are generally few. Probably, this very specialisation is largely responsible for their occurrence in a very restricted area of upper Burma.

In mastacembeloid fishes, a gradual broadening of the forehead is seen from Mastacembelidae. through Pillaiidae to Chaudhuriidae (Fig. 2). In Mastacembelidae, the forehead is extreamely conical due to the prolongation of the snout into an appendage, but in Pillaiidae it is rather conical (more conical in *P. khajuriai* than in *P. indica*) and in Chaudhuriidae it is less conical. The forehead in Mastacembelidae is well and Pillaiidae is well suited for their burrowing-type way of life but that of *Chaudhuria* appears better adapted for living under dense vegetation etc. rather than for burrowing.

The position of eyes in mastacembeloid fishes also show a gradual change in the field of vision. Both Mastacembelidae and Chaudhuriidae which move around in search

for food have lateral eyes, suited to see almost all sides. But in Pillaiidae, especially in *P. indica* where the eyes are placed dorsally due to remarkable depression of the forehead, the field of vision is mainly restricted to the dorsal side. The position of eyes in these fish is, therefore, well-suited for a dorsal vision while they are lying on the bottom either buried in mud or clinging to some vegetation.

The gradual loss of the fleshy rostral appendage from Mastacembelidae through Pillaiidae to Chaudhuriidae clearly suggests that it has occurred owing to change in habits of the latter two families. The members of Mastacembelidae have subterminal mouth and search their food at the bottom by the aid of tactile organ-the fleshy rostral appendage. But the fishes of other two families have terminal mouth and take in the moving food which they catch both at bottom and in midwater. This gives them a wider choice for food in streams or lake. The faint trace of fleshy rostral appendage in Pillaiidae appears to be a vestigial organ, showing a stage transitional between fully develoved rostral appendage, as in Mastacembelidae, and without any trace of it, as in Chaudhuriidae.

The upper jaw is non-protrusible in all the mastacembeloid fishes. However, it shows a greater range of adaptive radiation than what is known so far in any group of bony fishes. The loss of protrusion in the upper jaw appears correlated with their habit of catching food either from the bottom or by way of getting it into the mouth with respiratory current. In Mastacembelidae, the toothed premaxilla and a toothless maxilla, like that of a percoid fish, are present. But in the other families these bones have fused (presumably in Chaudhuriidae) to provide a stronger upper jaw bone for the purpose of catching live prey more efficiently. Since the function of maxilla in acathopterygian fish is to help protrude the upper jaw (See Alexander, 1967), the loss of free maxilla in Pillaiidae (and Chaudhuriidae) is a case of specialization, unparallel in the evolutionary history of acanthopterygian fishes.

The pectoral girdles and fins of mastacembeloid fishes also show loss or fusion of bony components from Mastacembelidae through Pillaiidae to Chaudhuriidae (Fig. 3C-E). The gradual reduction in the number of pectoral fin rays among the mastacembeloid fish is found in this order : *Mastacembelus* spp. 17-27 ; *Pillaia khajuriai* 19-20 *Pillaia indica* 7-9 and *Chaudhuria caudata* 6. A well-developed pectoral fin is generally found in fishes which are active swimmers because the pectorals are used as brakes. Since none of the mastacembeloid fishes are active swimmers, the pectoral fins and girdles appear to have undergone degeneration, more in Pillaiidae and Chaudhuriidae than in Mastacembelidae. This is in correlation with the fact that members of Mastacembelidae are more active than those of the other families.

The caudal fin is the main propulsive organ in fishes. It shows a great deal of variation among the mastacembeloid fishes. The members of Mastacembelidae possess a well-developed caudal skeleton to support the caudal fin, possessing a higher number of branched rays (15 or more). But the fishes of other families have caudal skeletons with reduced numbers of elements which appears correlated with the fact that both in Pillaiidae and Chaudhuriidae the caudal fins possess a rather small number of unbranched rays. The spiny eels are more active and possess a better developed caudal fin and caudal skeleton, whereas members of Pillaiidae and Chaudhuriidae are less active and possess a rather poorly developed caudal fin and caudal skeleton.

Among generalised perciform fishes the

number of vertebrae is 24. (See Greenwood *et. al.* 1966). In the mastacembeloid fishes, however, the number of vertebrae has increased owing to the elongation of body for an eel-like way of life. The members of Mastacembelidae grow to a large size and possess a high number (85-96) of vertebrae. The members of other families are small sized fishes and contain 62-70 vertebrae.

In all the mastacembeloid fishes, a few of the anterior vertebrae possess flattened neural spine which probably provides an additional support to the cranium. The number of anterior vertebrae, possessing flattened neural spine, in Mastacembelidae is higher than that of Pillaiidae and Chaudhuriidae. This seems to be correlated with the fact that spiny eels grow to a large size whereas the fishes of other two families do not.

The alimentary canal is basically similar in all the mastacembeloid fishes, but a gradual reduction in length has occurred from Mastacembelidae through Pillaiidae to Chaudhuriidae. As Suyehiro (1942) pointed out that the digestive organs of fishes depend upon their phylogeny as well as feeding habits it would seem reasonable to believe that the basic similarities in the alimentary canals between these three families is owing to their common descent, and the various modifications have occurred in relation to differences in their feeding habits.

Among mastacembeloid fishes, the pyloric caeca are present only in members of Mastacembelidae. Sinee the pyloric caeca are unrelated to the nature of diet (See Khanna, 1962) and their occurrence is believed to be meant for increasing the general surface of the intestine (Al-Hussaini, 1947) it seems probable that the pyloric caeca in spiny eels are also meant for increasing the surface area of the alimentary canal.

CONCLUSION

All the three families, Mastacembelidae, Pillaiidae and Chaudhuriidae share basic common characters. The gradual modification of various characters in each of these families has led to clear adaptive radiation.

These fishes appear to have evolved from a perciform stock through stages resembling spiny-eels. Pillaiidae is considered less specialised than Chaudhuriidae and it seems probable that the latter evolved from a stock resembling Mastacembelidae through stages comparable to Pillaiidae (see Fig. 7). Among Pillaiidae which shows affinities with both Mastacembelidae and Chaudhuriidae, *Pillaia khajuriai* exhibits a closer resemblance with the members of spiny-eels.

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The following abbreviations are used in figs. 3, 4 & 5.

a articular ; an anus ; c cranium ; cfr caudal fin ray ; cl cleithrum ; cor hypocoracoid ; d dentary ; e eye ; eb eye-ball ; hy hypural ; in intestine ; lc last centrum ; m maxila ; oe oesophagus ; p premaxilla ; pco post coracoid process ; p. tem. post-temporal canal bone ; py pylorus ; pyc pyloric caeca ; q quadrate ; r rays ; rd radials ; re rectum ; sc hypercoracoid ; scl supracleithrum ; st stomach.