

The Relationships of the Mastacembelid and Synbranchid Fishes

William A. Gosline

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Abstract Evidence is presented for a relationship between the Mastacembelidae, with *Chaudhuria*, and the Synbranchidae. In addition to a number of features associated with elongation of the body held in common by the two groups, there are similarities in head structure. Those of the olfactory apparatus, the upper jaw articulation, and the suspensorium are discussed. It is hypothesized that the mastacembelids and synbranchids have evolved in different directions from a common elongate ancestor which was itself a specialized derivative of the lower percoid fishes.

The mastacembelids, with the related *Chaudhuria* (Annandale and Hora, 1923), and the synbranchids are primarily freshwater fishes widely distributed in the tropics. All are elongate fishes, but in other respects they differ greatly. The mastacembelids, partly revised by Sufi (1956) and Roberts (1980), are spiny fishes which have developed a unique, flexible trunk-like extension of the snout. The synbranchids have neither spines nor snout extension, and many of their modifications are in a worm-like direction, e.g., the complete loss of rays in the dorsal and anal fins, the degenerate eyes, and the backward displacement of the heart (Rosen and Greenwood, 1976).

It is generally agreed that both mastacembelids and synbranchids are derived from higher teleosts. Among characteristics indicating such an origin are the exclusion of the maxillaries from the gape and features of the otoliths (Frost, 1929, 1930) and gill arches (Nelson, 1969; Rosen and Greenwood, 1976). Regan's (1912) conclusion that the mastacembelids have a perciform ancestry is also generally accepted. The derivation of the highly modified synbranchids is more obscure (Rosen and Greenwood, 1976). Among the various synbranchid affinities that have been suggested, McAllister's (1968) proposal of a relationship between the synbranchids and mastacembelids is supported here.

The synbranchids have evolved much farther in an eel-like direction than the mastacembelids, but certain features often found in elongate fishes are held in common by the two groups. These include the numerous vertebrae, the re-

duction in the caudal fin and the loss of the pelvic fins, the restriction of the gill openings to the lower half of the body, the reduction of the eye, and the wide separation of the two nostrils on each side of the head. Although these features are here considered to have been inherited from a common ancestor, an alternate interpretation is that they represent independent, parallel developments (Rosen and Greenwood, 1976). However, certain features apparently associated with the original elongation of the head in the two groups, a process that seems to have been partially obscured by secondary developments in the synbranchids (see below), do not occur elsewhere. It is these peculiarities, notably in the olfactory apparatus, the upper jaw articulation, and the suspensorium, that most clearly point towards a relationship between the two groups.

Material

The morphological features described in the following account are primarily based on *Mastacembelus tanganikae* (University of Michigan Museum of Zoology Cat. No. 199894) for mastacembelids and on *Ophisternon aenigmaticum* (UMMZ 202930) for synbranchids. These species seem to be fairly representative of their groups.

Comparative anatomy

In mastacembelids the nasal apparatus is peculiar in that the anterior nostril has been carried forward along the side of the trunk-like snout extension. This nostril leads back, via a long tube, into an expanded olfactory cavity.

The posterior nostril is a valved opening in front of the eye. The long olfactory cavity is broader than deep. It is completely roofed by a laminar nasal bone that has a long, firm medial attachment to the ethmoidal part of the cranium. The olfactory nerve enters through the posterior wall of the nasal cavity and is continued forward to its anterior end by the rachis of the olfactory organ. This rachis extends along the medial wall of the olfactory cavity, giving off two series of laterally-extending branches (lamellae), one passing across the roof of the cavity and the other across its floor. These two series nearly meet at their tips but have an interspace between their central portions. Posterolaterally, the floor of the nasal cavity has an opening which passes down into an accessory sac underneath the lacrimal bone.

The olfactory apparatus of the synbranchids appears to be a reduced and somewhat modified version of the specialized conditions present in mastacembelids. The anterior nostril is in the upper "lip". The posterior nostril is a valved opening in front of the eye in *Macrotrema*, but above the eye in other synbranchids (Rosen and Greenwood, 1976). In *Ophisternon aenigmaticum* the nasal bone is represented by tubular ossicles. The long nasal sac is only slightly expanded as compared to the tube that extends forward from it to the anterior nostril. This tube is straight and passes through a well-marked notch on the upper surfaces of the maxillary and premaxillary. The olfactory organ extends the length of the nasal sac but is represented only by a rachis with a few small lateral branches. A hole in the posterolateral part of the floor of the sac leads into an accessory lacrimal sac as in mastacembelids.

Of the olfactory features in mastacembelids and synbranchids, the valved posterior nostril and the lacrimal accessory sac occur in various other fishes (see, for example, Burne, 1909), but the anterior nostril and its tube appear to be more specialized than elsewhere.

In many long-snouted groups, e.g., the syngnathoids (Jungersen, 1908, 1910) and various triacanthoids (Tyler, 1968), the skull and suspensorium extend forward together. The mastacembelids and synbranchids, however, are among those fishes in which the skull and upper jaw articulation have extended anteriorly ahead

of the suspensorium, with the result that the usual articulation between the front end of the palatine and the maxillary has been lost. In fishes with this type of head elongation, which include such diverse forms as eels, *Indostomus* (Banister, 1970), and *Luciocephalus* (Liem, 1967), various modifications occur in both the upper jaw articulation and in the anterior part of the suspensorium.

As to upper jaw articulation, the mastacembelids and synbranchids have lost the usual acanthopteran premaxillary protrusion (Alexander, 1967; Gosline, 1981) and the structures associated with it. There is no rostral cartilage. The premaxillary has no ascending process, and the maxillary, as noted, has no palatine articulation.

In mastacembelids and synbranchids the maxillary and premaxillary are firmly attached to one another by membrane for almost their entire length and appear to move together. The maxillary has no firm proximal articulation with the skull. In both groups the premaxillary has a direct articulation with the lower surface of the anterior end of the skull. In synbranchids this articulation is of a ball-and-socket type, but in mastacembelids the premaxillary slides over the anteroventral end to the skull (see below).

The closest approach to the mastacembelid-synbranchid upper jaw articulation that I can find is that recorded for the armored *Indostomus* by Banister (1970).

The differences between mastacembelids and synbranchids are here considered to be the result of divergent trends of evolution from a common ancestor. Certain aspects of this divergence, namely the trunk-like extension of the snout in mastacembelids and modifications of structure associated with feeding in synbranchids, are discussed below.

The trunk-like extension of the snout is variably developed in mastacembelids and is absent in the related *Chaudhuria*. In its developed form the trunk seems to be a specialization for perceiving weak, local sensory stimuli, for it carries forward nearly to its tip the tubes from two different sensory systems: olfactory and lateralis. At its most highly specialized condition in *Macrogathus* the "trunk" also bears tooth plates on its ventral surface (Sufi,

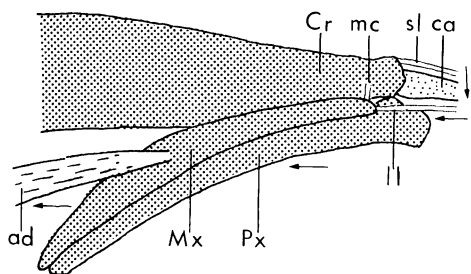


Fig. 1. Semidiagrammatic lateral view of the cranium and upper jaw of *Mastacembelus tanganikae*. Arrows indicate the presumed direction of movements when the maxillaris section of the M. adductor mandibulae contracts on both sides of the head. ad, Maxillaris section of the M. adductor mandibulae; ca, cartilaginous projection from the front of skull; Cr, skull; ll, lateral ligament to cartilaginous projection; mc, ligament from maxillary to skull; Mx, maxillary; Px, premaxillary; sl, median dorsal ligament to cartilaginous projection.

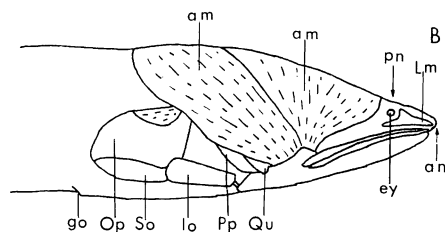
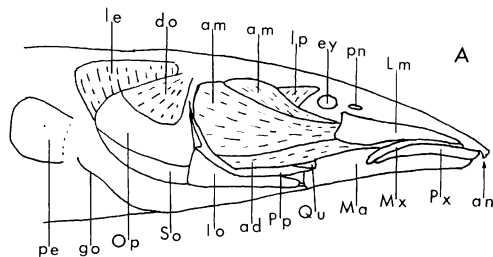


Fig. 2. Lateral view of heads of (A) *Mastacembelus tanganikae* and (B) *Ophisternon aenigmaticum*. Skin and nasal bones removed. ad, Maxillaris section of the M. adductor mandibulae; am, mandibular sections of M. adductor mandibulae; an, anterior nostril; do, M. dilatator operculi; ey, eye; go, gill opening; Io, interopercle; le, M. adductor plus levator operculi; Lm, lacrimal; lp, M. levator arcus palatini (covered by the M. adductor mandibulae in *Ophisternon*); Ma, mandible; Mx, maxillary; Op, opercle; pe, pectoral fin; pn, posterior nostril; Pp, preopercle; Px, premaxillary; Qu, quadrate; So, subopercle.

1956; Roberts, 1980). In the living mastacembelid the "trunk" can be moved in various directions (Walter Rainboth, pers. comm.). It is the association of the upper jaw with this movement that is discussed below.

In mastacembelids the central support for the "trunk" is provided by a cartilage-like extension from the anterior end of the skull (Fig. 1), and a ligament passes forward from the skull over this cartilage along its midline. Presumably tension in these two features tends to straighten out the "trunk". Lowering of the "trunk" appears to be brought about by the retraction of a pair of ligaments that extend along ventral to the "trunk" on either side. The cause of such retraction is apparently contraction of a maxillaris component of the M. adductor mandibulae acting through the maxillary bone. Two ligaments extend from the proximal head of the maxillary bone, which, as noted, has no direct articulation with the skull. One of the two passes upward to the skull and is long enough to permit fore and aft movements in the maxillary head. The other is the ligament noted earlier that passes forward along the lower side of the "trunk". Contraction of the maxillaris component of the M. adductor mandibulae apparently not only lowers the "trunk" but also

causes the premaxillaries to move posteriorly, causing the premaxillary heads to slide across their articulations with the skull.

In the mastacembelids the major specialization of the "trunk" affects preocular head structures. In synbranchids the most notable specializations are postocular. So far as the head is concerned they include the development of eel-like branchial pouches and, more pertinent for present purposes, a series of specializations associated with the development of a more powerful bite.

Mastacembelids are relatively small-mouthed fishes with a jaw bite. Synbranchids have a larger gape (Figs. 2B, 3B) with the principal bite between the mandible and ectopterygoid-palatine dentition on the roof of the mouth. The stronger bite is indicated by a number of features, most

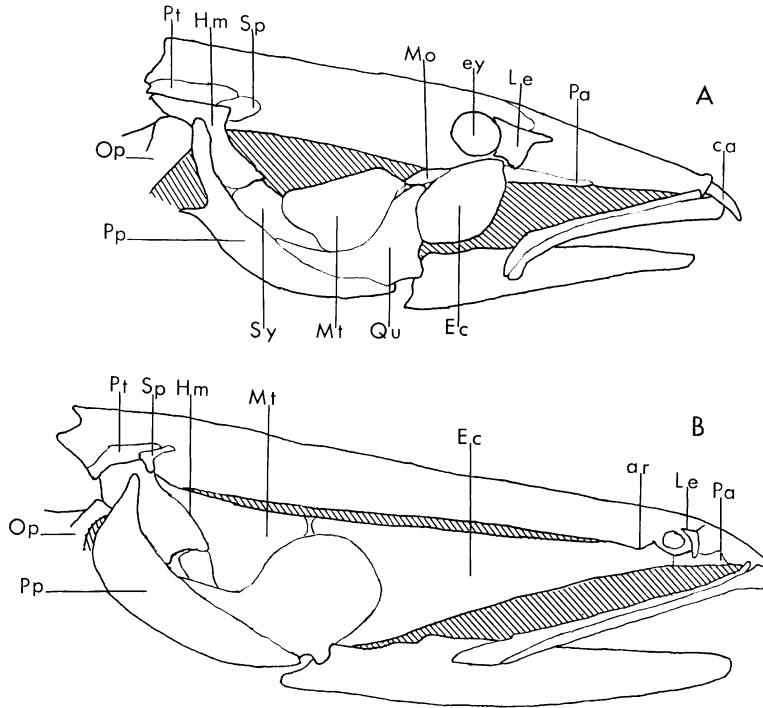


Fig. 3. Lateral views of the head skeletons of (A) *Mastacembelus tanganikae* and (B) *Ophisternon aenigmaticum*. Lacrimal and nasal bones removed; spaces between functional units cross-hatched. ar, Anterior suspensorial articulation with skull; ca, cartilaginous projection from the front of skull; Ec, ectopterygoid; ey, eye; Hm, hyomandibular; Le, lateral ethmoid; Mo, mesopterygoid; Mt, meta-
pterygoid; Op, opercle; Pa, palatine; Pp, preopercle; Pt, pterotic; Qu, quadrate; Sp, sphenotic; Sy, symplectic.

notably by the great expansion of the M. adductor mandibulae (Fig. 2B). This expansion seems to have had two secondary effects. First, it appears to have forced the rudimentary eye anteriorly. Second, presumably to strengthen the support against the contraction of this large muscle, an additional postoptic abutment has developed between the suspensorium and the skull. This additional abutment is well forward of that between the hyomandibular and the skull, between the frontal bone of the skull and the ectopterygoid (Fig. 3B), normally a preoptic component of the suspensorium. (In another fish with a greatly enlarged M. adductor mandibulae, the ophiocephalid *Channa*, there is also an additional abutment between the suspensorium and the skull. Primarily because of this Berg in 1940 suggested a possible relationship between ophiocephalids and synbranchids. However, among other differences the additional abutment in *Channa* is between the normally

postoptic metapterygoid, not the ectopterygoid, and the skull.)

The development of an additional abutment between the ectopterygoid and the skull in synbranchids can apparently be traced back to the original method of elongation in the mastacembelid-synbranchid head. In both groups the eye has been carried somewhat forward during skull elongation. This occurs elsewhere, for example, in the species *Lates calcarifer* within the genus *Lates* (Greenwood, 1976), and contrasts with a type of head elongation in which the snout lengthens but the eye remains well to the rear as in, for example, syngnathoids, *Indostomus*, and triacanthoids. However, in the mastacembelid-synbranchid group, as already noted, forward extension of the suspensorium has not kept up with elongation of the skull. In *Mastacembelus* the ordinarily subocular mesopterygoid has become small and mostly postocular, and a greatly enlarged

ectopterygoid is partly behind the eye (Fig. 3A). In *Ophisternon*, with the eye even farther forward, the mesopterygoid has disappeared, and a postocular part of the ectopterygoid meets the frontal (Fig. 3B), as previously discussed. Indeed, the enlargement of the ectopterygoid and the reduction or loss of the mesopterygoid appear to be diagnostic characteristics of the combined mastacembelid-synbranchid group.

Relation to other fishes

Of the two groups considered in this paper, the mastacembelids seem to have retained far more ancestral features than the synbranchids and hence provide more information about the derivation of their common ancestor. As to mastacembelids, Regan (1912) stated: "the skeleton indicates that these fishes are related to, but more specialized than, the Percomorphi, but they show no particular affinity to any group of Percomorphous fishes." I can only add that *Lates calcarifer* appears to provide an adequate morphological prototype for the line of specializations that developed in the mastacembelid-synbranchid ancestor. As to the teeth on the third hypobranchials of mastacembelids noted by Nelson (1969) and others, these seem to be foreshadowed by the third hypobranchial tooth plates in *Lates* (Greenwood, 1976). In the lengthening of the snout and the loss of premaxillary protrusion, the percoid genus *Percina* suggests a route over which the mastacembelid upper jaw articulation might have evolved. The above considerations merely suggest that the mastacembelids are derived from some rather basal type of percoid fish. However, there is a large morphological gap between any "percomorphous" fish and mastacembelids.

As to classification, my preference is to consider the mastacembelid-*Chaudhuria* group and the synbranchids as separate suborders of an Order Synbranchiformes. Such an order can be readily diagnosed as follows: elongate higher teleosts without pelvic fins, gill openings restricted to the lower half of the body, anterior nostril in the upper lip or farther forward, ectopterygoid enlarged, mesopterygoid reduced or absent, premaxillary excluding the maxillary from the gape, non-protrusile, without ascending process, articulating directly with the skull, and maxillary without palatine articulation.

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(Museum of Zoology, University of Michigan, Ann Arbor, Michigan 48109, U.S.A.)

トゲウナギ科とタウナギ科の類縁関係

William A. Gosline

トゲウナギ科 (*Chaudhuria* 属を含める) とタウナギ科は、体の伸長にともなう各種の形態的特性を共有するとともに、嗅覚器官の性状、上顎部の骨の接続状態や懸垂骨など頭部の構造で類似している。このような観察に基づいて、この両科は同一の祖先型から別方向に分化したものと推定される。分類学的には、両者をタウナギ目の別亜目とするのが適当と考える。このタウナギ目のなかではトゲウナギ亜目の方が原始的であるが、これとスズキ目のどの科が近いかは不明である。ただアカメ科や Percidae に若干の近似形質が認められるので、スズキ目の中の原始的な祖先型から分岐したと考えてよいであろう。