Movable head armature in higher teleostean fishes

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Synopsis

A general pattern of movable head armature, composed of serrations on the borders of the lacrimal and preopercle and of a spine on the opercle, evolved among early acanthopterygians and is retained among many basal percoid families. In the more specialized higher teleostean groups this pattern is modified in various ways. Scorpaeniform fishes develop a suborbital stay with which the lacrimal is rigidly united. Elsewhere lacrimal serrations are generally absent, but in some bottom-resting forms preopercular or opercular armature becomes highly specialized. An association between head armature, fin spines, and changes in locomotion in the development of the acanthopterygian state of teleostean evolution is suggested.

Introduction

The spines and serrations on movable head bones of higher teleostean fishes are a forward extension of the defensive armature provided by the fin spines on the body. These serrations or spines on the head, like the fin spines, can be erected or depressed by the fish. Such armature, when erect, provides sharp-pointed extensions to the perimeter of the fish and when depressed interferes minimally with forward movement. A different type of armor, not considered here, consists of bony plates on the body and/or head, and occurs somewhat sporadically throughout the teleostean series, e.g., in the catfish *Loricaria*, the pipefish *Syngnathus*, the pine-cone fish *Monocentris*, and in the boxfish *Ostracion*.

The serrations and spines discussed below are on the lacrimal, preopercular, and opercular bones and on the suborbital stay of scorpaeniform fishes. The suborbital stay is a new development within the Scorpaeniformes, but the armature on the other three units has a longer history going back,

among modern teleosts, to the percopsiform *Aphredoderus*.

Eversion of the lacrimal, preopercle, and opercle is caused by the lateral expansion of the oral-opercular cavities, a type of movement associated with feeding throughout much of teleostean history. Expansion and contraction of the preopercle and opercle are under direct muscular control, but eversion of the lacrimal seems to be the indirect result of movement in the maxilla.

Serrations on the lacrimal bone

Lacrimal serrae, when present, are along the lower rim of the posterior part of that bone (Fig. 1A). This lower border can be flared outward relative to the articulation between the dorsal part of the lacrimal and the lateral ethmoid bone of the skull. The shaft of the maxilla passes forward internal to the lower part of the lacrimal bone. The posterior end of the maxilla moves outward with lateral expansion of the oral cavity and its shaft then forces the
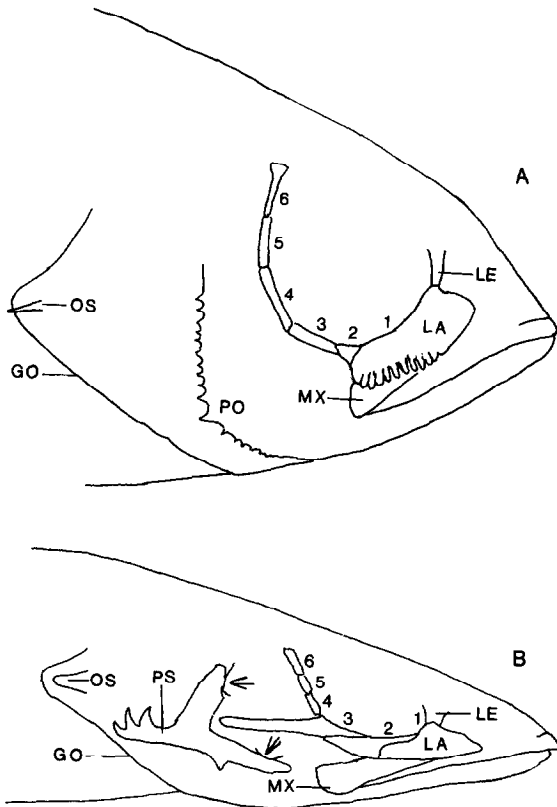
Fig. 1. Lateral view of head armature and infraorbital bones in (A) *Terapon jarbua* (UMMZ 100566) and (B) *Leptocottus armatus* (UMMZ 66222 and 128946). Infraorbital bones are numbered. Arrows in B indicate areas of articulation between the preopercle and the rest of the suspensorium. GO = gill opening, LA = lacrimal, LE = lateral ethmoid, MX = maxilla, OS = opercular spine, PO = preopercle, and PS = preopercular spine.

Table 1. Representative genera of different percoid families that have a serrated lacrimal bone. The families are listed alphabetically.

Ambassis (Ambassidae)	*Percichthys* (Percichthyidae)
Arripes (Arripidae)	*Perca*[1] (Percidae)
Archoplites (Centrarchidae)	*Holacanthus* (Pomacanthidae)
Lates (Centropomidae)	*Pomatomus* (Pomatomidae)
Enoplosus (Enoplosidae)	*Priacanthus* (Priacanthidae)
Diapterus (Gerreidae)	*Scatophagus* (Scatophagidae)
Kuhlia (Kuhliidae)	*Niphon* (Serranidae)
Kyphosus (Kyphosidae)	*Terapon* (Teraponidae)
Quinquarius (Pentacerotidae)	*Toxotes* (Toxotidae)

[1] In *Perca flavescens* lacrimal serrations vary from moderately well-developed to absent.

lower border of the lacrimal outward and upward. To judge from preserved specimens, these movements can occur with the mouth closed.

A serrated lacrimal occurs in *Aphredoderus* and in at least some members of the Caproidae, Beryciformes, Mugilidae, Anabantidae and Perciformes, as well as in some Scorpaeniformes in a modified form (see further). Lacrimal serrations thus seem to be an inherited character among lower acanthopterygian (acanthopteran, acanthomorph) fishes, even though they, like other components of the movable head armature, are very frequently lacking.

In the Perciformes, lacrimal serrations are present in at least some members of most lower percoid families (Table 1), but are absent in most of the derivative perciform suborders, the only exceptions known to me being the very different genera *Dascyllus, Trichodon,* and *Acanthemblemaria.* Lacrimal serrations are also absent in the more specialized higher teleostean orders Batrachoidiformes, Lophiiformes, Pleuronectiformes, and Tetraodontiformes. It appears that lacrimal serrations, once lost, have rarely been redeveloped and that, among perciform families the presence of lacrimal serrations often provide an indication of proximity to the base of the great perciform adaptive radiation.

The suborbital stay

The suborbital stay, a bony strut that extends back across the cheek (Fig. 1B) from the third infraorbital bone (counting the lacrimal as the first), is a defining character for the scorpaeniform fishes. It has been treated at length by Matsubara (1943) and others. Only certain aspects of this stay are discussed here.

To judge from its least developed and presumably primitive state in *Sebastes,* the stay originated as an unarmed ossification around an extension from the infraorbital lateralis canal. In *Sebastes* the stay ends well short of the preopercle. When, as in most scorpaeniform genera, the suborbital stay reaches to, or nearly to the preopercle the posterior end of the stay moves outward with the preopercle

(see further) and there is an extensive reorganization in the infraorbital series of bones.

In percoids, as in scorpaeniform fishes, there are two slightly different types of movement in the infraorbital chain of bones. In percoids the outward flaring of the lower border of the lacrimal usually carries the second infraorbital bone with it; there is no such flaring in the third and more posterior infraorbitals which, except the uppermost, simply move with the cheek; and a subocular shelf usually extends in under the eye from the third infraorbital (Smith & Bailey 1962). The differential in movements between the two parts of the infraorbital series in percoids is mediated by a slight swiveling between infraorbitals two and three. In the advanced type of scorpaeniform suborbital stay (Fig. 1B) the first three infraorbital bones are rigidly united to form a single structural unit; the subocular shelf (still present in *Sebastes*) is lost; and mediation of the differential in movement between the two parts of the infraorbital series has moved up to above the third infraorbital. This more specialized type of suborbital stay may have bony projections all along it, including spines on the lower border of the lacrimal, e.g., in *Scorpaena*.

The suborbital stay undergoes various types of further specialization within the Scorpaeniformes. For example, in *Prionotus* it becomes part of the general dermal plating of the head and loses its separate eversibility. At the other extreme, dactylopterids have evolved a method for everting the posterior end of the stay farther outward than the preopercle. In dactylopterids the stay is divided into two parts. As the preopercle moves out the short posterior part of the stay doubles under the long anterior section, forcing the posterior end of that section outward away from the preopercle.

Preopercular and opercular armature

Eversible armature is often present on the preopercle and opercle of higher teleosts (Fig. 1A). Movements in these two bones are related but different and are controlled by different muscles. With lateral expansion of the oral-opercular cavities during suction feeding the posteroventral part of the suspensorium including the preopercle moves outward. The front of the opercle also moves out, but outward movement of the posterior, armed border is limited by the necessity for maintaining a seal between the posterior rim of the gill cover and the body if a suction into the mouth is to be created.

In lower acanthopterygians a spine on the opercle and serrations on the preopercle are often present in the same fish. In some of the more specialized bottom-resting teleosts either the preopercular or the opercular armature may become highly specialized, but not both together.

In callionymids and various scorpaeniform groups the usual preopercular serrations are replaced by a long, often complex spine extending back from the posteroventral angle of the preopercle. In *Callionymus* this spine, when erected, moves out relative to the gill cover, to which it is connected by a distensible membrane. Here, most of the posterior border of the gill cover is not even free from the body, and the gill opening is reduced to a small hole.

The most extreme type of preopercular specialization occurs in certain cottids. In *Leptocottus* (Fig. 1B) the posteroventral part of the suspensorium not only moves out as usual, but the preopercular spine moves outward relative to the suspensorium. *Leptocottus* has a pair of movable, hinge-like articulations between the preopercle and the rest of the suspensorium. To judge from muscle attachments, when the m. levator arcus palatini contracts it not only pulls the suspensorium outward but swings the preopercular spine anterodorsally even farther.

The opercle is usually a large bone that forms the main component of the gill cover. Anteriorly it articulates relatively high on the posterior border of the suspensorium. It frequently ends posteriorly in a spine that extends to or slightly beyond the border of the gill cover (Fig. 1A). However, as noted, the amount to which such a spine can be everted is limited by the requirement for maintaining a seal between the border of the gill cover and the body.

In batrachoidids the usual opercular condition is considerably modified, and the opercle ends in strong armature that can be erected independently
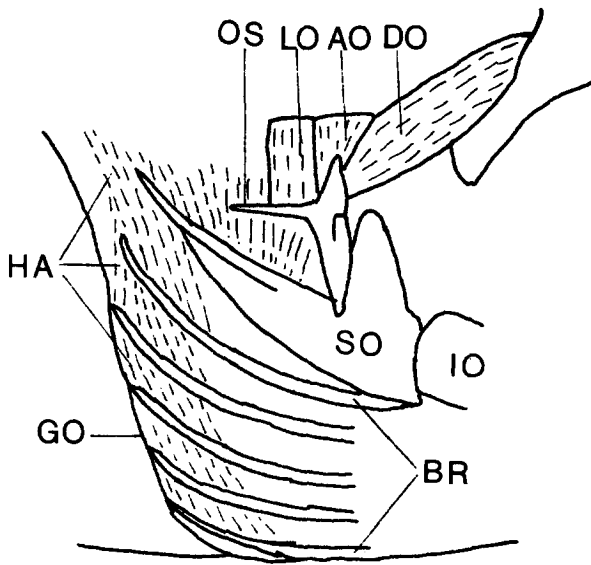
Fig. 2. Gill cover of *Porichthys notatus* (UMMZ 63601), right side. AO = adductor operculi, BR = branchiostegal rays, DO = dilatator operculi, GO = gill opening, HA = hyohyoidei adductores, IO = interopercle, LO = levator operculi, OS = opercular spine, and SO = subopercle.

of the gill cover that extends well behind it (Fig. 2). Here the gill cover can be closed against the body by contraction of the m. hyohyoidei adductores (Winterbottom 1974; see also Borcea 1907) which extend well up behind the opercle.

The evolution of movable head armature in teleostean fishes

Movable head spines of specialized types are present here and there among modern lower teleostean fishes, e.g., in the loach *Botia* and in the catfish *Ancistrus*. However, a pattern of head armature consisting of serrations on the lacrimal and preopercle and a spine on the opercle seems to be a development, first represented in *Aphredoderus,* that appeared in acanthopterygians at about the same evolutionary state as fin spines. The development of movable armature protecting both the head and body seems, in turn, to be associated with changes in locomotion during teleostean evolution.

With some specialized exceptions, lower teleosts

emphasize the forward component of locomotion, where armature can only cause a drag. To judge primarily from changes in paired-fin structure (see, for example, Gosline 1980) acanthopterygians have developed an increased ability to maneuver in restricted areas, and many of them capitalized on this ability. Here, eversible defensive armature seems to have been sufficiently advantageous to outweigh any drag it causes on forward swimming. In the more generalized acanthopterygians forward swimming, maneuvering, and defensive armature seem to provide an integrated series of systems that together diminish predation. These three acanthopterygian features are all represented in many lower percoids today.

This inverse relationship between forward locomotion and armature appears again in larvae and half-grown fishes. In these weakly-swimming developmental stages there is often, among oceanic forms of acanthoptherygians, extensive bony armature of various types (see Moser et al. 1984). Some of these types foreshadow a lesser development of the same armature in adults, but others, e.g., in chaetodontids, are quite different.

With the assumption that a pattern of spines or serrations on the lacrimal, preopercle, and opercle is an inherited character among lower acanthopterygians it becomes necessary to postulate that the absence of such armature in so many acanthopterygians is the result of secondary loss. This postulate is accepted here.

Among the more advanced acanthopterygian groups the movable head armature is usually absent, but in some bottom-resting forms its preopercular or opercular components have become specialized, and scorpaeniform fishes have evolved a different type in the suborbital stay.

Acknowledgements

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