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The Intercalar Bone in the Eel-pout Family Zoarcidae (Osteichthyes)

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With 17 Figures

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Abstract

The presence and relative development of an intercalar bone within the zoarcid family was studied. The bone, although reduced (anteriorly never reaching the prootic) is present in all "northern" (genera *Eucryphycus*, *Gymnelus*, *Lycodes* and *Macrozoarces*) and "southern" (senera *Austrolycus*, *Crossostomus*, *Dadyanos*, *Iluocoetes*, *Lycenchelys*, *Notolycodes*, *Phucocoetes*, *Piedrabuenia* and *Plesienchelys*) zoarcids examined. The reduction of the bone within the family clearly parallels the one observed in stichaeoid sister groups, related to their tendency toward an elongated body and eel-like movements, with a progressively reduced importance of the pectoral fin and girdle. The ontogeny of the bone, observed in southern species, clearly shows an extracranial dermal origin, and points to an only secondary skull-bone status.

Introduction

The intercalar or "opisthotic" bone of the hinder part of the neurocranium, although mentioned and illustrated in *Zoarces viviparus* by REGAN (1912) was explicitly regarded as absent in the eelpout family in the most recent comprehensive revision of the family (ANDERSON 1984). The presumed loss of this bone was considered as one of the apomorphies differentiating the zoarcids from other sister groups (ANDERSON 1984).

Research on the cranial osteology of Southamerican Zoarcidae has shown a well developed intercalar in all genera observed. To evaluate the extent of this character within the whole family, specimens of "northern" species were also examined.

Developmental stages of southern species were analyzed to learn about the ontogeny of the skull and pectoral girdle and their mutual relationships.

This work, although initially motivated by the finding of a structure not recognized by the last revisor, was performed putting a much heavier emphasis on the functional and evolutive significance of the bone than on its mere presence or absence.

Materials and Techniques

The osteological terminology employed follows that of MAKUSHOK (1958) and ROSEN and PATTERSON (1969).

List of institutional and anatomical abbreviations used

ISH: Ichthyological Collection of the Institut fuer Seefischerei Hamburg.

MLP: Idem, Museo de La Plata (Argentina).
NMC: Idem, National Museum of Canada, Ottawa.
AHF: anterior facet of hyomandibular.
BOC: basioccipital
EPI: epiotic
EXO: exoccipital
INT or I: intercalar
I-PL: intercalar-posttemporal ligament
PAS: parasphenoid
PHF: posterior hyomandibular facet
POT: posttemporal
PR: prootic
PT: pterotic
SOC: supraoccipital
TL: total length, as measured from the tip of snout to the end of the tail.
V–VII, IX, X: foramina of cranial nerves

Northern Zoarcidae examined

Eucryphycus californicus Anderson, 1984, (= *Maynea californica* Starks and Mann, 1911). One specimen ca. 185 mm TL, 36°48.1′ N, 121°48.5′ W, 75 fathoms, 16 Oct., 1974, R. Kliever coll. Uncatalogued.

Gymnelus viridis Fabricius, 1780. One specimen 158 mm TL. Assistance Bay. 74°38.4′ N, 94°18.4′ W, 25 July, 1962. (Formerly NMC 62 0399)

Lycodes pacificus (Collett, 1879). One specimen 230 mm TL. Burke Channel, 52°06.5′ N, 127°24′ W, 28 May 1965, Arai and Scoggan coll. (Formerly NMC 65259, as *Lycodopsis pacificus*).

Lycodes palearis Gilbert, 1895. One specimen 255 mm TL, female, Behring Sea, 53°58.0 N, 166°33.0 W, 274 m, 28 Nov. 1965, (Formerly NMC 700027).

Lycodes reticulatus Reinhardt, 1835. One specimen, 150 mm TL, 48°24.8 N, 70°49.0 W, 101 m, 21 June 1962. (Formerly NMC 700027).

Lycodes vahli Reinhardt, 1831. Two specimens 240 and 290 mm TL. Labrador Sea, 58°58.5′ N, 60°12′ W, 27 October, 1964, J. Hannan coll. (Formerly NMC 64762).

Macrozoarces americanus (Schneider, 1801), Two specimens, 240 and 305 mm TL, Northumberland Strait. 46°40′ N, 64°33′ W, July 1959, (Formerly NMC 590322).

Southern Zoarcidae examined

Austrolycus depressiceps Regan, 1913. Ten specimens, 66 to 310 mm TL., from the intertidal zone of Ushuaia and Isla de los Estados (Tierra del Fuego, Argentina). Nov. 1967 to Dec. 1967. Uncatalogued.

Austrolycus laticinctus (Berg, 1895). Eight specimens, 370 to 760 mm TL, from the intertidal zone of Puerto Deseado, Argentina, 1969–1972. Uncatalogued.

Crossostomus chilensis (Steindachner, 1898). One specimen, male 410 mm TL. Ushuaia, Tierra del Fuego. Uncatalogued.

Crossostomus fasciatus (Loennberg, 1905). Thirteen specimens, 79–322 mm TL, from the intertidal zone of Puerto Deseado. Uncatalogued.

Dadyanos insignis (Steindachner, 1898). Seven adults, 183–263 mm TL, from the intertidal zone of Puerto Deseado, June 1962 – May 1972. Eight postlarvae and young fish (24–46 mm TL), either obtained with the parents or reared in the laboratory between April and December 1972. All uncatalogued.

Iluocoetes effusus (Smitt, 1898). Eight specimens, 72–165 mm TL from the intertidal zone of Puerto Deseado, March 1965–July 1972. Postlarvae and young fish, 25–32 mm TL, obtained with their parents, some of them reared in the laboratory. Uncatalogued.

Iluocoetes fimbriatus Jenyns, 1842. Five specimens, 74—370 mm TL, obtained in Puerto Deseado, Ushuaia and Mar del Plata. Uncatalogued.

Lycenchelys bachmanni Gosztonyi 1977. One specimen, 207 mm TL, "Shinkaimaru" cruise I, St. 62, 48°58.0′ S, 59°00′ W, 554—558 m. Uncalalogued.

Notolycodes schmidti Gosztonyi, 1977. One specimen, 427 mm TL, "Shinkaimaru", cruise I, St. 14, 38°59′ S, 55°25′ W, 420—430 m. Uncatalogued.

Phucocoetes latitans Jenyns, 1842. Two adults: one male 123 mm TL, one female 122 mm TL. One young fish ca. 32 mm TL. All from the intertidal zone of Puerto Deseado. Uncatalogued.

Piedrabuenia ringueleti Gosztonyi, 1977. One specimen, 191 mm TL. "Shinkaimaru" cruise V, St. 66, 47°26.3′ S, 60°29.3′ W, 509 m. MLP 25.4.80.20.

Plesienchelys stehmanni (Gosztonyi, 1977) Anderson, 1984. One specimen, 229 mm TL, male, same data as *P. ringueleti*.

Most of the observations were made in whole specimens, either cleared and stained with my enzime-based presoaker method (Gosztonyi 1984) or dissected and locally stained with a few drops of alizarin solution. Two technical or observational points were relevant to the success of this research. The first one concerned the observation medium after alizarin staining of the skulls. Instead of pure glycerine in which the observations are usually made, water or strongly dilluted ethanol were used. The latter media make the connective tissues along the sutures opaque and thus whitish under incident light, making the limits of the different bones much easier to detect and follow, which is not usually the case with pure glycerine. The second point refers to the proper identification of the intercalar bone itself. This can be easily made since the bone acts as the attachment point of the intercalar-posttemporal ligament joining the lower arm of the posttemporal bone to the hinder part of the skull (Devillers 1958, Makushok 1958).

Results

A) General osteological pattern of the hinder part in a zoarcid fish

The following description is mainly based on the skull of an adult *Austrolycus laticinctus*, 245 mm TL, (Fig. 6—7), but it also includes information obtained from smaller specimens and from a disarticulated skull of a much larger, 760 mm long specimen.

The hinder part of the skull is roughly triangular when seen from behind, with its dorsal surface almost flat. It is formed by the usual ring of concentric bones surrounding the foramen magnum.

The ventralmost bone is the more or less fan-shaped basioccipital with a massive facet for the attachment of the first vertebral centrum. It has a pointed anterior process which is lodged in a "V" shaped groove of the parasphenoid, and a "W" shaped system of grooves in which the posterior forked part of the latter bone is lodged. Laterally the basioccipital joins the exoccipitals through internally interdigitating and externally smooth sutures.

The exoccipitals are roughly triangular from behind, they are pierced by cranial nerves IX and X and bear well developed facets for the attachment of the upper facets of the first vertebra. The IXth nerve emerges from the ventrolateral face of the bone and the Xth from near its lower apex just short of the articular condyle.

Dorsally each exoccipital meets its homologue at the middle of the upper rim of the foramen magnum, and, through a single suture, joins the hinder part of the supraoccipital which is thus excluded from the latter foramen.

Anteriorly the exoccipitals join the prootics through a wide cartilaginous smooth suture. Dorsally they join the pterotics and opisthotics through strongly interdigitating sutures. Posterodorsally, also through an interdigitating suture, each exoccipital joins the epiotic and, centrally the centralmost apex of its homologue as stated above closing the bony ring. Internally, the exoccipitals along with the prootics and pterotics contribute to the various cavities lodging the internal ear system.

The strongly developed pterotics acting as dihedral angles form the outermost border of the skull, closed posteriorly by a roughly vertical plate joining the exoccipitals. Their dorsolateral portion, parallel to the outer rim, bears a partly closed furrow lodging the hinder part of the postorbital canal of the cephalic lateral-line system. The posterior tip of these bones, which protrudes as a strut is connected to the lateral tabulars in which the cephalic canal goes backward to the pectoral girdle. At about their lateral mid-point they have a concave articular facet for the posterior attachment of the hyomandibular bone. Their medialmost dorsal part joins the epiotics and parietals through strongly interdigitating sutures. At the pterotic-epiotic suture both bones are bent downward forming a conspicuous furrow or fossa parallel to the lateral rim.

The epiotics form the upper posterior edge of the skull. A strong, pointed process protrudes from their upper angle for the attachment of the upper arm of the posttemporal. Internally the epiotics are divided in two concave areas by a sort of columnar structure uniting the upper and lower posterior planes of the bones. Anteriorly the epiotics are joined to the parietals, laterally to the pterotics and ventrally to the exoccipital bones. All the corresponding sutures are very strong and externally almost indistinguishable, but very well seen from within the brainkase as cartilaginous smooth sutures which are triradiate in the sense Gregory (1933).

The intercalars or "opisthotics" are roughly rectangular and lie upon the hinder part of the exoccipital-pterotic suture, covering less than one half of the latter suture. They are extended as a blade protruding from the posterior lateral edge of the braincase, continuous with similar blade-like expansions of the pterotics and exoccipitals. Their dorsal portion serves as attachment point of the ligament coming from the lower arm of the posttemporal bone, and therefore has an important role in the support of the pectoral girdle.

B) The intercalar in Northern species

Eucryphycus californicus, (Fig. 1). Intercalar well developed, quadrangular, covering about one third of the exoccipital-pteoric joint, with its hinder apex conspicuously protruding from posteroventral margin of skull. The sutures with exoccipital and pterotic are smooth but the bone is strongly attached to the neurocranium.

Gymnelus viridis, (Fig. 2). Intercalar well developed, subcircular, covering about one half of the exoccipital-pterotic articulation. Its hinder apex beyond posterior tip of pterotic. Easily detachable.

Lycodes pacificus, (Fig. 4). Well developed, more or less quadrangular, joined to exoccipital and pterotic through an interdigitating and a smooth suture respectively. It is strongly attached to the neurocranium and it covers about one half of the exoccipital-pterotic joint.

Lycodes palearis. Intercalar well developed, quadrangular and strongly attached, covering about one half of the exoccipital-pterotic articulation. Suture with exoccipital interdigitated, suture to pterotic smooth.

Lycodes reticulatus. Intercalar well developed, subtriangular, its hinder apex only slightly protruding, and nearer to the tip of prootic than to its own tip. Easily detachable.

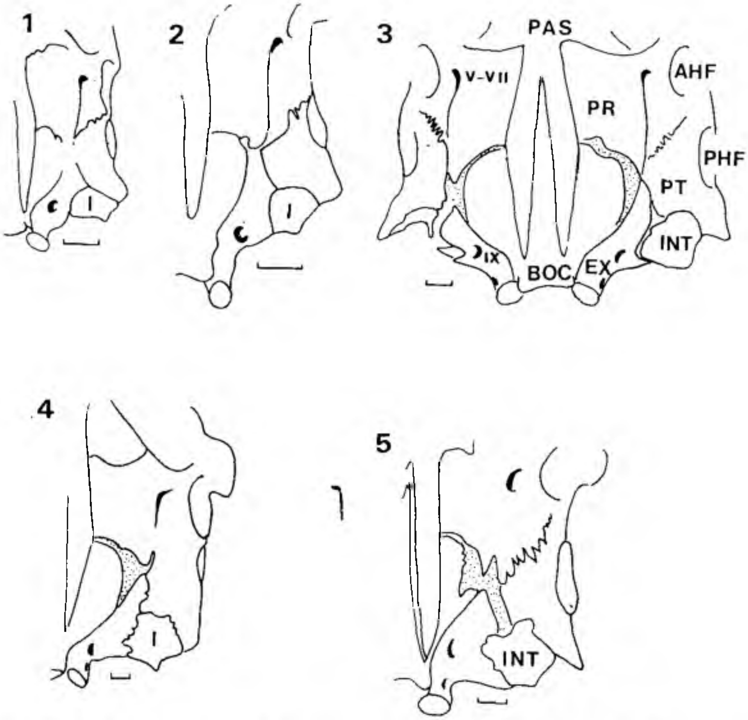

Fig. 1—5. Ventral view of the posterior part of basicranium in Northern zoarcid fishes. (Scale 1 mm)

Fig. 1. *Eucryphycus californicus*, ca. 185 mm TL
Fig. 2. *Gymnelus viridis*, 158 mm TL
Fig. 3. *Lycodes vahli*, 240 mm TL, the right intercalar was lost during dissection
Fig. 4. *Lycodes pacificus*, 230 mm TL
Fig. 5. *Macrozoarces americanus*, 240 mm TL

Lycodes vahli, (Fig. 3). Well developed, hinder apex protruding from posteroventral margin of skull, and about equidistant from the prootic and its own tip. Sutures with with exoccipital and pterotic interdigitating and smooth respectively. In the examined specimen, the right opisthotic was removed to show the attachment area, just above and at each side of the pterotic-exoccipital suture.

Macrozoarces americanus (Fig. 5). Well developed, roughly quadrangular, covering about one half of the exoccipital-pterotic joint and protruding from the posteroventral margin of skull. Sutures with exoccipitals and pterotics smooth or only slightly interdigitating producing a very loose attachment to the neurocranium.

C) The intercalar in Southern species

Austrolycus depressiceps. In very young specimens, about 66 mm TL, the intercalar is triangular, very small (covering less than one third of the exoccipital-pterotic suture) and apposed to the ventrolateral wall of the skull. It is very loosely attached to the neurocranium, since the articulations with both the pterotic and the exoccipital are wide and not interdigitating. In older specimens the bone becomes longitudinally elongated (reaching to about the mid-point of the exoccipital-pterotic joint) with the articulation to the exoccipital interdigitated, but the articulation to the pterotic remaining smooth, as a parallel line with the lateral margin of the skull.

Austrolycus laticinctus (Fig. 6—7). In specimens longer than 374 mm TL, the intercalar is well developed and well attached to, but never fused to the neurocranium. It covers less than one half of the exoccipital-pterotic articulation. The suture with the exoccipital is always interdigitating and the one with the pterotic is smooth and straight, but becomes interdigitated in very large specimens (about 700 mm TL).

Crossostomus chilensis (Fig. 8). Only one very large, 410 mm TL, specimen was available. The intercalar is indistinct, apparently by the fusion with the exoccipital, which is articulated to the pterotic through a strongly interdigitating suture. The fusion to the exoccipital seems to be the particular scheme in genus *Crossostomus* as will be seen in *C. fasciatus*.

Crossostomus fasciatus (Fig. 9). The intercalar is present although in a markedly regressive state, somewhat difficult to interpret.

In the largest specimens it is undoubtedly not distinct, and seems to be fused to the exoccipital and articulated to the pterotic through an interdigitating suture.

In rather large specimens, about 230 mm TL, though small, triangular, it is distinct and easily detachable, but in the smallest specimen examined it is indistinct and seems to be fused to the exoccipital at an earlier stage. In specimens of intermediate lengths the intercalar is either distinct or fused without following any length dependant pattern.

Dadyanos insignis (Fig. 10). The intercalar is well developed, longitudinally elongated and articulated to the exoccipital and pterotic through smooth sutures. It covers from one third to one half of the exoccipital-pterotic joint. The attachment to the neurocranium is very light in younger specimens but becomes stronger with age through the fusion to either the exoccipital or pterotic bones.

The ontogenetic development of the bone was followed in alizarin-stained larvae, postlarvae, and young fish, and no trace of it could be detected in specimens below 40 mm TL. The bone is well developed and distinct in two young fishes 42.0 and 46.0 mm TL, reared in the laboratory between May and December 1972.

Iluocoetes effusus (Fig. 11). The intercalar is distinct in adults and specimens beyond 70 mm TL. In alizarin-stained postlarvae and young fishes, in which the skull ossification was taking place, no intercalar could be detected. In older specimens the bone is roughly triangular and mainly apposed on the lateral flange of the exoccipital and becomes strongly attached through a strongly interdigitating suture to the latter, covering about one half of the exoccipital-pterotic joint. No fusion to either the pterotic or exoccipital was detected even in the largest specimen examined.

Iluocoetes fimbriatus. In adults the intercalar is well developed, roughly triangular and strongly attached to the neurocranium, through strongly interdigitating sutures to the exoccipital and pterotic bones. In the smallest specimen examined (74 mm TL) the bone is very small and easily detachable from the skull, in adults it covers about one half of the exocciptial-pterotic suture.

Lycenchelys bachmanni (Fig. 12). In the only specimen available, the intercalar is well developed, large, with its anterior apex nearer to the hinder tip of the prootic than to its own posterior margin.

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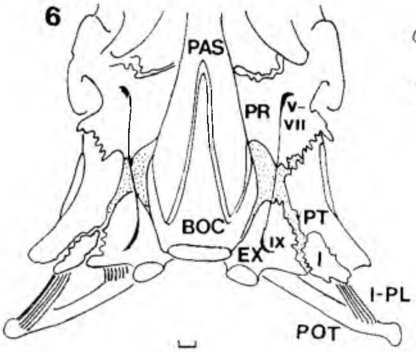

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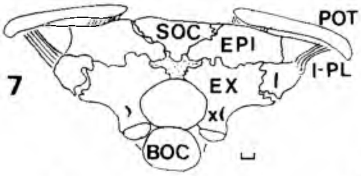

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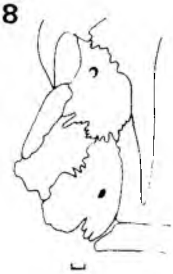

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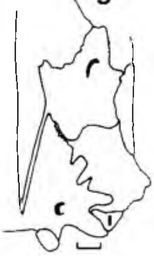

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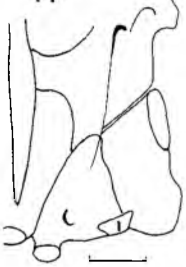

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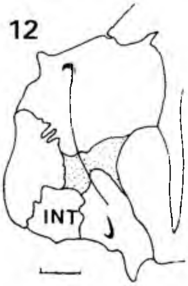

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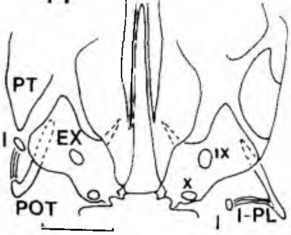

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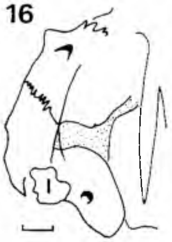

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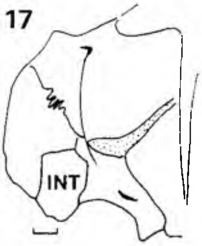

Fig. 6–17. Posterior part of basicranium in Southern zoarcid species (Scale 1 mm).

Fig. 6. *Austrolycus laticinctus*, female, 380 mm TL

Fig. 7. *Austrolycus laticinctus*, specimen as in Fig. 6, occipital view

Fig. 8. *Crossostomus chilensis*, male, 410 mm TL

Fig. 9. *Crossostomus fasciatus*, male 233 mm TL

Fig. 10. *Dadyanos insignis*, female, 236 mm TL

Fig. 11. *Iluocoetes effusus*, 111 mm TL

Fig. 12. *Lycenchelys bachmanni*, 207 mm TL

Fig. 13. *Notolycodes schmidti*, 727 mm TL

Fig. 14. *Phucocoetes latitans*, 32 mm TL, showing developing intercalars, with the left one displaced from its normal position

Fig. 15. *Phucocoetes latitans*, adult female, 121 mm TL

Fig. 16. *Piedrabuenia ringueleti*, 191 mm TL

Fig. 17. *Plesienchelys stehmanni*, male 229 mm TL

Notolycodes schmidti (Fig. 13). In the only specimen examined, the intercalar is well developed and large, comprising about two thirds of the pterotic-exoccipital suture. The bone is strongly attached to the skull through strongly interdigitating sutures.

Phucocoetes latitans (Fig. 15). The intercalar is very small, its length covering only one third of the exoccipital-pterotic suture. It is easily detachable even in the largest adults examined.

In an alizarin-stained young fish, about 32 mm TL (Fig. 14), the just ossifying intercalar could be observed. It is worth noting that the bone is developing not as a part of the skull but as an ossification of the membranes covering the adjacencies of the exoccipital-pterotic articulation. This observation confirms the membranous, i.e. non-endochondral, origin of the intercalar bone.

Piedrabuenia ringueleti (Fig. 16). In the single specimen available, the intercalar is well developed, roughly quadrangular and well attached to the skull. Its anterior tip is nearer to its own hinder margin than to the prootic. The joints to the pterotic and exoccipital are moderately interdigitating.

Plesienchelys stehmanni (Fig. 17). In the single specimen examined, 229 mm TL, the intercalar is well developed and rather large, its anterior tip almost reaching the tip of the prootic. It is articulated to the pterotic and exoccipital through smooth sutures.

Discussion

Despite its important role as one of the anchoring points of the pectoral girdle to the skull, not too much attention has been given to the intercalar or opisthotic in the literature.

Even within the morpho-functional analysis of the fish skull in GREGORY (1933), in which much attentions is given to particular bones or bone-groups as regards their response to the strains coming from different directions, no mention of the function of the intercalar is made. Nevertheless, much information about the presence and development of the bone in different fishes and fish groups can be pieced together from the numerous illustrations, in this otherwise most valuable work.

Quoting previous authors in his anatomical monograph, DEVILLERS (1958), establishes the non-homology of the fish "opisthotic" or intercalar with that of the tetrapods and the dermic origin of the bone.

GOSLINE (1971) in his description of the pectoral girdle, its functions and relations to the skull, clearly illustrates the role of the intercalar as the lower attachment point of the posttemporal in the two-plane lateral "hinge system" between the skull and the upper end of the cleithrum.

More recently, JOLLIE (1984), dealing with the development of the skull and pectoral girdle in *Lepisosteus,* considered the lack of an intercalar as one of the specializations of the genus, related to the "aborted development of the posttemporal and its close relationship to the pterotic-epiotic".

YABE (1985) specifically refers to the reduction of the intercalar as a derived condition, common to all cottoid fishes as opposed to a large one reaching the prootic, which is considered as the basal condition in the general percoid fishes.

Before analizing the intercalar within the zoarcidae, it seems worthwhile commenting on the variations of the pectoral fin, its relations to the skull and the development of the intercalar in the closely related sister group of stichaeoid fishes, according to their revision by Makushok (1958).

In these fishes the pectoral girdle is composed of a forked posttemporal (with the lower arm in various levels of ossification), a supracleithrum, a *cleithrum*, a *coracoid*, four radials, a variable (or null) number of fin rays, and one or two postcleithra. The hinder part of the postocular lateral line canal pierces the upper arm of the posttemporal and the upper part of the supracleithrum.

The modifications toward the reduction of the pectoral fin or girdle in the stichaeoidea are the following, in that order: a) the loss of one or two of the postcleithra, b) the reduction or complete loss of fin-rays and c) loss of the radials.

There is a wide spectrum of variation in the relative development of the intercalar (designated as opisthotic by Makushok) vs that of the pectoral girdle and fin. Although there are fishes with a reduced pectoral and a large intercalar (*Pseudalectrias* sp.), the reduction of the girdle or fin is normally accompanied by a reduction of the intercalar. The latter reduction takes place gradually, starting with the reduction of the intercalar-prootic suture, followed by the loss of the latter suture by the backward migration of the anterior tip of the intercalar. The most dramatic example in this respect is that of the stichaeid *Azygopterus coralinus*, in which the loss of the pectoral fin rays, the postcleithra and radials, is accompanied by a marked reduction in the intercalar (Makushok 1958). The latter bone looses its contact with the prootic and has its anterior tip well removed from that bone. In a lesser degree, in the ptilichthyid *Ptilichthys goodei*, which has a reduced pectoral fin, the intercalar is also small and well removed from the prootic (Makushok 1958).

This parallel reduction of both the pectoral fin and the intercalar would seem to be correlated with the progressive elongation and eel-like mode characteristic of the littoralized stichaeoids.

Taking into account the functional definition of the original teleostean pectoral fin, which is undoubtedly closely related to the efficiency in the swimming of fishes, (Gosline 1971) the departures from the original scheme in partly sedentary or bottom-dwelling percoid derivatives should not be surprising.

Within the eelpout or zoarcid family, as a result of the present investigation the following pattern can be put forward:

The presence of an intercalar, although in an apparently regressive state, seems to be a general characteristic, probably leading to its complete disappearence. The regressive nature of the intercalar can be inferred from the fact that even in the most generalized zoarcids examined (*Macrozoarces americanus*) (Fig. 5) the intercalar does not extend forward to the end of the prootic, thus departing from the general percoid pattern (a large intercalar reaching the prootic (Yabe 1980).

A review of the relative development of the bone in "northern" vs "southern" zoarcids, shows no clear-cut difference between the two groups. However, there seems to be a tendency toward a less developed intercalar in the second group, In fact, whereas in most of the northern genera examined the bone comprises one half or more of the exoccipital-pterotic articulation (the only exception is *Eycryphycus californicus* with an intercalar only one third as long as the latter articulation), in most of the southern genera the intercalar covers only one half or less of the mentioned suture. Two notable exceptions are the deeper-water species *Notolycodes schmidti* and *Plesienchelys stehmanni*

(Fig. 13 and 17), in which the intercalar is large, covering two thirds or more of the exoccipital-pterotic articulation.

The general tendency toward the reduction of the intercalar in the Zoarcidae could be interpreted as an homoplasic phenomenon paralleling, on a stronger degree, the one mentioned in the sister group of stichaeoid fishes. Remembering that in the latter group the reduction of the pectoral fin or girdle (as a step toward a progressively elongated eel-like form) is normally accompanied by a reduction of the intercalar, it is not surprising that the zoarcids, with a more advanced starting point (an advanced postemporal-supracleithrum not pierced by the lateral-line canal and a completely eel-like body), could have a reduced intercalar. This applies particularly well to the most completely littoralized Patagonian forms.

A somewhat disturbing case from the Patagonian fauna must be considered in some detail. It is the strictly littoral genus *Crossostomus* in which, as mentioned in the descriptive part, the intercalar is difficult to detect due to its fusion to the exoccipital bone.

This can be explained by the fact that in this genus the head has a very strong complexion. The jaws and suspensorium are strongly built and massive (GOSZTONYI 1977) and the head musculature, especially that of the hinder part is very strong and fibrous, reinforcing the whole structure including the anchoring of the pectoral girdle. The need of a strongly built head and pectoral girdle is apparently related to the feeding habits of this genus. As mentioned in my previous paper (GOSZTONYI 1977) *Crossostomus fasciatus* is highly specialized in its feeding habits. It feeds on polychaete worms, probably digging them up by hammering the bottom with its reinforced head and anterior body. The fusion of the intercalar to the skull could be interpreted as a contribution to the reinforcement of the whole system in which one the building parts — the intercalar — is apomorphically reduced.

It can be concluded from the present study that the presence of an intercalar bone, although reduced, seems to be general within the zoarcid fishes. Its reduction could be interpreted as an adaptation to an eel-like habit, with a reduced importance of the pectoral fin and girdle.

The ontogeny of the bone consisting in a non-endochondral development and a subsequent apposition and eventual fusion to the neurocranium, points to an only secondary "skull-bone" status of the intercalar within the zoarcid fishes.

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