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Gill Arches of some Teleostean Fishes of the Families Salangidae and Argentinidae

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Abstract Gill arches of salangids, despite certain embryonic features, resemble those of argentinids in having an elongate basihyal and basihyal tooth plate. The arrangement of basihyal teeth in *Argentina* is in a distinctive pattern, found also among galaxiids, osmerids and salmonids, suggesting that these groups are more closely related among themselves than to esocoids. A relationship between osmerids and stomiatoids is not supported by gill-arch structure.

The problem of the relationships of salangid fishes has been mentioned by a number of recent authors (Gosline, 1960; Weitzman, 1967b; McDowall, 1969). By them, salangids have been compared with galaxiids and osmerids, as if there were an informed consensus that salangid relationships are with one or the other (or both) of these two groups. Regan (1908), however, referred to the salangids as "Argentinidae with the dorsal fin placed far behind the pelvics, the head depressed, flat above, and the body elongate, subcylindrical anteriorly and compressed posteriorly." Weitzman (1967b) argued for a close relationship between stomiatoids and osmerids, believing them to be more closely related among themselves than to salmonids or esocoids. Thus, the problem of the relationships of salangids is a complex one, involving many groups. This problem will probably not be solved simply by intensive study of salangids (however desirable that might be in itself), but will require comparative study of all groups so far mentioned, and perhaps others as well (e.g., Alepocephalidae; see also Gosline, 1969).

The present paper deals with gill-arch structure. An attempt is made to consider its relevance to the problem of relationships of salangids. But of interest also are the peculiarities of their gill arches, some of which make salangids unusual if not unique among teleostean fishes.

Salangidae

The gill arches have few endoskeletal ossifications (Figs. 1–2). The ventrohyal, anterohyal and posterohyal (terminology of Nelson, 1969:481) are perichondrally ossified in all material examined. The only other endoskeletal (perichondral) ossification observed was in *Salanx chinensis*, which has the basihyal slightly ossified in its posterior part. Peculiar calcifications (as evidenced by alizarin staining) were seen in the fourth arch of one specimen (of two examined) of *Salangichthys microdon* (for mention of similar calcifications, see Nelson, 1969:519). For the cartilaginous endoskeleton, two or three copulae are present, depending on whether the basihyal is a separate element. Divisions could not be observed in the hyoid arch, but the gill arches are subdivided in the usual fashion into hypo-, cerato-, epi-, and (infra) pharyngobranchials. Of interest are the well developed fourth hypobranchials, which so far as known are absent from all other adult teleostean fishes. Rudimentary fourth hypobranchials occur in some adult cobitids (Nelson, 1969) and as transitory rudiments in embryos of some other teleosts (e.g., characins; Bertman, 1959; see also Nelson,

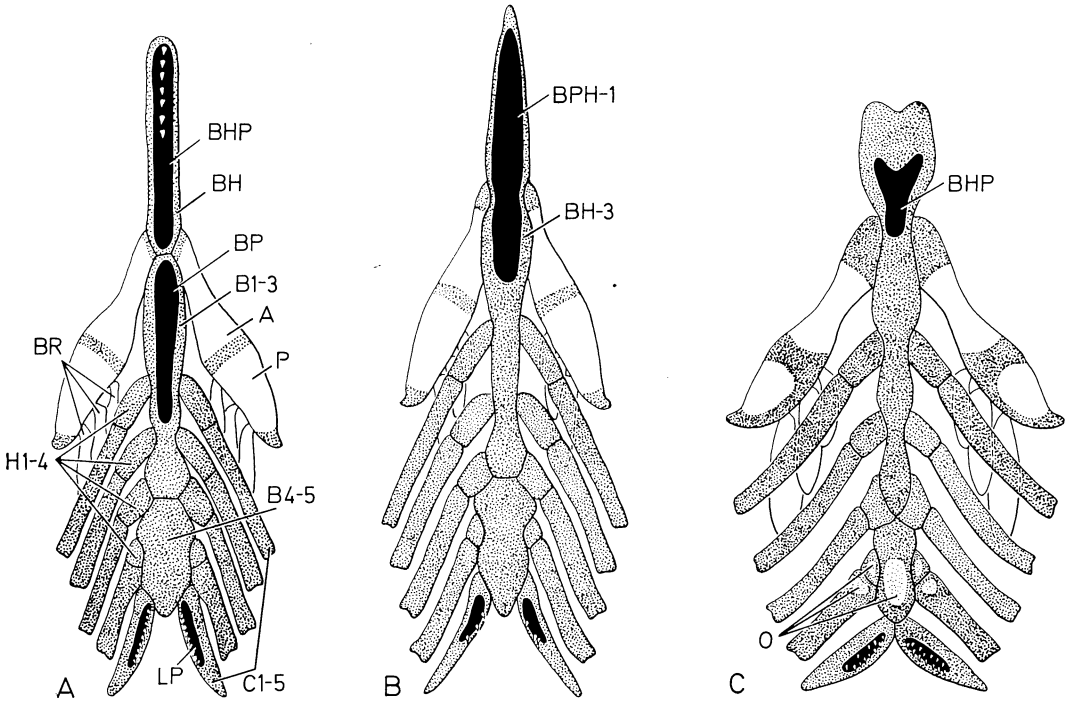

Fig. 1. Gill arches, ventral parts, dorsal view. A, *Salanx chinensis* (Amer. Mus. Nat. Hist. 10336, ×4); B, *Salanx cuvieri* (AMNH 10327, ×4); C, *Salangichthys microdon* (AMNH 10337, ×10). Cartilage stippled, perichondral bone clear, dermal bone black. A, anterohyal; B1-5, basibranchials 1-5; BH, basihyal; BH-3, basihyal + basibranchials 1-3; BHP, basihyal plate; BP, basibranchial plate; BPH-1, basihyal plate + basibranchial plate; BR, branchiostegal rays; C1-5, ceratobranchials 1-5; H1-4, hypobranchials 1-4; LP, lower pharyngeal plate; O, endochondral mineralization; P, posterohyal.

1969: 508, note 2). In salangids, dermal elements consist of one or more median basibranchial plates, one pair of lower pharyngeal plates, and one pair of upper pharyngeal plates. The basibranchial plates may be toothed or not. The pharnygeal plates are toothed. The form of the basibranchial plates varies interspecifically, but the form of the pharyngeal plates is relatively constant. There is some variation in the number and arrangement of teeth, but teeth in general are few in number and weakly developed.

Argentinidae

The endoskeleton of the gill arches of *Argentina* is ossified in the pattern usual in teleosts (Fig. 2). Dermal elements include a long basihyal plate toothed anteriorly, a toothless basibranchial plate fused to the second basibranchial, toothed lower pharyngeal plates fused with the fifth ceratobranchials, and two pairs of upper pharyngeal plates supported by the cartilaginous fourth pharyngobranchial. Posterior to the fourth epibranchial is a small diverticulum with gill rakers (the like of which might be called a vestigial, weakly developed or rudimentary epibranchial organ; see, however, Nelson, 1970). Gill-arch structure of *Glossanodon* is similar, but the basihyal plate is shorter, its teeth are smaller and perhaps fewer in number, and in a different arrangement (Cohen, 1964; personal observations). To judge from published descriptions of structure of other argentinids, they are generally similar but have the dermal elements further reduced (Trewavas, 1933; Chapman, 1942, 1943, 1948).

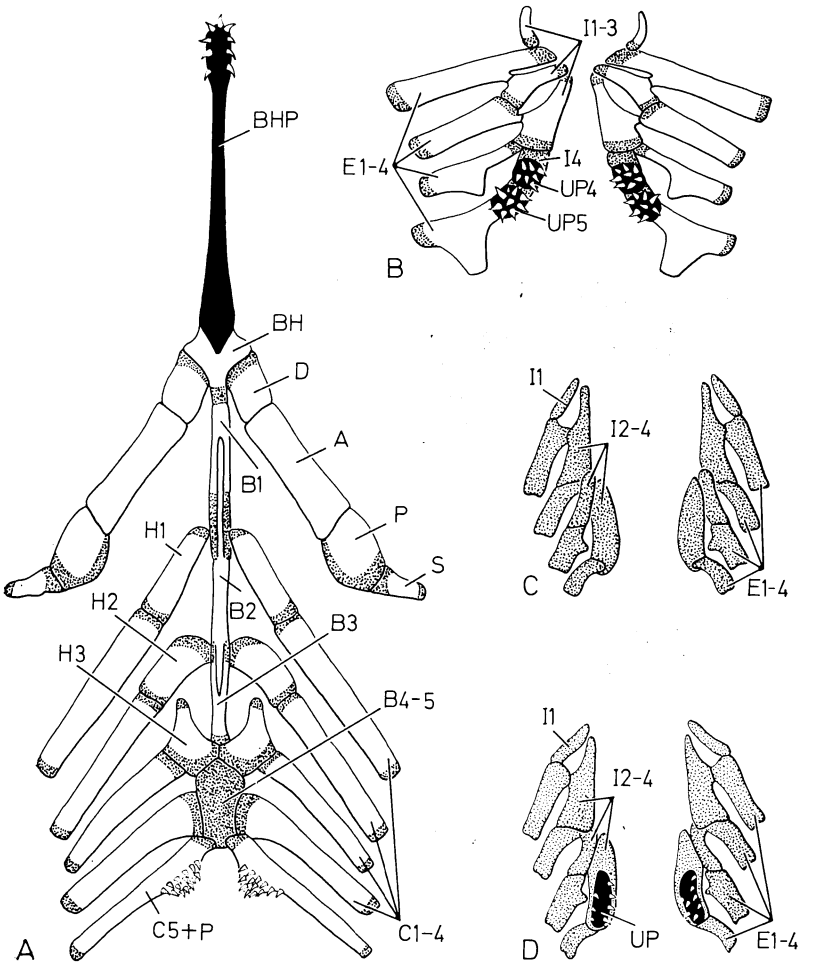

Fig. 2. A–B, *Argentina striata* (AMNH uncatalogued, ×4), gill arches: A, ventral parts, dorsal view; B, dorsal parts, ventral view. C–D, *Salanx cuvieri* (AMNH 10327, ×4), gill arches: C, dorsal parts, dorsal view; D, dorsal parts, ventral view. C5+P, lower pharyngeal plate fused with C5; D, dorsohyal; E1-4, epibranchials 1-4; I1-4, (infra) pharyngobranchials 1-4: S, stylohyal; UP, upper pharyngeal plate. Other symbols as in figure 1.

Discussion

Whether or not salangids really are neotenic derivatives of their ancestral stock (Berg, 1947; Gosline, 1960), their gill arches have embryonic aspects: the general absence of endoskeletal ossification, and the persistence of independent and well developed fourth hypobranchials. In these respects the gill arches of salangids are unusual if not unique among those of mature teleostean fishes.

Gosline (1960) compared salangids with an apparently neotenic galaxiid (*Lovettia*). Gill arches of *Lovettia* are well ossified and generally similar to those of other galaxiids. They lack the embryonic aspects of salangid gill arches (personal observations). A more fruitful comparison might be that between salangids and apparently neotenic argentinids (e.g., *Dolichopteryx*; Cohen, 1960, 1964).

Despite the embryonic aspects of their

gill-arch endoskeleton, salangids exhibit a trend toward reduction of dermal gill-arch elements. In *Salanx chinensis* there are separate basihyal and basibranchial plates comparable to those apparently primitive for the Teleostei as a whole. The single basibranchial plate of *Salanx cuvieri* perhaps represents the two of *S. chinensis* secondarily fused together (a condition suspected to occur also in some Osteoglossomorpha; Nelson, 1968, 1969). The small plate of *Salangichthys*, whether it corresponds to one or to both of those of *S. chinensis*, probably represents the most advanced condition of those shown. If the condition in *S. chinensis* is close to that primitive for the Salangidae as a whole, it can be compared to that of *Argentina*. In both, the basihyal and its dermal plate are elongate, with teeth occurring only at the front (see however, Fang, 1934: fig. 1; Wakiya and Takahasi, 1937: fig. 23). In *Argentina* the teeth are enlarged and are in two rows, in *Salanx* they are small and in one row (two rows occur in some other salangids). Dorsally *Argentina* has two pharyngeal plates and *Salanx* only one, which might, however, represent the two of *Argentina* secondarily fused (fusion of this type is believed to occur elsewhere in teleostean fishes; Nelson, 1969: 490). *Argentina* has some dermal elements (basibranchial plate, lower pharyngeal plates) fused with their endoskeletal supports, whereas salangids do not, perhaps because of a retention of embryonic features (some argentinids have the basibranchial plate unfused; Chapman, 1948: fig. 7).

The similarity in gill-arch structure between *Argentina* and salangids is not detailed, striking or convincing, but it is greater than that between salangids and any other group whose gill-arch structure is known to the writer. Thus, the elongation of the basihyal and its associated dermal plate, and the reduction of upper pharyngeal dentition to one or two plates supported by the fourth pharyngobranchial, may be indications of a close relationship between these groups. But the basihyal dentition of *Argentina*, with enlarged teeth in two rows along the sides of the plate, is similar to that occurring in galaxiid, osmerid and salmonid fishes (a similar but not identical condition occurs in some Osteoglossomorpha; Nelson, 1968, 1969), and the upper pharyngeal dentition is similarly reduced in some galaxiids, and nearly so in some osmerids and salmonids. In the writer's opinion the basibranchial plate in particular, with its enlarged and differentiated dentition, is a feature distinctive for these groups and is probably some indication of a relationship between them all (Osteoglossomorpha excepted?). Of course, some members of each group (e.g., *Prototroctes, Mallotus, Thymallus*) are without the distinctive tooth arrangement, either because the basihyal teeth are small or absent altogether, or because the teeth tend to occur over the entire surface of the plate (personal observations). Whether these aberrant members are primitive or advanced in these respects is difficult to say.

Stomiatoids have a basihyal which is reduced and at least sometimes ventrally deflected (a condition found also in engraulids; Nelson, 1970), and, so far as known, toothless (Günther and Deckert, 1953, 1955, 1959; Tchernavin, 1953; Weitzman, 1967a, 1967b.) Stomiatoid gill-arch structure as a whole (with toothed third infrapharyngobranchials equipped with retractor muscles, and in some cases a secondary basibranchial dentition of paired plates with well developed teeth) represents a specialization different from that of argentinids, galaxiids, osmerids, salangids and salmonids, resembling more closely that of the Neoteleostei (Nelson, 1969: 493, 528). Some esocoids have well developed basihyal and basibranchial tooth plates in a condition probably more primitive in some ways than that of argentinids, galaxiids, osmerids, salangids and salmonids (e.g., Nelson, 1969: pl. 85, fig. 2).

The fishes discussed above have been "classified" in various ways in the past, but a consistently phyletic arrangement of them is a task yet to be achieved. Recent discussion of their classification has led toward

proliferation of higher categories (suborders, superfamilies, families) to serve purposes other than the objective of phyletic classification, i.e. the classification together of species related by common ancestry. As regards the problem of relationship, there is some agreement that argentinids, galaxiids, osmerids, salangids and salmonids may be more closely related among themselves than to any other fishes, a proposition supported by gill-arch structure. These "salmonoid" fishes may therefore be grouped together in a taxon coordinate with that including their nearest relatives. Possible salmonoid relatives include a number of groups listed by Greenwood *et al.* (1966) as salmoniform suborders (Esocoidei, Stomiatoidei, Alepocephaloidei, Bathylaconoidei and Myctophoidei). Of these, the Myctophoidei have subsequently been argued to have their relationships with the Paracanthopterygii and Acanthopterygii (Rosen and Patterson, 1969) and have been grouped with them in a superorder Neoteleostei (Nelson, 1969: 534). Of the remaining salmoniform "suborders," the Esocoidei have most often been considered close relatives of salmonoids, a proposition consistent with, but not particularly supported by gill-arch structure. If closely related, esocoids and salmonoids may be classified together. To rank them as superfamilies (suborder Salmonoidei, order Salmoniformes, superorder Protacanthopterygii) can express their probable relationship as "sister-groups" without requiring that the Stomiatoidei, Alepocephaloidei and Bathylaconoidei be raised to the ordinal level, but requires consolidation of some currently recognized families and may require further consolidation when the interrelationships of the various salmonoid groups become established with reasonable certainty. The writer finds this alternative preferable to any further proliferation of higher categories inconsistent with the phyletic classification of the Vertebrata as a whole.

Suborder Salmonoidei

Superfamily Esocoidae

Families Esocidae

Umbridae (incl. Dalliidae, Novumbridae)

Superfamily Salmonoidae

Families Argentinidae (incl. Bathylagidae, Microstomidae, Opisthoproctidae)

Galaxiidae (incl. Aplochitonidae, Prototroctidae, Retropinnidae)

Osmeridae (incl. Plecoglossidae)

Salangidae

Salmonidae (incl. Coregonidae, Thymallidae)

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シラウオ科，ニギス科の若干の魚類の鰓弓

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シラウオ科の類縁についての定説はなく，キウリウオ，ガラクシス，ニギス類との関係も不明である．よって，シラウオとニギスの鰓弓の構造と性格を研究して知見を求めた．シラウオ類は第4鰓骨の発達により他の硬骨魚類(成魚)と特徴的に異なる．シラウオ類が祖先型の幼生成熟として出現したか否かは別として，内部骨の骨化の一般的欠如と上記の下鰓骨の発達より，鰓弓構造の胚仔的であることは明らかである．ニギス類の鰓弓構造は他の硬骨魚類と近似してはいるが，その基舌骨の延長と舌咽歯の1，2列である点でシラウオ類と類似している．また，ニギス類の基舌骨歯の配列は特異であり，その形質はガラクシス，キウリウオ，サケ類にもみられ，彼等の近縁を示すものと思われる．ワニトカゲギス類の鰓弓は上記の魚類よりも特化し，パイク類のある種類ではより原始的である．以上より，次の如き構想に到達した．

最近の魚類の分類の理念は上位分類段階(亜目，上科，科)の増加にむかい，これは，共同祖先に発した類似種の総合的分類には役立つが，系統分類の目的とは離れている．鰓弓の構造と性格より，ニギス，ガラクシス，キウリウオ，シラウオ類は，その近縁群を含めて，1群と考える．そして，上記の理念のもとに，これらの魚類の系統分類(p. 65)が，現在，適切と考えられる．

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