PHYLOGENY AND ZOOGEOGRAPHY OF SALMONIFORM FISHES AND RELATIONSHIPS OF *LEPIDOGALAXIAS SALAMANDROIDES*

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ABSTRACT

THE AFFINITIES of the tiny, freshwater Australian fish *Lepidogalaxias salamandroides* have remained uncertain since its original description in 1961. Comparisons of *Lepidogalaxias* with various salmoniforms, which it superficially resembles, uncovered a number of major problems in salmoniform taxonomy. A review of the anatomy of salmoniform gill arches, caudal skeletons, and secondary sexual characters suggests that *Lepidogalaxias* is an esocoid, that galaxiids and aplochitonids are related to salmonids (as salmonoids), and that retropinnids and prototroctids are related to osmerids, salangids, and plecoglossids (as osmeroids). A comparison of possible salmoniform phylogenies based on various anatomical features indicates that the phylogeny derived from gill arch evidence leads to the most economical hypothesis involving the fewest assumptions of independent origin of similar character states. The proposed phylogeny recognizes salmonoids and osmeroids (each as redefined to include parts of the former galaxioid assemblage) as sister groups. Argentinoids are considered a plesiomorph sister group of these two, and esocoids plus *Lepidogalaxias* the plesiomorph sister group of all other salmoniforms. Salmoniforms are amphitropical, panboreal, and panaustral in distribution and their worldwide and southern hemisphere distributions correspond partly or wholly with those of chironomid midges, southern beech trees (*Nothofagus*), and other plant groups. Alternative biogeographic interpretations of these distributions are considered: chance dispersal over uninhabitable gaps in relation to the present continental landscape versus an original and ancient Pangaean distribution followed by continental drift. Waif dispersal hypotheses are found to be aprioristic, wanting in evidence, highly imaginative, and untestable, whereas the continental drift model simply and directly accounts for the present distributions of varied organisms with different mobilities and other biological properties. Acceptability of the continental drift model would place the minimum age of the main groups of salmoniforms at 180 million years and of some of the southern assemblages at 90 million years. Reasons for rejecting the concepts of primary and secondary division freshwater fishes as applied to the solution to zoogeographic problems are given. A return to the concepts of continental and oceanic fish groups is advocated, the zoogeographic interpretations of which are determined not by what we imagine to be the habits of the fishes and their possible dispersal mechanisms but by their distributions in relation to phylogeny and in relation to the distributions of other organisms.

INTRODUCTION

THE TINY Western Australian fish *Lepidogalaxias salamandroides* was included without comment in the Galaxiidae by its describer, Mees (1961). Subsequently Scott (1966) disputed its inclusion in that family. He provided a brief comparative survey of the external anatomy of *Lepidogalaxias* in relation to the galaxiids and concluded that various of its features are "difficult to harmonize . . . with our present concept of the Galaxiidae." Most recently, and in the only other published account of its structure, Nelson (1972) wrote that "*Lepidogalaxias* may be the sister group of all other galaxiines (Frankenberg, MS), but sensory canal and pore data are inconclusive."

Specimens of *Lepidogalaxias* were sent in 1967 by R. M. McDowell to P. Humphry Greenwood and me for study, and preliminary inspection of their osteology confirmed that a problem did exist in assigning them to the Galaxiidae. Two years later, in the spring of 1969, many additional specimens, including a number of adult males and females, were collected by G. J. Nelson, W. H. Butler, and the writer. Cleared and alizarin-stained examples from this material revealed that the adult males have a sexually modified anal fin of great complexity, and its specialized structure seemed to hold out some hope of identifying the nearest relatives of the species. The hope proved vain, for, although several other groups of teleosteans—an osmerid, the salangids, and two groups of cyprinids— have somewhat similar sexually dimorphic anal fins, their other anatomical traits are discordant with those of *Lepidogalaxias*.

During a search for some clear indication of the relationships of *Lepidogalaxias*, principally among the various groups of salmoniforms some of which *Lepidogalaxias* superficially resembles, it became evident that salmoniform classification is in a somewhat confused state. It was equally evident that some attempt to resolve the larger confusion of salmoniform taxonomy would

have to be made before resuming the search for relatives of *Lepidogalaxias*.

ACKNOWLEDGMENTS

MATERIALS AND METHODS

Cleared and alizarin-stained preparations, X-rays, and dissections were prepared from the following comparative materials. Wherever possible an effort was made to secure specimens of nearly comparable size for study. Because the galaxiid-like fishes are generally small, the largest attaining a fork length of about 15 cm., it was necessary to use the younger individuals of the northern salmoniforms, some of which (*Salmo, Oncorhynchus*, and *Esox*) grow to a very large size. This procedure was followed partly to make direct comparisons of similarly prepared specimens (that is, alizarins), and partly to be able to study osteological features such as dentition and the various dentigerous bones that often are strongly modified during sexual maturation. The method proved fortunate because one of the features of the head of the young salmonid, the pattern of basihyal teeth, which was found to have significance in phylogenetic analysis, is altered substantially and difficult to interpret in the breeding adult.

APLOCHITONIDAE
  Aplochiton taeniatus Jenyns, AMNH 30802
  Aplochiton zebra Jenyns, AMNH 27468, 31048
  Lovettia seali (Johnston), AMNH 27459
ESOCIDAE
  Esox americanus Gmelin, AMNH 8754
  Esox lucius Linnaeus, AMNH 27438
  Esox masquinongy Mitchill, AMNH 30881
  Esox niger Lesueur, AMNH 21878
GALAXIIDAE
  Brachygalaxias bullocki (Regan), AMNH 31038
  Galaxias brevipinnis Günther, AMNH 30885
  Galaxias divergens Stokell, AMNH 31034
  Galaxias fasciatus Gray, AMNH 27467
  Galaxias maculatus (Jenyns), AMNH 27466, SAM F.3028
  Galaxias paucispondylus Stokell, AMNH 30889
  Galaxias truttaceus (Cuvier), SAM F.3188
  Galaxias vulgaris Stokell, AMNH 30887
  Galaxias zebratus (Castelnau), AMNH 32998
  Neochanna apoda Gunther, SAM
  Nesogalaxias neocaledonicus (Weber and de Beaufort), AMNH 31036
LEPIDOGALAXIIDAE
  Lepidogalaxias salamandroides Mees, AMNH 24114, WAM P.8124, 7578
MEGALOPIDAE
  Megalops atlantica Valenciennes, AMNH 27478
OSMERIDAE
  Allosmerus elongatus (Ayres), USNM 188125
  Hypomesus olidus (Pallas), AMNH 27417
  Mallotus villosus (Müller), AMNH 26286
  Osmerus mordax (Mitchill), AMNH 292, 30800
  Spirinchus thaleichthys (Ayres), AMNH 2637, USNM 104690
PLECOGLOSSIDAE
  Plecoglossus altivelis Temminck and Schlegel, AMNH 27476
PROTOTROCTIDAE
  Prototroctes maraena Günther, MCZ 6867
RETROPINNIDAE
  Retropinna abbreviata McDowall, AMNH 27469
  Retropinna osmeroides Hector, AMNH 27457

Retropinna retropinna Richardson, AMNH 30890
Stokelia anisodon (Stokell), AMNH 31037
SALANGIDAE
  Neosalanx anderssoni (Rendahl), UMMZ 180141
  Neosalanx hubbsi Wakiyawa and Takahashi, UMMZ 180147
  Salangichthys microdon Bleeker, AMNH 10337
  Salanx chinensis (Osbeck), AMNH 10336
  Salanx cuvieri Valenciennes, AMNH 10327
SALMONIDAE
  Coregonus artedi Lesueur, AMNH 20096
  Cristivomer namaycush (Walbaum), AMNH 27239
  Oncorhynchus kisutch (Walbaum), AMNH 7626
  Prosopium cylindraceum (Pallas), AMNH 31044
  Salmo gairdneri Richardson, AMNH 21975
  Salmo trutta Linnaeus, AMNH 21164
  Salvelinus fontinalis (Mitchill), AMNH 23791
  Salvelinus malma (Walbaum), AMNH 27400
UMBRIDAE
  Dallia pectoralis Bean, AMNH 16215, USNM 111669
  Novumbra hubbsi Schultz, UMMZ 187427
  Umbra krameri Walbaum, AMNH 28653
  Umbra limi (Kirtland), AMNH 21108
  Umbra pygmaea (DeKay), AMNH 17699

ABBREVIATIONS USED IN FIGURES

ACC, accessory hemal spine or parhypural
ACC PHYP, accessory parhypural
ART, articular
BB, basibranchial
C, ceratobranchial
DBB, dermal basibranchial plate, with or without teeth
DBH, dermal basihyal plate, with or without teeth
DETH, dermal ethmoid
DN, dentary
E, epibranchial
EA-5, passage for fifth efferent branchial artery
END, endopterygoid
EP, epural
EPO, epiotic

EXOC, exoccipital
$F\text{-}BB_1$ or $F\text{-}BB_2$, dermal basibranchial plate fused with first or second endochondral basibranchial
FR, frontal
F-RNA, rudimentary neural arch fused with centrum
HYO, hyomandibular
HYP, hypural
IM, intermuscular bone
IO, infraorbital bone
IOP, interopercular
LAT, lateral ethmoid
LEV, levator process of fourth epibranchial
LIG, ligament
MES, mesethmoid
MX, maxilla
NA, nasal
NPU, preural neural spine
OP, opercular
PA, parietal
PAL, palatine
PB, infrapharyngobranchial
PHYP, parhypural
PMX, premaxilla
POP, preopercular
PTO, pterotic
PTT, posttemporal
PU, preural centrum
QU, quadrate
RET, retroarticular
RNA, rudimentary neural arch
SO, supraorbital
SOC, supraoccipital
SOP, subopercular
SPHO, autosphenotic
SYM, symplectic
U, ural centrum
UD, urodermal
UN, uroneural
UNC, uncinate process of epibranchial
$UN_1\text{-}F$, first uroneural fused with terminal centrum
UP, upper pharyngeal teeth
VO, vomer

GALAXIOID ANATOMY AND INTERRELATIONSHIPS

McDOWALL (1969) PROVIDED a list of characters that he believed unite all galaxioid fishes (Galaxiidae, Aplochitonidae, Retropinnidae, and Prototroctidae). Most of these are "loss" characters: absence of a mesocoracoid, reduction in the number of urostylar vertebrae and caudal fin rays, loss of proethmoids, reduction in the number of pyloric caeca, loss of supramaxillae, loss of the lower arm of the posttemporal, loss of maxillary teeth. Gain characters specified by McDowall include: increase in the area of the parietals in the posterior cranial roof and an increase in the length of the premaxillary alveolar process. None of these characters, taken either singly or in combination, seem decisive to me. With the exception of the moderately sized *Prototroctes*, all galaxioids are small fishes that may show a paedomorphic reduction of ossifications as is often encountered in the smaller species of other fish groups. With regard to the two gain characters, it seems not established that a more extensive parietal ossification is an advanced, and not a primitive, feature, and that an increase in the length of the premaxillary alveolar process has occurred in a way peculiar to galaxioids. The tendency of the premaxillary alveolar end to enlarge is characteristic of every primitive teleostean assemblage. McDowall also provided a table comparing five galaxioid genera (*Galaxias, Lovettia, Aplochiton, Prototroctes*, and *Retropinna*) with respect to 16 features. This table is reproduced here in somewhat modified form (table 1). Of the 16 character states given, nine are advanced and shared among *Galaxias, Lovettia*, and *Aplochiton*, and six are advanced and shared between *Prototroctes* and *Retropinna*. Only one attribute, caudal fin ray reduction, is shared among all five genera, although *Galaxias, Lovettia*, and *Aplochiton* have one count (12–14 branched rays) and *Prototroctes* and *Retropinna* another (16). Three of the remaining five advanced features shared by *Prototroctes* and *Retropinna* occur also in some or all osmerids, viz., the cucumber odor, a short vomerine shaft, and a posterior pubic symphysis. Wiley and Collette (1970) have also found similarities among several osmerids, *Plecoglossus*, and *Retropinna* in the presence and characteristics of their breeding tubercles: "The tubercles of *Plecoglossus*, the various smelts, and the retropinnids all have similar morphology, the chief differences being in shape and size. All are characterized by slight to moderate amounts of cellular hypertrophy and none to slight amounts of keratinization in the surface layers." Although there appears to be some indication of relationship between osmeroids and retropinnids, it is my opinion that only Nelson (1972) has offered some specific evidence of relationship of *Retropinna* and *Prototroctes* with *Galaxias, Lovettia*, and *Aplochiton*. He showed that in *Retropinna* and *Prototroctes* the infraorbital branch of the cephalic lateral line sensory canals is interrupted below the eye and that the anterior segment of this branch is deflected downward toward the preopercular canal which it crosses. In *Brachygalaxias* and *Aplochiton*, and in other galaxiids not figured, only an anterior segment of the infraorbital canal persists, and this is deflected downward toward the anterior arm of the preopercular canal which, however, it does not contact. Nelson had pointed to the possibly spurious nature of the comparison, as galaxiids have a type of infraorbital canal reduction and reorientation that occurs also in various species of atheriniforms. Moreover, in retropinnids and prototroctids, the anterior canal segment is represented by three infraorbital bones, and the posterior segment behind the orbit by two, so that there appears to be only a single bone missing (the fourth infraorbital) from the primitive series as defined by Nelson (1969a). In contrast, galaxiids, *Aplochiton* and *Lovettia* have never more than the first two bones in the entire series, the bones and the associated canal often are very short, not approaching the preopercle, and the bones and the canal are sometimes not deflected downward as in some examples of *Galaxias divergens* and *Neochanna apoda*. The following comparisons offer some alternative schemes of relationships of galaxioid fishes, which point to the possibility that the Galaxioidei as construed by McDowall and others is a polyphyletic group.

Patterson (1970), largely on caudal skeleton

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TABLE 1

A COMPARISON OF SOUTHERN HEMISPHERE SALMONIFORM GROUPS (FROM McDOWALL, 1969)

(Bars indicate shared advanced characters.)

Character	Galaxias	Lovettia	Aplochiton	Prototroctes	Retropinna
Scales	—	—	—	+	+
Horny keel	—	—	—	+	+
Cucumber odor	—	—	—	+	+
Pyloric caeca	+	—	+	—	—
Vomerine shaft	long	long	—	short	short
Vomerine teeth	—	—	—	+	+
Basibranchial teeth	—	—	—	+	+
Palatine teeth	—	—	—	+	+
Extrascapular	—	—	—	+	+
Ectopterygoid	—	—	slender splint	+	+
Mesopterygoidal teeth	U	U	U	M	M
Coracoid-cleithrum process	—	—	—	+	+
Posterior pubic symphysis	—	—	—	+[a]	+
Pubic foramen[b]	—	—	—	+	+
Caudal skeleton	1–5[c]	1–5	1–5	1–6	1–6
Branched caudal fin rays	12–14[d]	14	14	16	16

[a] Trait questioned by McDowall.

[b] Primitive or advanced condition of trait not known.

[c] Parhypural plus hypurals.

[d] Trait given as 14 by McDowall, 1969.

Symbols: —, character lacking; +, character present; M, multiserial; U, uniserial.

evidence, was the first to propose that the Retropinnidae and Prototroctidae are related to the osmerid fishes and not to the other galaxioids. Evidence concerning the hyobranchial apparatus, some additional features of caudal anatomy, and male sexual dimorphisms agrees with this proposal.

SALMONIFORM HYOBRANCHIAL APPARATUS

DERMAL BASIHYAL AND BASIBRANCHIAL ELEMENTS

Nelson (1969b) suggested that the condition of the basibranchial dentition of *Elops* is close to that primitive for teleosteans. In *Elops* a small tooth plate occurs over the basihyal, and behind this an elongate tooth plate over basibranchials 1–3. Following the elongate tooth plate is a small round or oval tooth plate or patch of teeth over the fourth endoskeletal basibranchial. A similar condition occurs in what seem to be primitive representatives of most lower teleostean groups: Osteoglossiformes (*Hiodon*), Ostariophysi (*Ichthyoborus*), Elopiformes (*Megalops*),

Clupeiformes (*Chirocentrus*), Salmoniformes (*Retropinna, Osmerus*). The teeth characteristic of this primitive arrangement of tooth plates, when present, are small, uniform, and close-set. Among salmoniforms this basic pattern of teeth and tooth plates is modified in various ways. In esocoids the elongate tooth plate is subdivided into a long and a short section, which in umbrids is reduced to two small tooth plates over the first and third basibranchials; in both families there is a well-developed tooth plate over the fourth basibranchial (fig. 1). Among osmerids the basihyal tooth plate is large and in most cases oboval and the elongate basibranchial tooth plate has a low, blunt ridge medially. When this tooth plate is reduced, as in *Mallotus*, only the median ridge remains (fig. 2B). The marginal teeth are differentiated. On the basihyal the marginal teeth of most species are large and recurved, and arranged irregularly or in alternating positions on the right and left sides. The basihyal is terminated by a single large tooth. The nonmarginal teeth are relatively sparse, patchily distributed, and
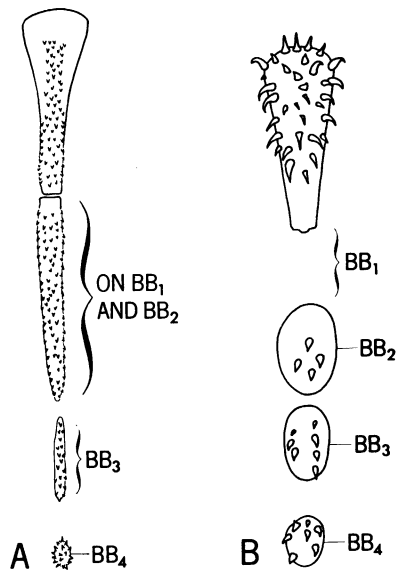
FIG. 1. Dermal basihyal (top) and basibranchial elements in esocoids. A. Pattern in all examined species of *Esox*. B. *Novumbra hubbsi*. Positions of underlying endoskeletal basibranchials shown by symbol BB.
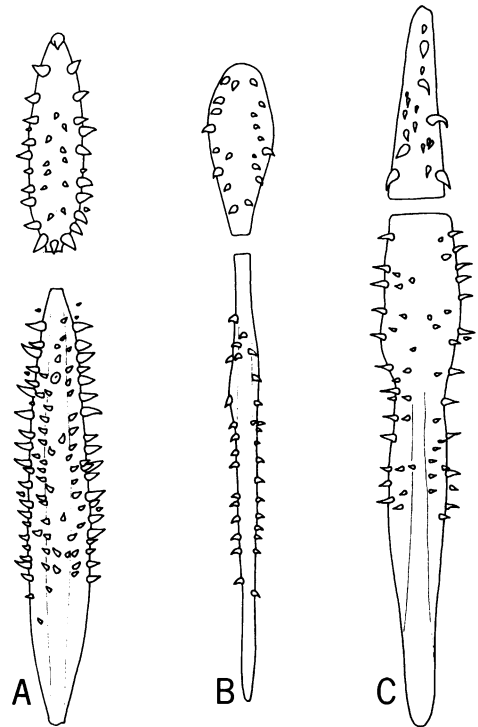

FIG. 2. Dermal basihyal (top) and basibranchial elements in osmeroids. A. *Hypomesus olidus*; pattern also present in most osmerines. B. *Mallotus villosus*. C. *Plecoglossus altivelis*. Basibranchial tooth plate (bottom) extends over endoskeletal basibranchials 1, 2, and 3. Note median basibranchial ridge in A and C; ridge only persists in B.

small (fig. 2). The teeth on the elongate basibranchial tooth plate are differentiated in much the same way, although the marginal ones tend to be somewhat smaller than those on the basihyal. In the reduced dentition of *Mallotus*, tooth differentiation is less evident (fig. 2B). In *Plecoglossus* the pattern is like that of most osmerids (fig. 2C). Salangids, however, generally lack a basibranchial dentition (but see below and Nelson, 1970). Among argentinoids, the searsiids have only a marginal fanglike dentition on the basihyal; the basibranchial tooth plate when present is edentulous and fused with the second endoskeletal basibranchial. Even the basihyal dentition is reduced in most searsiids, and basihyal and basibranchial teeth are absent in all alepocephalids examined. In the argentinids basihyal teeth, often fanglike (in *Argentina*), are present only along or around the distal margin of a greatly elongate basihyal; the basibranchal tooth plate is edentulous and, as in the alepocephaloid groups, fused with the second endoskeletal basibranchial. In argentinoids the basibranchial tooth plate is invariably elevated medially into a sharp ridge in connection with the development of a specialized pharyngobranchial structure, the cru-

menal organ (see Greenwood and Rosen, 1971, p. 8, figs. 19, 20). Among salmonids, the salmonines show a massive development of the marginal, fanglike basihyal teeth and the virtual or complete loss of smaller, inner teeth. These large teeth are distributed in right and left pairs along the sides of the large basihyal tooth plate. The arrangement is notably symmetrical, and the salmonine basihyal is almost always terminated by a distinct terminal pair of teeth, rarely by a single tooth (fig. 3). The basibranchial tooth plate is either edentulous or it has a much reduced dentition, and the tooth plate itself is reduced or fragmented into two smaller plates. When present and well developed, it is fused with the second endoskeletal basibranchial (figs. 3A–D, F). Thymallines and coregonines show a general reduction of tooth plates and dentition over their condition in salmonines (fig. 3F; Norden, 1961).
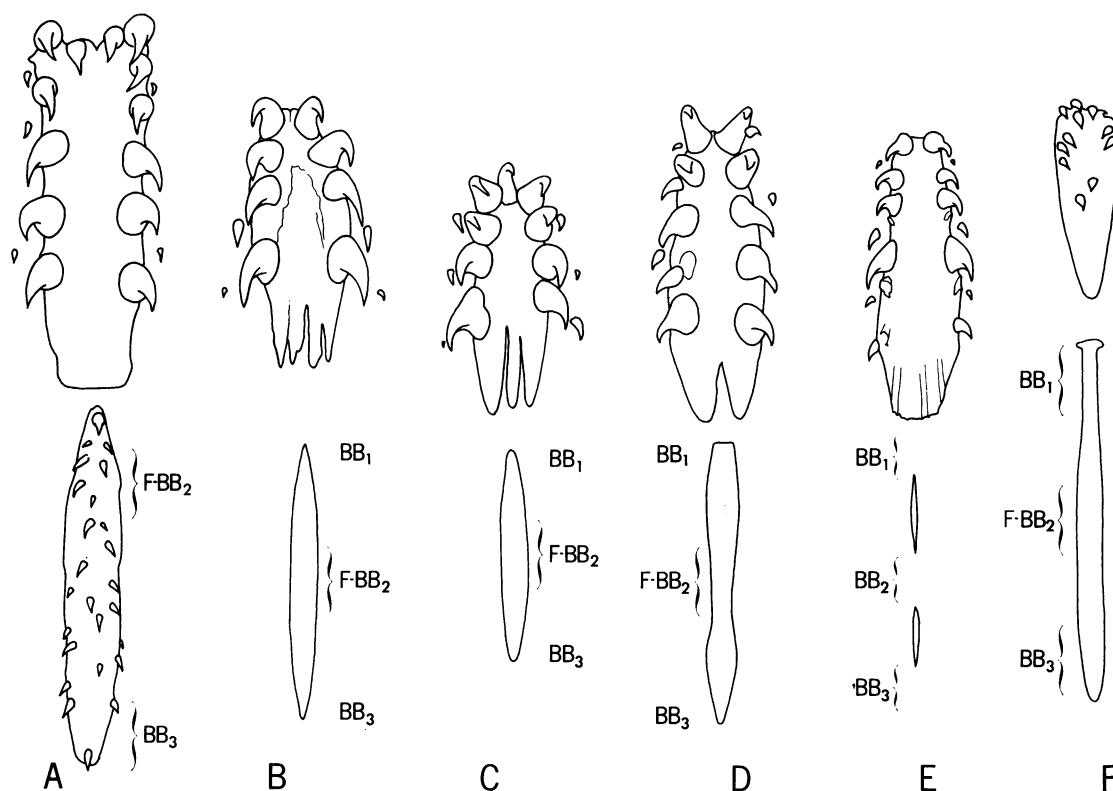
FIG. 3. Dermal basihyal (top) and basibranchial elements in salmonids. A. *Cristivomer namaycush*. B. *Salvelinus malma*. C. *Salvelinus fontinalis*. D. *Salmo trutta*. E. *Oncorhynchus keta*. F. *Prosopium cylindraceum*. Separation between basihyal and basibranchial in A–E reduced for purposes of illustration. Positions of underlying endoskeletal basibranchials shown by symbols BB and F–BB (signifying fusion between dermal and endochondral elements).

Galaxioids exhibit two types of basihyal and basibranchial tooth plates and dentition. The species of *Retropinna*, *Stokelia*, and *Prototroctes* have basihyal tooth plates and dentition like those of osmerids and plecoglossids, including even the tendency of the fanglike marginal basihyal dentition to be represented by a single tooth distally (fig. 4). The only difference is to be found in the basibranchial tooth plate of *Prototroctes*, which is rather wide in relation to its length and lacks a median ridge. The unusual width of this bone suggests the possibility that the ridge has been lost secondarily by a general flattening of the plate (fig. 4D). *Retropinna* and *Stokelia* are indistinguishable from the more generalized osmeroids in this branchial dentition (figs. 2A, C; 4A–C). *Aplochiton*, *Lovettia*, and the species normally included in the Galaxiidae, on the other hand, have basihyal and basibranchial tooth plates like those of

salmonines (fig. 5B–D). The resemblances between galaxiids-aplochitonids and the salmonines is particularly striking in the highly symmetrical basihyal fangs and in the presence of a distinct pair of teeth distally, which in *Brachygalaxias* are greatly enlarged (figs. 3, 5–7). Unlike the basibranchial tooth plate of salmonines, this invariably edentulous bone in *Aplochiton*, *Lovettia*, and galaxiids is not fused with the second endoskeletal basibranchial in the specimens examined although it is fused to the first endoskeletal element in one (fig. 5D).

Finally, *Lepidogalaxias salamandroides* has greatly reduced basihyal and basibranchial tooth plates that are edentulous in all specimens examined. The endoskeletal basihyal is ossified in two pieces—a short distal and a longer proximal section; it supports a thin sliver of dermal bone and in the largest available specimen, an adult female 56.5 mm. in standard length, a few small
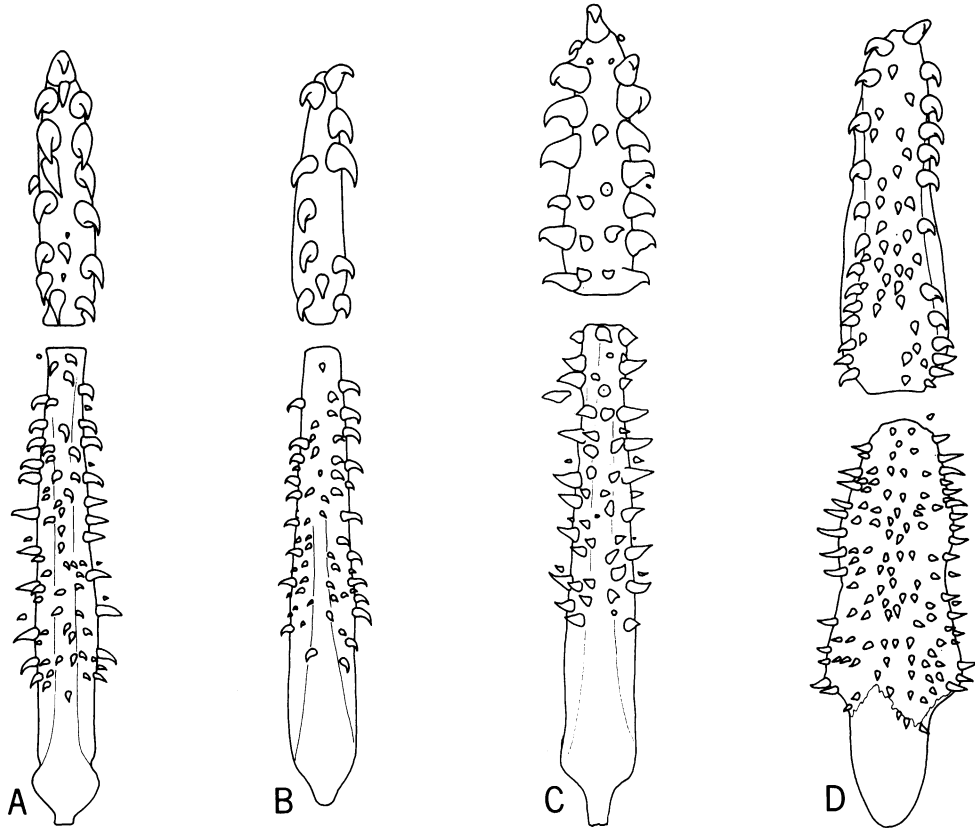
FIG. 4. Dermal basihyal (top) and basibranchial elements. A. *Retropinna osmeroides*. B. *Retropinna retropinna*. C. *Stokelia anisodon*. D. *Prototroctes maraena*. Basibranchial tooth plate (bottom) extends over endoskeletal basibranchials 1, 2, and 3. Note median basibranchial ridge in A–C, and see text regarding its absence in D.

distal ossifications that resemble, and may be, rudimentary tooth bases. The only other dermal ossification is a tooth plate that lies over the fourth endoskeletal basibranchial, a condition found elsewhere among salmoniforms only in esocoids, but the occurrence of this structure is almost certainly primitive.

In summary all salmoniform fishes have basihyal and basibranchial tooth plates and dentition that in most features are advanced relative to the primitive conditions found in osteoglossiforms, elopiforms, and clupeiforms. Esocids have the most primitive arrangement of all salmoniforms, and are advanced only in having the tooth plate over basibranchials 1 to 3 divided into a long anterior and shorter posterior section. All other groups of salmoniforms, except *Lepidogalaxias*, have specialized, fanglike marginal teeth. Of these, osmerids retain the greatest number of primitive features of the tooth plates and teeth. Their relatively few advanced features are shared with plecoglossids, retropinnids, and prototroctids. The argentinid and some searsiid argentinoids, salmonine salmonids, aplochitonids, and galaxiids share a different and distinctive set of derived characters. Other searsiids, the alepocephalids, and the coregonines and thymallines show a great reduction in each of these dermal branchial components. Salangids also have greatly reduced basihyal and basibranchial dermal elements, which, even in the species of *Salanx* with basihyal teeth do not closely resemble those of other salmoniforms (Nelson, 1970). The greatest reduction in this ventral branchial dentition is shown by *Lepidogalaxias*.
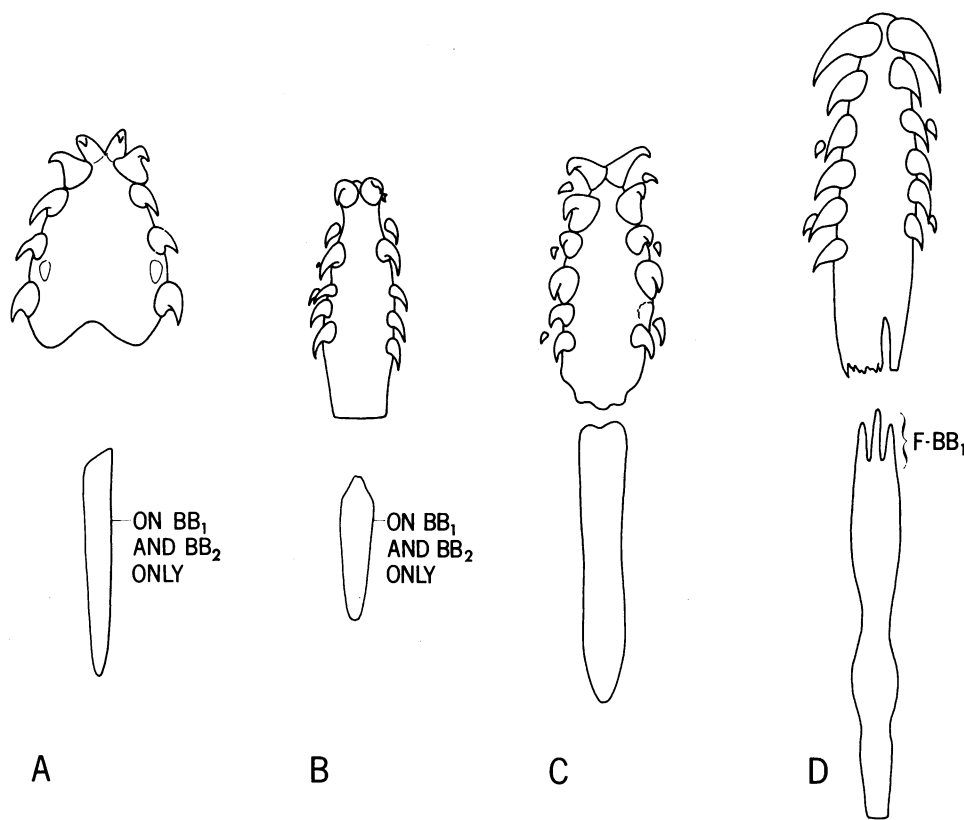
FIG. 5. Dermal basihyal (top) and basibranchial elements. A. *Lovettia seali*. B. *Galaxias divergens* C. *Galaxias vulgaris*. D. *Brachygalaxias bullocki*. Positions of underlying endoskeletal basibranchials shown by symbols BB and F–BB (signifying fusion between dermal and endochondral elements); basibranchial plate in C and D extends over endoskeletal basibranchials 1, 2, and 3.

The evidence indicates, therefore, that the Galaxioidei is a polyphyletic category with some members (retropinnids and prototroctids) being assignable to an osmeroid assemblage consisting of osmerids, and plecoglossids, and the remaining members (aplochitonids and galaxiids) being assignable to a salmonoid assemblage. The evidence further indicates that argentinoids, salmonoids, and osmeroids share various advanced features of tooth plate and tooth development and form a monophyletic group. Dermal basihyal and basibranchial evidence neither supports nor opposes a relationship of esocoids, and *Lepidogalaxias*, or salangids, to other salmoniforms.

POSTERIOR EPIBRANCHIAL ELEMENTS

The posterodorsal part of the gill arch skeleton in representatives of all major teleostean groups was illustrated by Nelson (1967a). His figures indicate that in teleosteans the primitive condition is for the fourth and fifth epibranchials to be separate, for the fifth to be a small oval or cylindrical cartilage articulating with the posteroventral end of the fourth, and for the fourth epibranchial to be a relatively simple bone, narrow anteriorly and much wider posteriorly, and with an expanse of cartilage posteriorly that more or less follows the contours of the bone. The fourth epibranchial is, nevertheless, a bone that assumes a variety of distinctive specialized shapes and relationships to the fifth epibranchial characteristic of a particular lineage. Often the distinctive modifications are associated with the development of a particular kind of mechanism, such as an epibranchial organ, for concentrating small food particles. Among euteleosteans the fourth
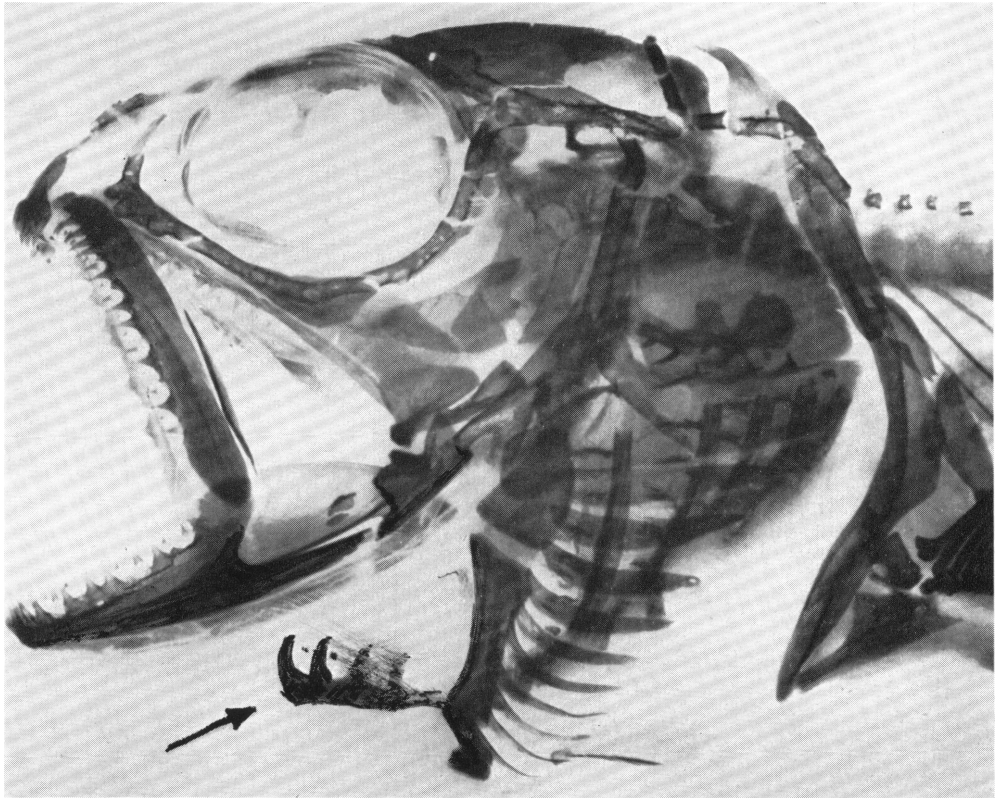
FIG. 6. Photograph of alizarin preparation of head of young *Salvelinus fontinalis* to show position of basihyal fangs (arrow) when mouth is widely opened.

epibranchial primitively has several characteristic features: 1) posteroventrally, above its articulation with the fourth ceratobranchial, it supports the fifth epibranchial; 2) anteroventrally it supports the fifth upper pharyngeal tooth plate, the dentition of which together with that of the fourth pharyngobranchial forms the main upper pharyngeal dentition; 3) it articulates anteriorly directly with the fourth pharyngobranchial; 4) dorsally it forms an elevation or specific process for insertion of the fourth external levator muscle; and 5) anterior to this elevation on the dorsal edge it bears a short uncinate process that forms the pylon of a connective tissue bridge between it and a corresponding uncinate process on the third epibranchial. Hence, the fourth epibranchial is mechanically connected to the third via the uncinate processes, it is joined to the basicranium by the fourth external levator muscle, and it supports part of the main upper pharyngeal dentition in

primitive euteleosteans. All of these features are present in *Megalops*, *Albula*, *Pterothrissus*, and in some anguilliforms (Nelson, personal commun.). In *Elops* the elevated dorsal margin of the fourth epibranchial is simply reflected forward in a long arc, there is no uncinate process, and the presumption is that the uncinate process is secondarily missing. In other words, the process is present in one of the two groups of elopoids as well as in all examined members of the albuloid-anguilloid assemblage and was therefore probably present in the common ancestor of these two main lineages. In osteoglossomorphs there is neither a distinct dorsal process for the external levator nor an uncinate process for articulation with the third epibranchial. In clupeomorphs a variety of different dorsal processes are present, but never an uncinate process. The same is true of some gonorynchiform and characoid ostariophysans. In the remaining euteleosteans, salmoniforms, and neoteleosteans (Rosen, 1973a),

FIG. 7. Photograph of alizarin preparation of head of young *Galaxias maculatus* to show position of basihyal fangs (arrow) when mouth is widely opened.

each of the five main attributes of this bone, as listed above for Elopomorpha is present in some representatives of all the principal assemblages. It appears, therefore, that the common ancestor of all euteleosteans shared many of the same dorsal gill arch features as those in elopomorphs. If this set of epibranchial attributes is advanced for teleosteans, its shared presence suggests that elopomorphs and euteleosteans are sister groups, and the absence of an uncinate process and the development of a specialized levator process in *Chanos*, *Hoplias* (Nelson, 1967a), and the characids I examined (and see Weitzman, 1962) may be additional evidence of gonorynchiform relationship to other ostariophysans (see Rosen and Greenwood, 1970). Clearly, however, before such conclusions can be proposed formally, it is necessary to decide which of these features of the fourth epibranchial are shared advanced features of elopomorphs and euteleosteans, which are primitive for all modern teleosteans, whether

some or all the structures have been lost independently by osteoglossomorphs, clupeomorphs, and ostariophysans, or whether they are similar and independent specializations in elopomorphs and in the nonostariophysan euteleosteans. It would be instructive to attempt a study of this bone in some of the fishes that appear to be primitive sister groups to some or all living forms, for example, in ichthyodectids and in some of the fishes called leptolepids.

The dorsal, or levator, process of the fourth epibranchial has a distinct topographic relationship to the posterior branchial arteries. In *Elops* and *Megalops* the reflected dorsal section (the levator process) forms a notch with the anterior arm of the bone, and the fourth efferent branchial artery passes through this notch (Nelson, 1967b). The fifth efferent branchial artery passes through the notch formed by the posteroventral corner of the fourth epibranchial and the fifth epibranchial. These two efferent arteries

have tended to become enclosed in canals in various groups of teleosteans. In clupeomorphs the passage of the fourth efferent has been enclosed in bone, presumably by the development of a bridge across the notch formed by the reflected anterodorsal levator and narrow anteroventral parts of the fourth epibranchial (Nelson, 1967a, figs. 2a, b of *Etrumeus* and *Clupea*). The fifth efferent has been enclosed in clupeomorphs by the enlargement and growth upward of the cartilaginous fifth epibranchial around this artery. A complete canal is formed when the dorsal tip of the fifth epibranchial

contacts the posterodorsal cartilaginous part of the levator process. The fifth epibranchial often fuses with the fourth in clupeomorphs. Apparently fusion takes place first dorsally and then ventrally, for the fifth epibranchial of clupeomorphs is either in contact with the fourth ventrally and dorsally, articulated with the fourth ventrally and fused with it dorsally, or fused with it dorsally and ventrally. In no case is the fifth epibranchial fused ventrally and articulated dorsally with the fourth. In one group, represented by *Chirocentrodon*, the posterior epibranchials are so reduced that the posterior wall

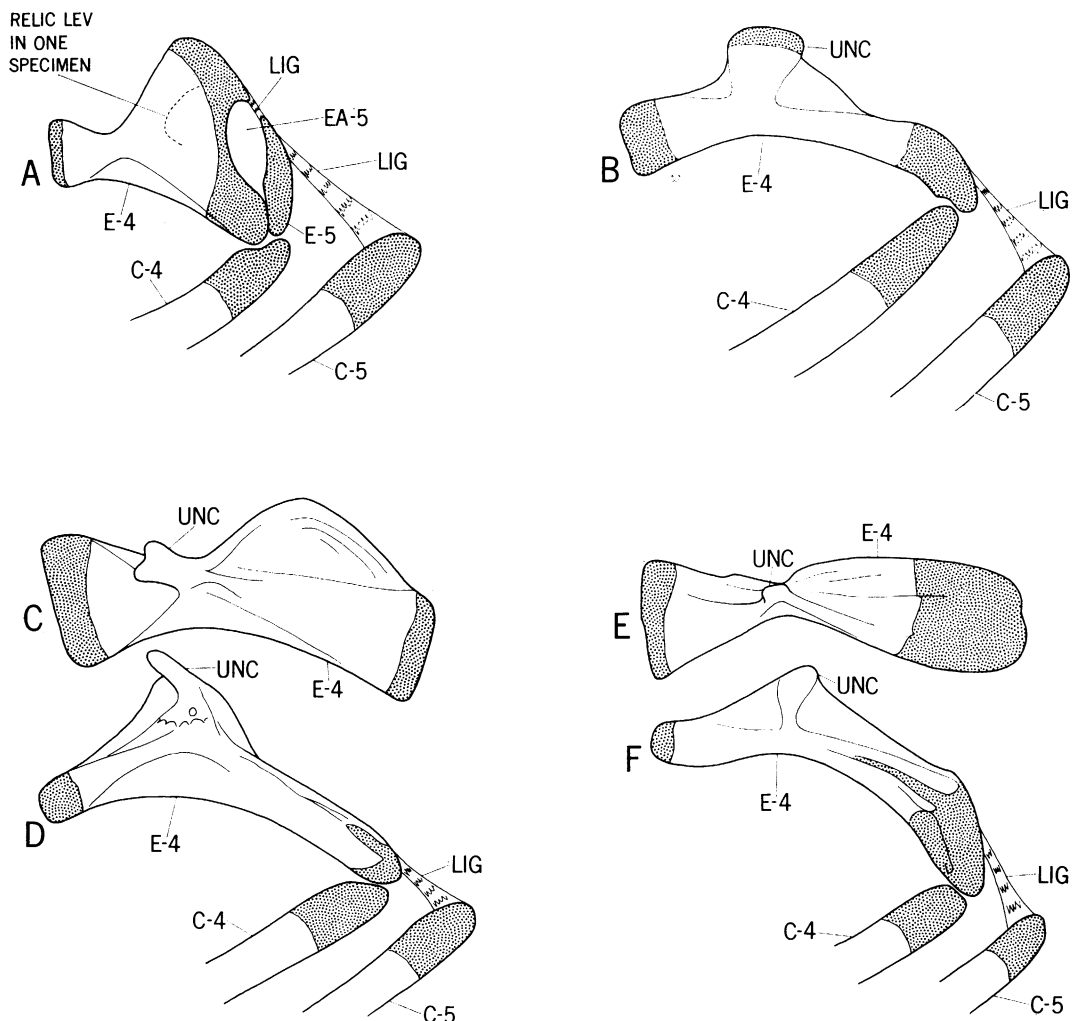Fig. 8. Epibranchial structure in esocoids, lateral view, anterior to right. A. *Umbra pygmaea*; pattern present in all species of *Umbra*. B. *Esox americanus*; pattern present in all examined species of *Esox*. C, D. *Novumbra hubbsi* (C shows E–4 in dorsal view). E, F. *Dallia pectoralis* (E shows E–4 in dorsal view). Note absence of E–5 and presence of UNC in all but *Umbra* (A). Cartilage stippled.

of the fifth efferent canal has been lost, deceptively appearing as if the fifth epibranchial had fused ventrally with the fourth. The fifth efferent canal of clupeomorphs has been secondarily enlarged in many forms by the disappearance of the adjacent cartilage and bone of the fourth epibranchial so that the canal has the appearance of having gradually sunk into the posterior substance of the fourth epibranchial. A triradiate bone is thus formed in which the anterior arm contacts the fourth pharyngobranchial, the posterior arm (which borders the arterial canal ventrally) contacts the fourth

ceratobranchial, and the dorsal arm (which borders the arterial canal dorsally) receives the insertion of the external levator muscle. Hence, this triradiate structure appears to have been the direct result of the formation of an arterial canal by the enlargement of the fifth epibranchial. The fifth efferent arterial canal seems to have been formed in much the same way in osteoglossomorphs (see Nelson, 1967a, figs. 1–3). A triradiate fourth epibranchial occurs also in various primitive and generalized euteleosteans, for example, in characoids, argentinids, and osmerids, but it is not associated with the
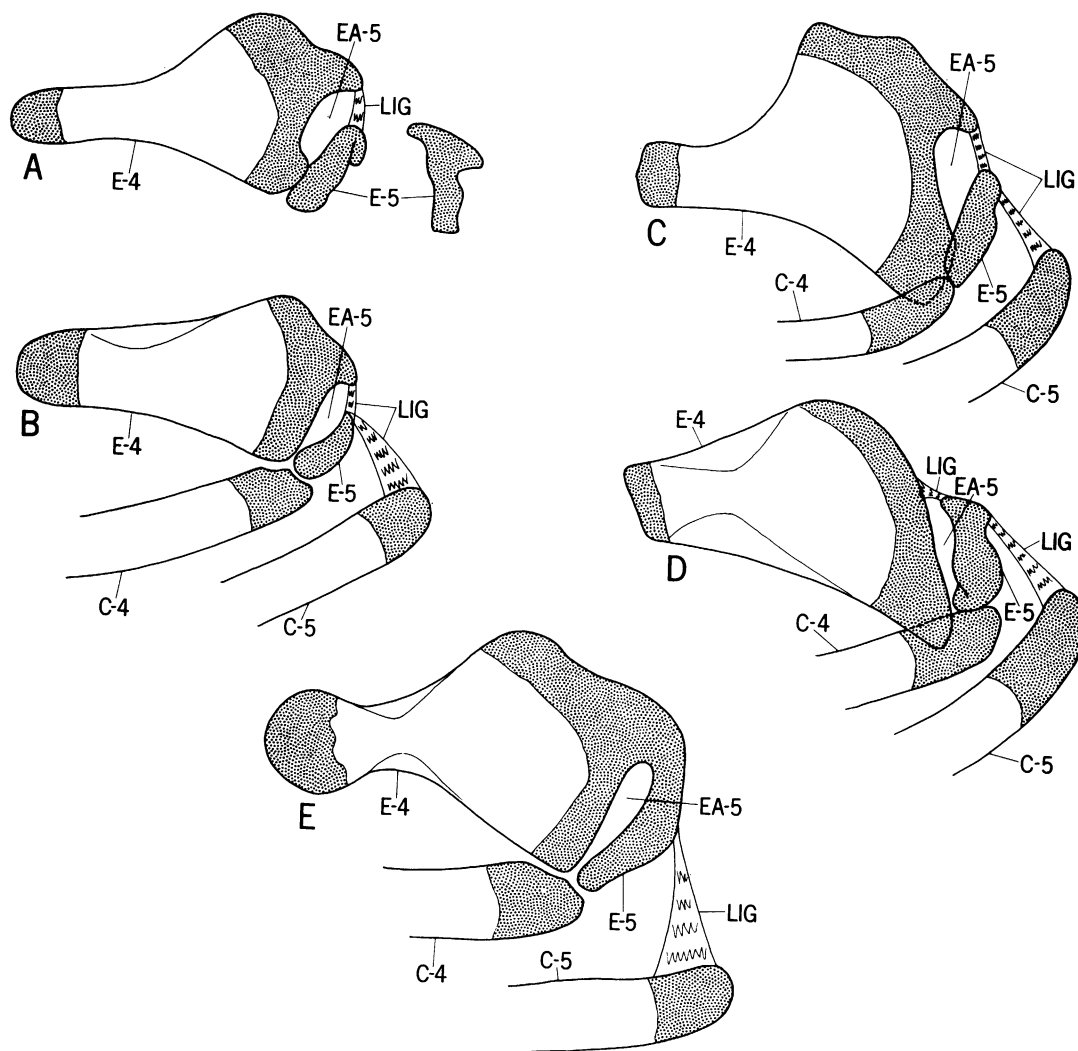

FIG. 9. Epibranchial structure in salmonids, lateral view, anterior to right. A. Pattern in *Salmo gairdneri* and *Oncorhynchus kisutch* (posterior view of E–5 shown to right). B. *Salvelinus fontinalis*. C. *Coregonus artedi*. D. *Cristivomer namaycush*. E. *Prosopium cylindraceum* (cf. fig. 10A).

development of an arterial canal or enlarged fifth epibranchial. The triradiate bones of primitive euteleosteans appear, therefore, to have evolved independently and to have arisen for different reasons than those in clupeomorphs.

The occurrence of a triradiate fourth epibranchial with an uncinate process in front of a distinct levator process, without necessarily involving the formation of a fifth efferent arterial canal or enlarged fifth epibranchial, is not known outside of the Euteleostei. Such an epibranchial occurs in argentinids, osmerids, and among the Neoteleostei. Among esocoids, an uncinate process occurs on a simple cylindrical fourth epibranchial in esocids (fig. 8B) and a triradiate epibranchial appears as an apparent relict in some umbrids (fig. 8A) although there is no uncinate process. Both structures apparently are being reduced and lost in esocoids. In fact, when these modifications of the fourth epibranchial do not occur in euteleosteans, in general it is simpler to assume that they have been reduced and lost than to assume that they have been repeatedly evolved independently, an assumption that would be required if the simpler structure were primitive.

In argentinoid fishes the absence of an uncinate process and a tiradiate structure is associated with a general reduction in ossification. Within the superfamily Argentinoidea, the rather well-ossified argentinids have a full complement of fourth epibranchial structures (Greenwood and Rosen, 1971, fig. 4), and the less-ossified bathylagids from deeper waters lack an uncinate process and, in *Opisthoproctus*, also the triradiate structure (Greenwood and Rosen, 1971, figs. 5, 6). Within the superfamily Alepocephaloidea, the rather generalized and comparatively well-ossified searsiids lack the triradiate structure but retain the uncinate process (Greenwood and Rosen, 1971, fig. 1a), and the very poorly ossified alepocephalids lack both the triradiate structure and the uncinate process (Greenwood and Rosen, 1971, figs. 1b, 2, 3).

No aplochitonid, galaxiid, or salmonid has a triradiate fourth epibranchial or uncinate process (figs. 9–11). In aplochitonids and galaxiids notable reductions in ossification are evident in the loss of a dermopalatine, ectopterygoid, supramaxilla, most infraorbital bones (fig. 13), and in reduction of the basibranchial tooth plate (fig. 5) and upper pharyngeal
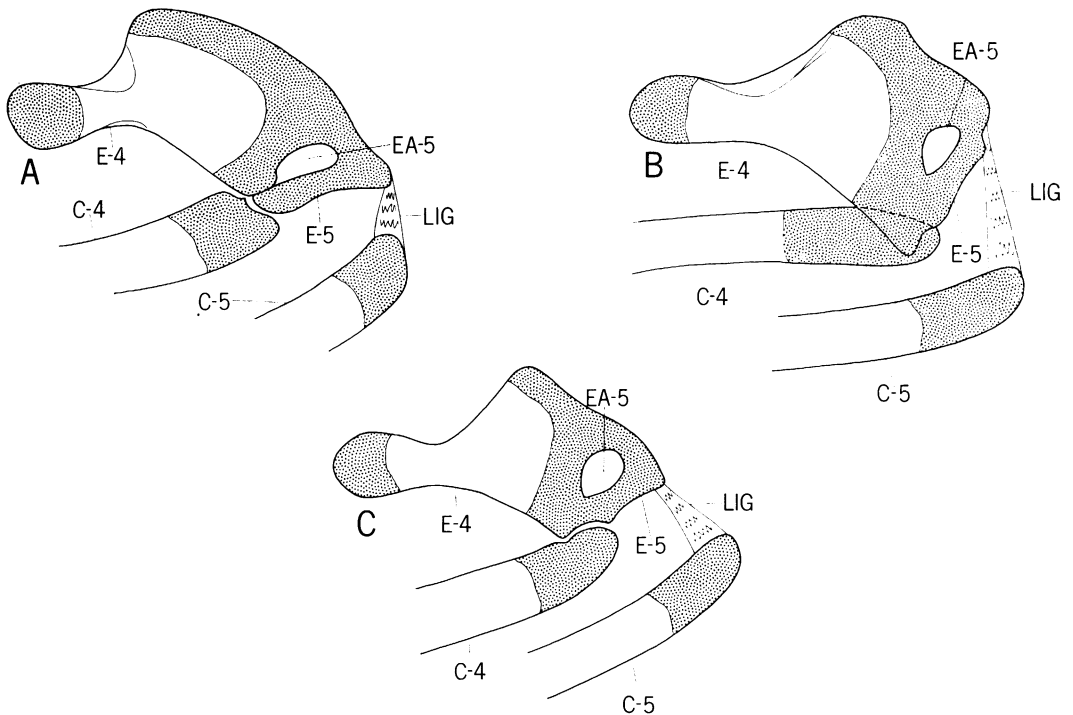

FIG. 10. Epibranchial structure in galaxioids, lateral view, anterior to right. A. Pattern in *Galaxias divergens* and *Nesogalaxias neocaledonicus* (cf. fig. 9E). B. *Aplochiton taeniatus*. C. *Galaxias maculatus*.

dentition (fig. 11, cf. fig. 12). Salmonids show significant reductions in the basihyal (in core-gonines and thymallines, fig. 3F) and basi-branchial tooth plate (fig. 3A–E) and are well known for the amount of cartilage retained in the skull of the adult, particularly in the ethmoid region (fig. 6).

Lepidogalaxias also lacks an uncinate process and triradiate structure in the fourth epibran-chial (fig. 14), and its loss or reduction in ossi-fication are evident from head to tail. In the head skeleton there is no supramaxilla, no rem-nants of the circumorbital series, only minor remnants of the basihyal and basibranchial tooth plates, a reduced urohyal, no dermal com-ponents on the second or third pharyngobran-chials (fig. 15B), and a thin, flexible operculum with deep indentations of unossified tissue.

The absence of an uncinate process or tri-radiate structure is not specifically correlated with other reductional trends in esocoids and in osmeroid-like fishes. For example, in esocoids, *Esox*, *Dallia*, and *Novumbra* retain the uncinate process but have greatly reduced the height of the posterior end of the epibranchial to a single, low cartilaginous process that articulates only with the fourth ceratobranchial; the fifth epi-branchial has been lost (fig. 8B–F). In *Umbra* the fourth epibranchial lacks the uncinate pro-cess and has a large triangular posterior end which in a specimen of *Umbra limi* shows a relict of the triradiate structure; a small fifth epibran-chial of apparently primitive design articulates with the cartilage of the posteroventral corner of the bone (fig. 8A). *Dallia* is the least ossified member of the group, yet it shows no greater sign of epibranchial simplification than that in *Novumbra* or *Esox*. Among osmeroid-like fishes (fig. 16), all except the salangids are rather well ossified, yet salangids appear to lack only the
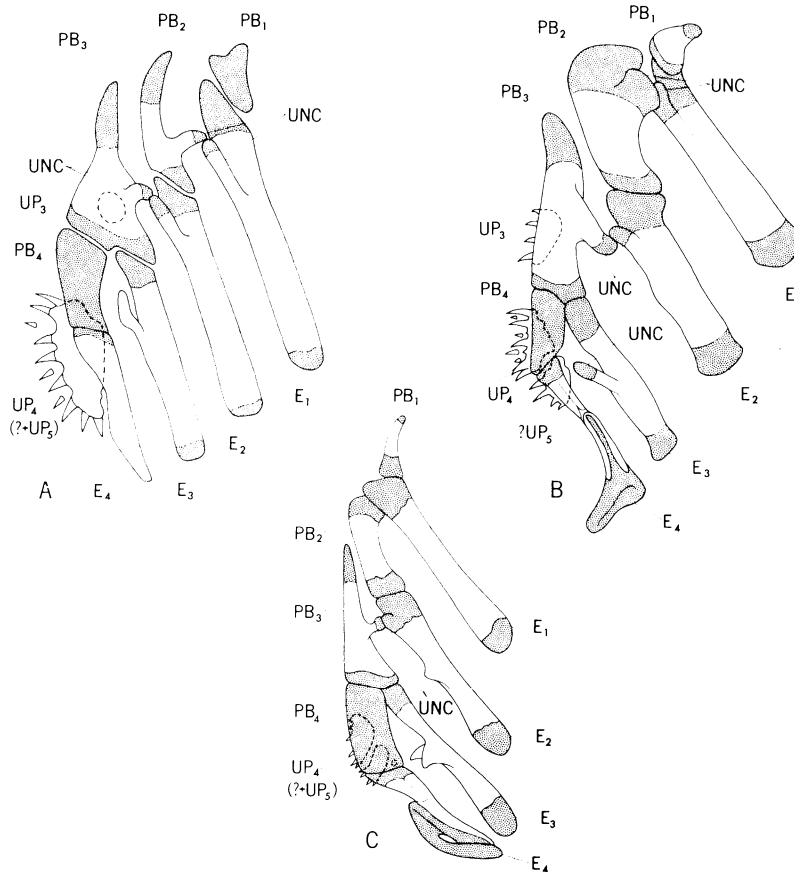

FIG. 11. Dorsal gill arch skeleton, dorsal view of right side. A. *Salmo gairdneri*. B. *Galaxias vulgaris*. C. *Nesogalaxias neocaledonicus*.
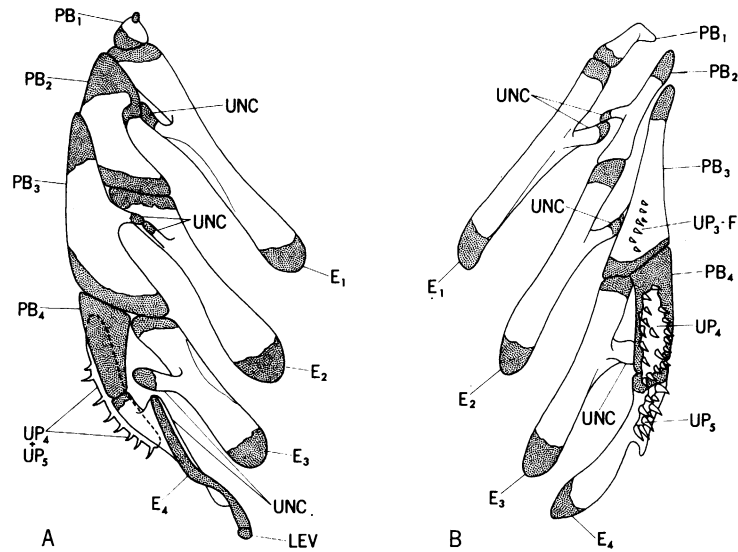
FIG. 12. Dorsal gill arch skeleton, right side. A. *Stokelia anisodon*, dorsal view. B. *Hypomesus olidus*, ventral view. Note elongate tooth plates on PB$_4$ and E$_4$.

uncinate process, which is also absent in *Hypomesus* and *Mallotus* (fig. 16C, D, G). In the retropinnids (fig. 16E, F), *Stokelia* lacks a triradiate structure (that is, a distinct levator process as present in osmerids, plecoglossids, and salangids).

The fifth epibranchial has a distinctly different fate in each of the main groups of salmoniforms. In esocoids it is simply lost in *Esox*, *Dallia*, and *Novumbra* (fig. 8B, D, F), as well as in *Lepidogalaxias* (fig. 14). In argentinoids it articulates ventrally with the posteroventral corner of the fourth epibranchial and dorsally with the accessory cartilage of the fifth ceratobranchial that is unique to this group (Greenwood and Rosen, 1971). In the group including salmonids, galaxiids, and aplochitonids it is free in some salmonids, and it is fused with the posterodorsal corner of the fourth epibranchial in other salmonids and in some galaxiids. Aplochitonids and other galaxiids have this cartilage fused both dorsally and ventrally with the fourth epibranchial (figs. 9, 10). There is no evidence that in aplochitonids or galaxiids the fifth epibranchial ever first fuses ventrally with the fourth. Among osmeroid-like fishes, the opposite is true. When the fifth epibranchial is fused with the fourth in *Hypomesus*, *Mallotus*, *Spirinchus*, *Allosmerus*, *Salangichthys*, and *Retro-*

pinna, the fusion invariably takes place ventrally with the lower posterior arm of the fourth epibranchial (fig. 16A–D, F, G). In *Stokelia* (fig. 16E) and *Osmerus* (Greenwood and Rosen, 1971, fig. 7) the fifth epibranchial is unfused, and in *Plecoglossus* (fig. 16H) it is greatly
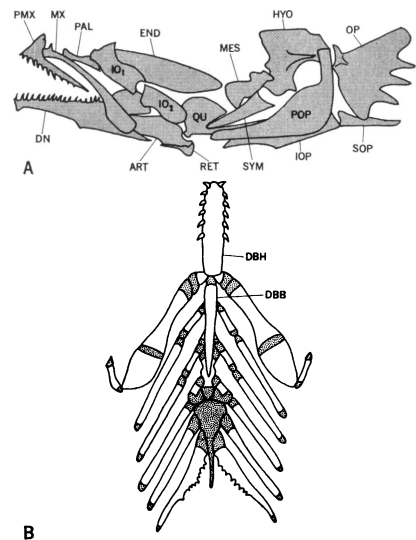

FIG. 13. *Nesogalaxias neocaledonicus*. A. Jaw suspension, opercular apparatus, and infraorbital bones, left side. B. Ventral gill arch skeleton; stippling represents cartilage in B only.
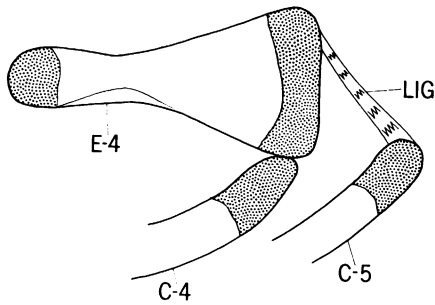
FIG. 14. Epibranchial structure in *Lepidogalaxias salamandroides*, lateral view, anterior to right.

enlarged so that it extends between but does not fuse with the tips of the two posterior arms of the fourth epibranchial.

If one assumes that the presence of an uncinate process and a separate and distinct levator process of the fourth epibranchial are primitive for salmoniforms, as suggested above, then no phylogenetic conclusions can be drawn regarding the interrelationships of the four main groups of salmoniforms based on epibranchial structure alone. Nor can *Lepidogalaxias* be related on this basis since, like *Umbra*, salmonids, aplochitonids, galaxiids, *Retropinna*, and *Opisthoproctus*, it has lost both the uncinate and levator processes. The fifth epibranchial appears to be in

a primitively simple condition in *Umbra, Salvelinus, Cristivomer, Salmo, Oncorhynchus, Coregonus, Osmerus,* and *Stokelia,* and it has been lost in *Novumbra, Dallia, Esox,* and *Lepidogalaxias.* Various specializations of the branchial elements suggest certain lower level phylogenetic inferences, as follows:

1. In the reduction in height of the posterior end of the fourth epibranchial and in the loss of the fifth, *Dallia* and *Novumbra* are more closely related to each other, and possibly to *Esox,* than to *Umbra.* The common absence of the fifth epibranchial in the esocoids *Novumbra, Dallia,* and *Esox* and in *Lepidogalaxias,* might be significant, but only as parallel trends arising independently from phylogenetically more distantly related branchial systems (cf. fig. 15A and B). The posterior end of the fourth epibranchial in *Esox* is simple and cylindrical and may be independent of the reduction in height of the bone in *Dallia* and *Novumbra* in which the posterior arm is also expanded laterally.

2. The argentinoids are defined by the presence of a complex branchial structure, the crumenal organ (Greenwood and Rosen, 1971).

3. The Galaxioidei is polyphyletic, with the Galaxiidae and Aplochitonidae being related to salmonids and the Retropinnidae to osmerids (prototroctid material was not available for this
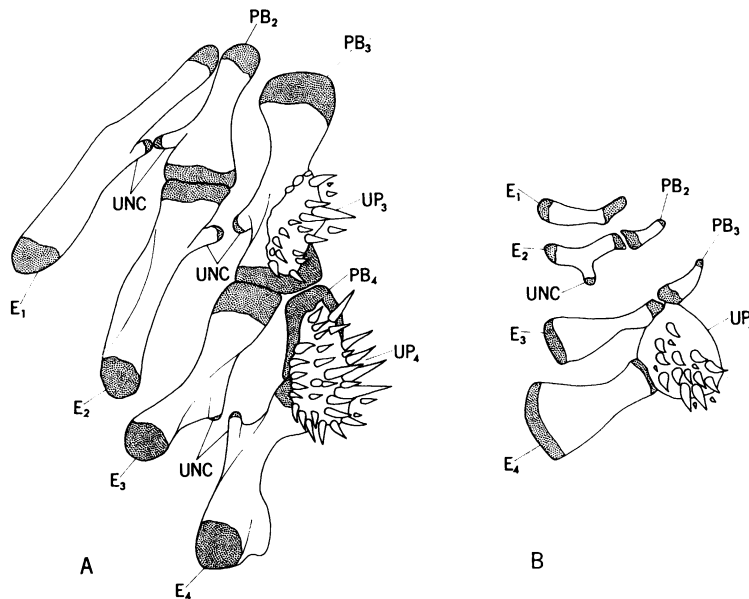
FIG. 15. Dorsal gill arch skeleton, right side ventral view. A. *Novumbra hubbsi.*
B. *Lepidogalaxias salamandroides.*
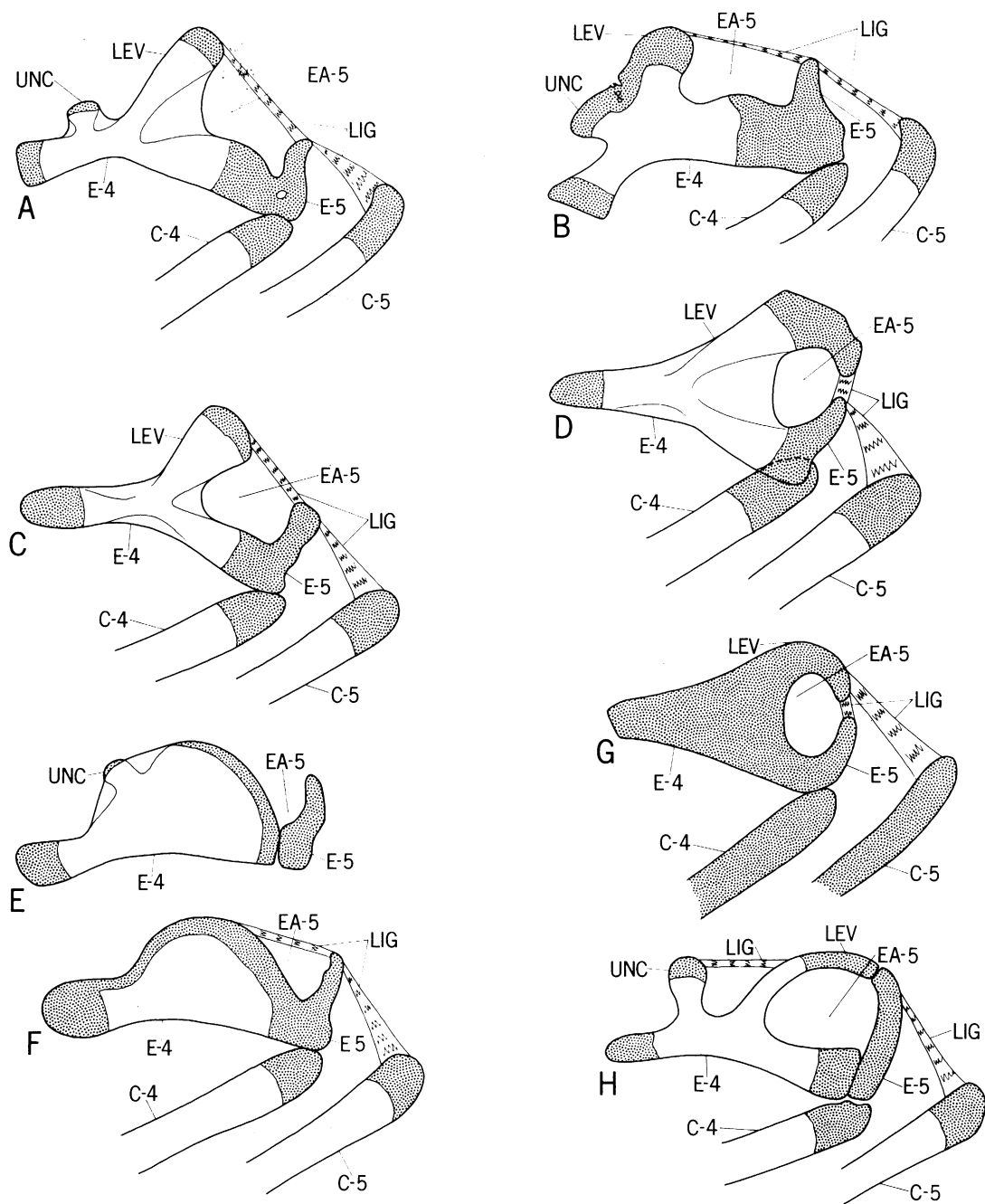
FIG. 16. Epibranchial structure in osmeroids, lateral view, anterior to right. A. *Spirinchus dilatus*. B. *Allosmerus attenuatus*. C. *Mallotus villosus*. D. *Hypomesus olidus*. E. *Stokelia anisodon* (epibranchials only). F. *Retropinna retropinna*. G. *Salangichthys microdon*. H. *Plecoglossus altivelis*.

part of the study) on the basis of specializations of the fourth epibranchial and the manner in which this bone fuses with the fifth epibranchial.

4. In having the fifth epibranchial apparently incorporated into the lower posterior arm of a triradiate fourth epibranchial, salangids are

related to the Osmeridae. Epibranchial structure is similar in *Salangichthys* and *Hypomesus*.

SALMONIFORM CAUDAL SKELETON

Numerous advanced attributes are present in the caudal skeletons of salmoniform fishes. The major features are as follows (table 2):

1. Vertebral centra of the caudal skeleton are lost or combined. The first preural centrum (PU_1) is combined with the first ural (U_1) to produce a compound centrum (PU_1+U_1). The second ural centrum (U_2) is lost or combined with the compound centrum (as $PU_1+U_1+U_2$).

2. The number of uroneurals is reduced from three to two or one. The first to be lost is the uppermost, or third. The second uroneural is either lost or fused with the first.

3. The first uroneural is foreshortened, develops dorsal outgrowths of laminar bone, and fuses with a compound centrum PU_1+U_1 or $PU_1+U_1+U_2$. The first uroneural is withdrawn anteriorly from its position over the second preural centrum to the first (PU_1) and in some cases to the first or second urals (U_1 or U_2). Fusion of centra is invariably accompanied by reduction of the first uroneural, but the reverse is not true. Similarly, the first uroneural is sometimes fused to the compound centrum, but never to unconsolidated centra. Dorsal outgrowths of laminar bone develop on the first uroneural whether or not it is foreshortened or fused to a compound centrum.

4. The dorsal outgrowth of laminar bone of the first uroneural fuses with an entire autogenous rudimentary neural arch and spine from the first or second preural centrum (PU_1 or PU_2) to produce an anteriorly directed prong on the dorsal margin of the uroneural.

5. The dorsal outgrowth of laminar bone of the first uroneural fuses with the laminar bone of the sessile rudimentary neural arches and spines of a compound centrum to produce a bony plate (or plates) that fills the area between the arch and spine of PU_2 and the first uroneural and ventral to the epurals when these are present.

6. Rudimentary neural arches and spines of PU_2, PU_1, U_1 or of the compound centrum fuse with epurals.

7. Rudimentary neural arches and spines of PU_2, PU_1, U_1 or of the compound centrum are reduced or lost.

8. Epurals are reduced in number from three to none by loss or consolidation.

9. The upper hypurals are reduced in number from four to one by loss or consolidation.

10. The lower hypurals fuse into a single plate or they fuse with each other and with the parhypural.

11. The first, or lowermost, hypural fuses only with the parhypural.

12. Preural centra fuse to produce doubling of neural or hemal spines and arches, or both, or to produce free or semidetached spines.

TABLE 2

DISTRIBUTION OF ADVANCED CHARACTERS OF THE CAUDAL SKELETON IN SALMONIFORM FISHES

	Argentinoids	Galaxioids	Salmonids	Osmeroids	Esocoids	*Lepidogalaxias*
Character[a]						
1	+	+	—	+	—	—
2	+	+	+	+	+	+
3	+	+	+	+	+	+
4	—	—	+	+	—	—
5	+	—	—	—	—	—
6	—	+	—	—	+	+
7	—	—	+	+	+	+
8	+	+	+	+	+	+
9	—	+	—	—	+	?+
10	—	+	—	—	—	?+
11	—	—	—	+	—	—
12	+	+	+	+	+	+

[a] See above for explanation.

Symbols: +, present in at least some members of group; ?+, character difficult to interpret and may not be the same attribute.

ARGENTINIDAE   BATHYLAGIDAE   SEARSIIDAE   ALEPOCEPHALIDAE

BATHYLAGINAE

OPISTHOPROCTINAE

$(PU_1 + U_1), U_2$

$(PU_1 + U_1), U_2$

$(PU_1 + U_1 + U_2)$

PU_1, U_1, U_2

PU_1, U_1, U_2

PU_1, U_1, U_2

$[(PU_1 + U_1), U_2]$
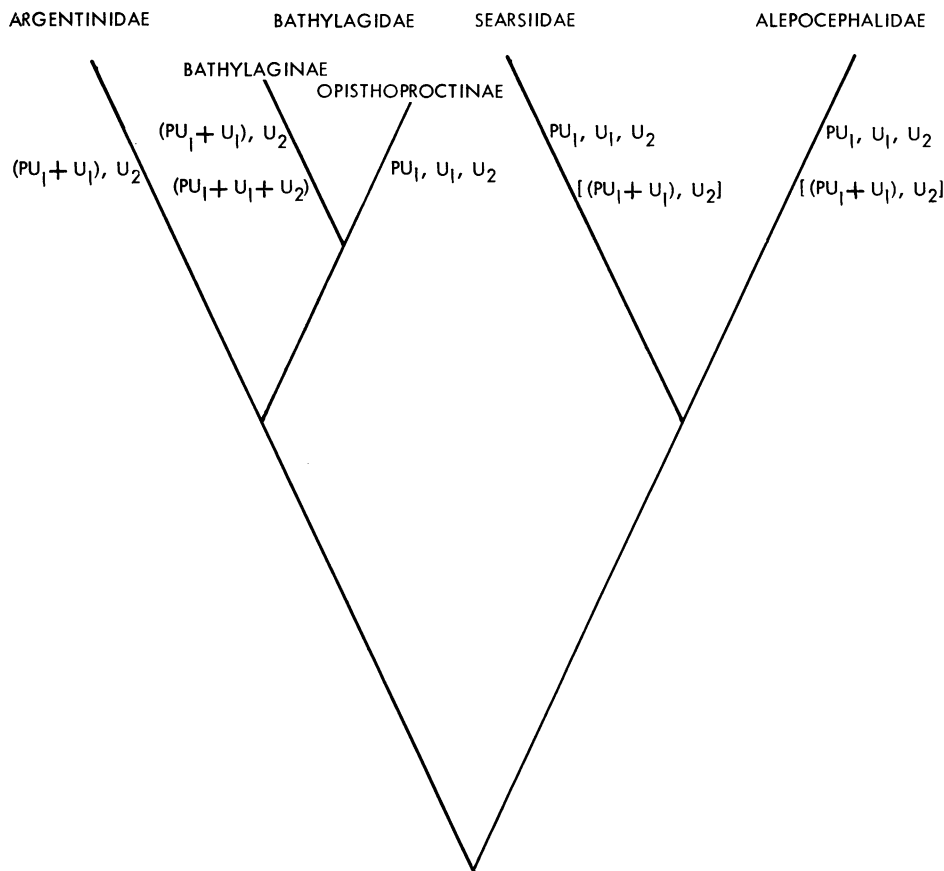
PU_1, U_1, U_2

$[(PU_1 + U_1), U_2]$

Fig. 17. Phylogeny of argentinoid fishes, after Greenwood and Rosen (1971), showing pattern of distribution of fused and unfused ural and preural centra (U and PU) in caudal skeleton. Symbols for unfused centra are separated by commas, fused centra by +, and groups of fused centra are enclosed in (). [] signify an uncommon or rare condition. *Bathyprion*, of uncertain relationship to other alepocephaloids, is omitted from the diagram.

A review of the occurrence of some of these caudal traits in argentinoids is instructive as the caudal skeleton of these fishes seems to be based on a relatively primitive format. Character number 1 (vertebral fusion), for example, is usually thought of as an advanced feature in many fish groups in which the number of separate skeletal elements are reduced and consolidated (that is, simplified) as a means of achieving increased strength and rigidity. Indeed, the pattern of occurrence of vertebral fusion in the alepocephaloid argentinoids (fig. 17) seems clearly to point this way: PU_1, U_1, and U_2 are present and unfused in most searsiids and alepocephalids, and only PU_1 and U_1 are fused in an occasional species or individual.

Within other argentinoid groups, however, the pattern is not so clear. In the Argentinidae and Bathylaginae (family Bathylagidae) PU_1 and U_1 are invariably fused into a compound centrum, and in one bathylagid, *Bathylagus stilbius*, U_2 is either also incorporated (as $PU_1+U_1+U_2$) or it has been lost (fig. 17). The examined opisthoproctine bathylagids, on the other hand, have all the caudal centra unfused. In a scheme of relationships in which the bathylagines and opisthoproctines are sister groups and both form a sister group (as the Bathylagidae) of the argentinids, the evolution of vertebral fusion can be explained in two ways. Either the common ancestor of the whole group had unconsolidated centra and they were independently fused

in argentinids and bathylagines, or the common ancestor had consolidated centra and the opisthoproctines redeveloped separate centra paedomorphically. The former scheme thus requires two assumptions (of independent origin) and the latter, only one. In general, the latter hypothesis seems to be contrary to our general understanding of evolutionary direction in this trait, but nevertheless it cannot be ruled out. Unfortunately, an insufficient number of ontogenetic studies have been carried out to determine the extent to which unconsolidated centra are present in the larvae or juveniles of groups in which the centra are compound in the adults, and I have seen no small juvenile argentinoids in which the hypothesis of paedomorphosis can be tested and therefore possibly rejected. Character state number 1, therefore, appears to be presently of little significance in phylogenetic studies unless the consolidation occurs in unusual or unique ways, for example, in connection with the fusion of centra to hypurals or uroneurals prior or subsequent to the formation of a compound centrum (PU_1+U_1) and the loss or consolidation of U_2. The fact that argentinoids share this trait with galaxioids and osmeroids, but not with salmonoids and esocoids, cannot therefore at this time be taken to be significant phylogenetically. Of the five other advanced caudal skeletal characters in argentinoids (2, 3, 5, 8, 12), character number 5, the formation of supraneural plates or laminae associated with rudimentary neural arches but never with epurals, is unique for argentinoids. The remaining four characters (2, 3, 8, 12) are shared with all other groups of salmoniforms including *Lepidogalaxias*. In having advanced attributes shared with all groups of salmoniforms, and none shared with any one or two groups (other than the doubtfully interpretable vertebral fusion), argentinoids qualify on caudal skeleton evidence as the primitive sister group of all other salmoniforms.

The remaining salmoniform caudal skeletons fall into three groups, one consisting of galaxioids (galaxiids and aplochitonids), a second of esocoids and *Lepidogalaxias*, and a third of salmonids and the osmeroid fishes (osmerids, plecoglossids, salangids, retropinnids, and prototroctids).

Galaxiids (fig. 18) and aplochitonids (fig. 19) are characterized by some primitive and some advanced caudal features. Like argentinoids,

the galaxioids retain rudimentary neural arches and spines over PU_1 and U_1 which have fused to form a compound centrum, a fusion that is quite complete except in an occasional individual of the Chilean *Brachygalaxias bullocki* (Greenwood et al., 1966, fig. 4). Such small posterior neural arches and spines are undoubtedly primitive for teleosteans generally, as they occur in clupeomorphs, elopomorphs, osteoglossomorphs, and in various leptolepid-like fishes. Remnants of these relict structures occur in other salmoniforms, but they are never so well developed as in galaxioids. Galaxioids have, in fact, maintained these elements in a relatively stable condition and have incorporated them in various ways to reenforce the epaxial part of the caudal skeleton. They are only infrequently autogenous, as in individual specimens of *Aplochiton taeniatus* (fig. 19B). Otherwise they are fused with the compound centrum and sometimes even with the anterior arm of the first uroneural as in the highly consolidated skeleton of *Galaxias maculatus* (fig. 18E). In only a few instances are there two arches combined into a single structure, as in *Lovettia seali* (fig. 19C). Also as in argentinoids the ural neural arches of galaxioids have become invested with platelike bone and it is evident in certain cases in *Aplochiton taeniatus* that epurals have fused with them (cf. fig. 19A and B). The general rule in galaxioids seems to be, in fact, that the number of free epurals is reduced in most species either by fusion with the spines of the ural neural arches or by being crowded out by the extensive bony laminae on those spines. There are two uroneurals in galaxioids in most cases, although they are sometimes reduced to one in *Lovettia seali* and in *Galaxias divergens* (figs. 18C, D; 19C). In *Galaxias maculatus* there are two uroneurals but the first has fused with the compound centrum and with the ural neural arches (fig. 18E). The first uroneural may also develop dorsal laminae which extend forward toward the tip of the nearby ural neural arch. The galaxioid caudal skeleton is specialized in several additional ways. There are never more than three upper hypurals or 14 branched rays. Hypurals tend to fuse with one another, the most common fusion being between the first and second. More extensive fusion occurs in cases where all upper hypurals are fused to form a single plate and the two lower hypurals and the parhypural are fused to form a second plate. In no case have the first hypural and
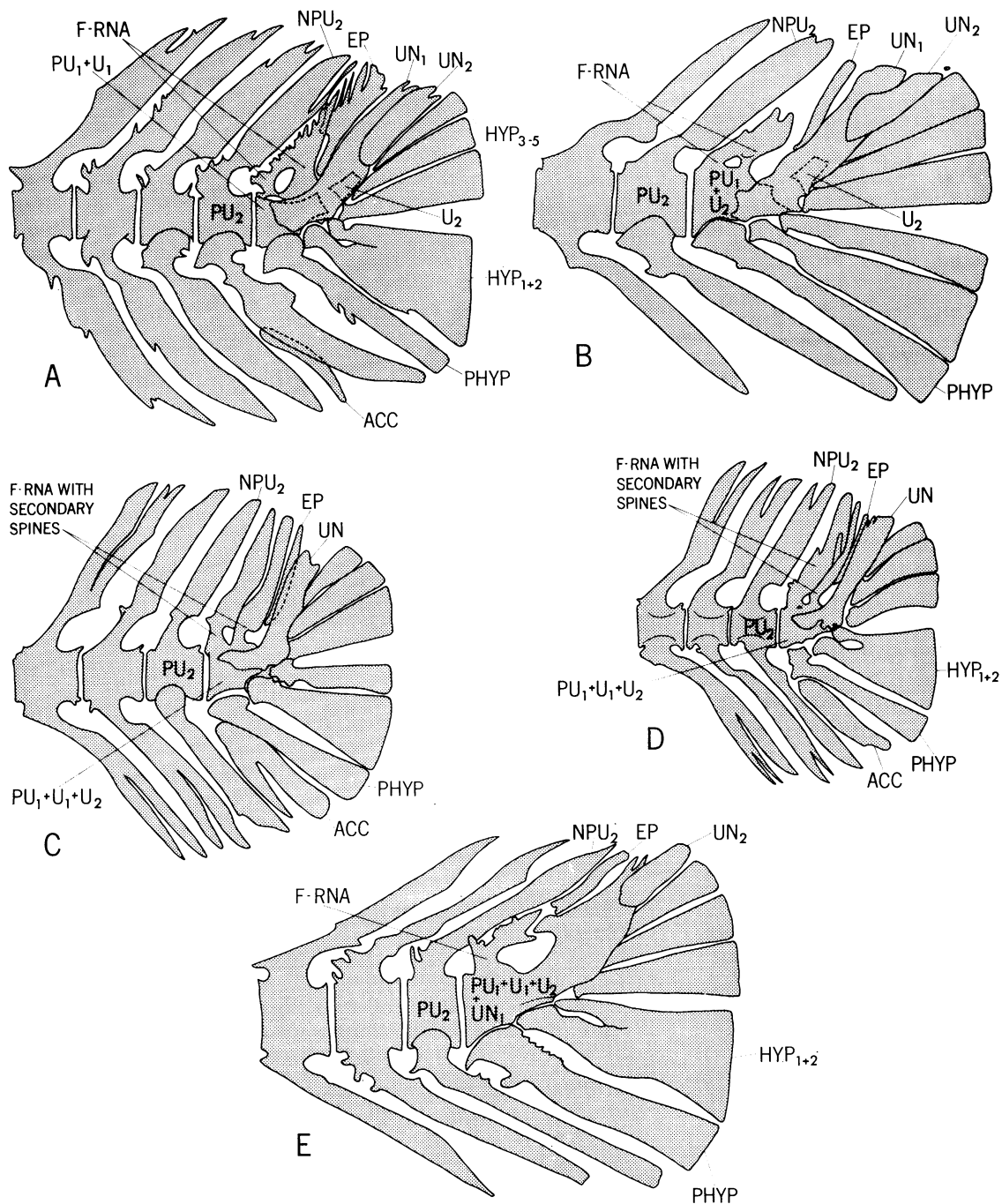
FIG. 18. Caudal skeletons of galaxiines. A. *Galaxias vulgaris*. B. *Nesogalaxias neocaledonicus*. C, D. *Galaxias divergens*. E. *Galaxias maculatus*.
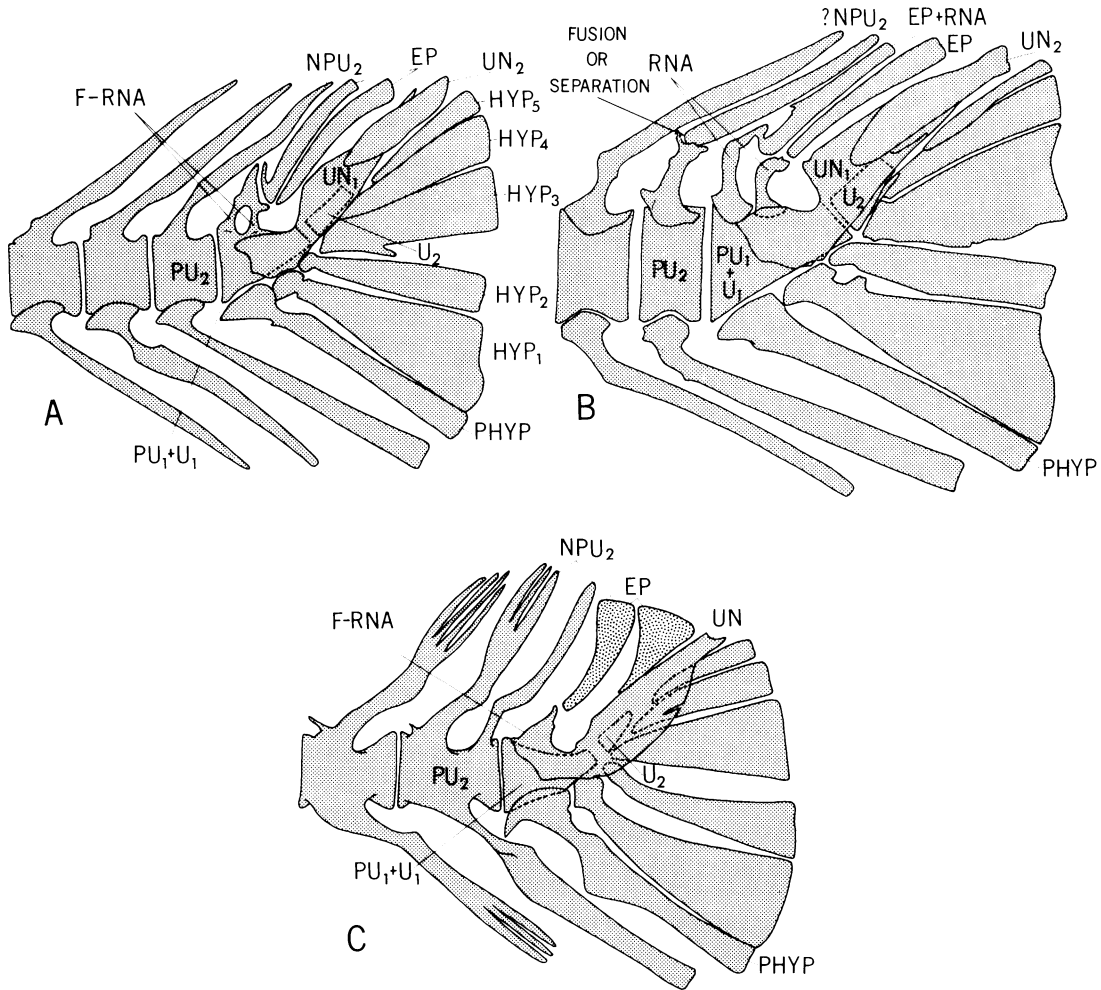
Fig. 19. Caudal skeletons of aplochitonines. A, B. *Aplochiton taeniatus*. C. *Lovettia seali*. Epurals are cartilaginous in C.

parhypural been found fused without also incorporating the second hypural, suggesting that the primary fusion is between the lower two hypurals followed by fusion with the parhypural. In their figure 4 of *Brachygalaxias*, Greenwood et al. (1966) have shown the extent of fusion between the two lower hypurals to be greater than that between these hypurals and the parhypural, and this is generally so for other galaxiids examined. Finally, galaxioids develop extensive amounts of platelike bone on the posterior neural and hemal spines and there is a considerable amount of spine doubling in this region presumably as a result of the loss or consolidation of centra.

In the aggregate, galaxioids have a rather specialized caudal skeleton that shares advanced features exclusive of vertebral fusions with those of esocoids (characters 6 and 9) and *Lepidogalaxias* (character 6). The latter resemblance is considered below in the discussion of *Lepidogalaxias*. The specific resemblances of galaxioids to argentinoids all appear to be in primitive characters.

Esocoids also have a rather primitive type of caudal skeleton with relatively few advanced features (figs. 20–23). All the ural centra are free (except in a single example of an unusual $U_1 + U_2$ fusion, fig. 22B), the upper hypurals are
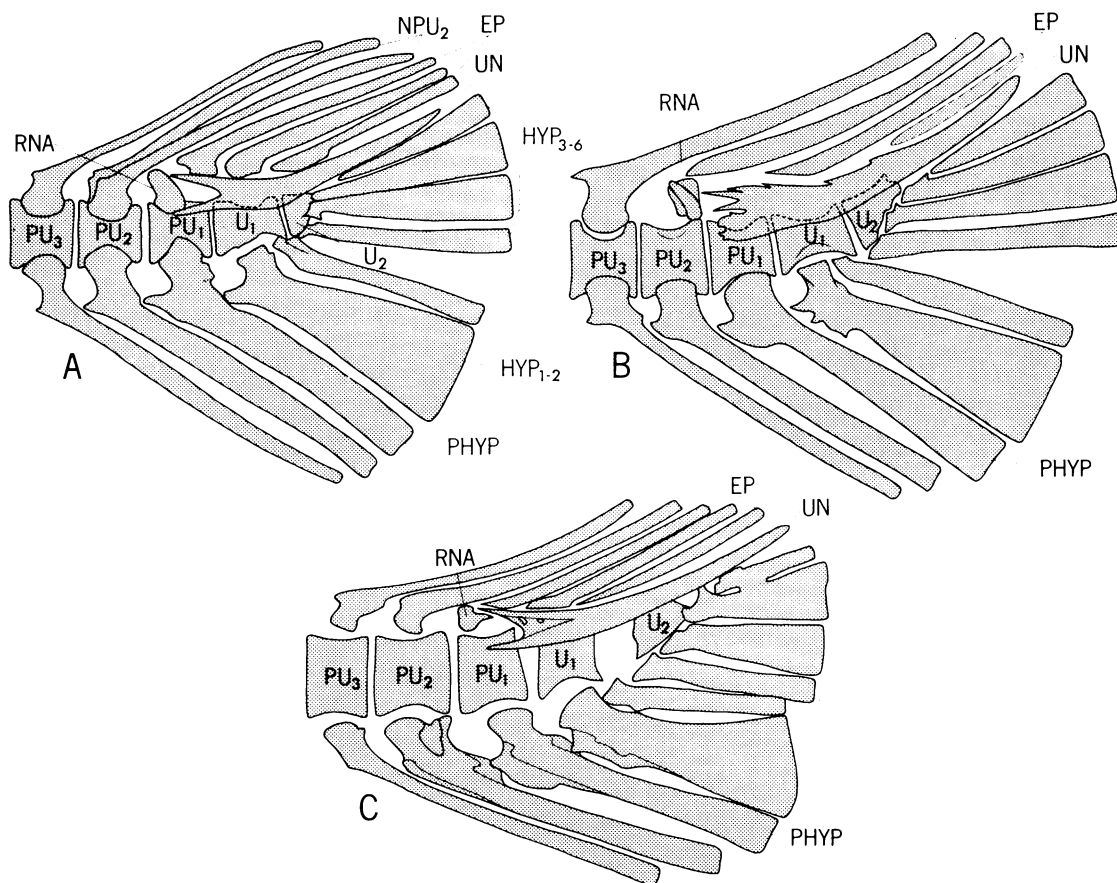
Fig. 20. Caudal skeletons in species of *Esox*. A. *E. lucius*. B. *E. americanus*; the third epural may be present or absent; same as pattern in *E. niger*. C. *E. masquinongy*.

four in number in most species, there are no special modifications of the posterior neural and hemal spines, and there is only a slight tendency to elaborate laminar bone. All esocoids have only a single uroneural which tends to be long and straplike and extends forward to PU_1 in all but two species. Anterodorsally, this uroneural develops one or more acuminate processes except in the specimens of *Umbra krameri* and in about half of the examples of *Dallia pectoralis* at hand (figs. 22C, 23B, D, F). A single pair of rudimentary, or ural, neural arches is present variably on PU_2 or PU_1 in *Esox* and the three species of *Umbra* (figs. 20, 22). In *Novumbra* and *Dallia* this neural arch evidently has fused with an anterior epural to produce a structure that appears as a normal neural arch and spine. A single specimen of *Novumbra* shows what appears

to be an incomplete fusion between this neural arch and an epural (fig. 21A). Hence, *Novumbra* and *Dallia* have the consistently lowest epural number (usually one) and are the only esocoids to bear a full neural spine on PU_1. *Novumbra* and *Dallia* are also distinctive in having the uroneural foreshortened so that usually it does not extend farther forward than the anterior border of U_1. In a single individual of *Dallia* the uroneural has been withdrawn behind the joint between U_1 and U_2 (fig. 23F), and this specimen now bears a small neural arch on U_1. The possibility is thus raised that the esocoid uroneural incorporates a ural neural arch in this position which may be the genesis of the acuminate processes that appear on the anterodorsal surface of the longer esocoid uroneural. These processes normally arise above the first ural centrum.
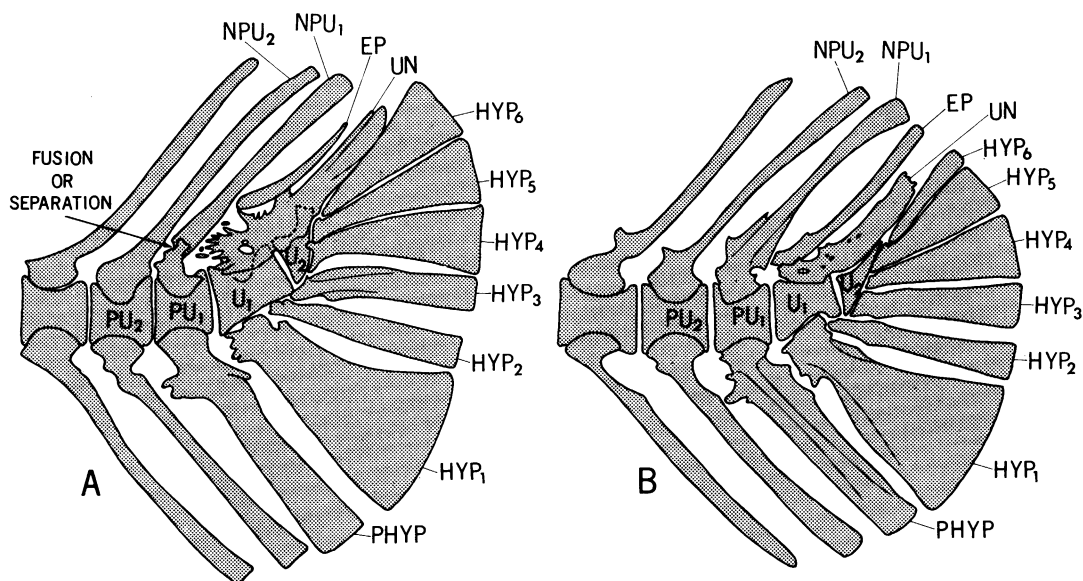
FIG. 21. Caudal skeleton in *Novumbra hubbsi*. Compare neural arches on PU_1 in A and B.

Both Cavender (1970) and Norden (1961) have suggested such an origin of the specialized uroneural laminae in salmonids. An apparent second uroneural has been found in esocoids as a relict structure in only a single specimen of *Umbra limi* (fig. 22B). Hypural number has been reduced from four to three in the species of *Umbra*. In *Dallia* there may be one, two, or three hypurals, and this varies in accordance with the number that have fused together. Whether hypural reduction in *Umbra* and *Dallia* is due solely to hypural fusion or partly to loss of the uppermost element in one or both cases cannot be decided. Fin ray number has also been reduced in esocoids: there are 16 or 17 branched rays in *Esox* (Gosline, 1960) and as few as eight or nine in umbrids (Nelson, 1972). Nelson (1972) proposed that *Dallia* is most closely related to *Umbra* partly on the basis of the subequal size attained by the two lower hypurals as compared with the distinctly larger first hypural and slender second in *Novumbra* and *Esox*. *Dallia*, however, is an extremely variable form (fig. 23), and one must examine many specimens in order to define the characteristics of its caudal skeleton. In contrast, the condition of the lower hypurals of *Umbra* is very stable (fig. 22).

Evidence from the epaxial part of the caudal skeleton indicates, therefore, that *Dallia* and

Novumbra are sister groups within the Umbridae, whereas evidence derived from hypural structure suggests a relationship between *Dallia* and *Umbra*. Umbrids, but not esocids, resemble galaxioids in the tendency for epurals to fuse with ural neural arches, but unless galaxioids are really umbrid esocoids—a conclusion that is not supported by other evidence—the similar conditions of the epurals must be independent in the two groups. The closest parallel of the esocoid caudal skeleton is found in *Lepidogalaxias*, as described below.

In *Lepidogalaxias* (fig. 24) the ural centra are unfused and there is only a single long and straplike uroneural that, in occasional specimens, develops anterodorsal acuminate processes (fig. 24B). There is but one uroneural that tends to fuse with the single, small remaining ural neural arch of PU_1. Also, as in umbrids, the principal caudal fin rays are reduced to nine, although these rays as well as those of the other fins are unbranched. It is not possible to decide whether in *Lepidogalaxias* there are four upper hypurals and one lower or three upper and two lower elements. The second hypural from the bottom in sequence supports the middle, or fifth, principal caudal ray, and it lies parallel to and on the plane of the vertebral axis. There is no sign that the first hypural is
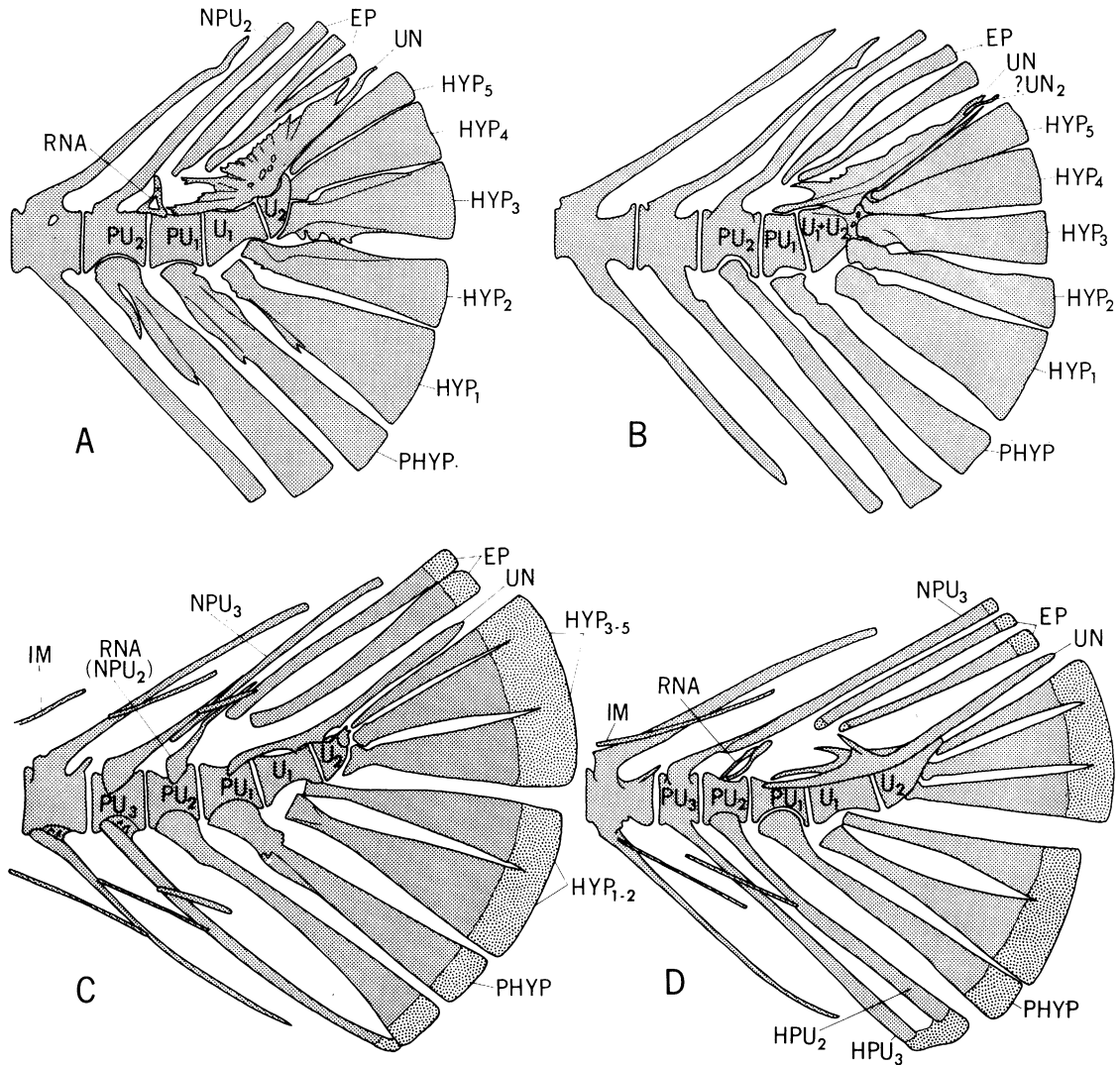
Fig. 22. Caudal skeleton in species of *Umbra*. A, B. *U. limi*. C. *U. krameri*. D. *U. pygmaea*. Note fused U_1 and U_2 in B. Cartilage (coarse stippling) and intermuscular bones shown in C and D.

of compound origin, yet the base of the second hypural occupies the position of the third in fishes with unfused ural centra and four upper hypurals (that is, the hypural base lies partly over the intervertebral joint between PU_1 and U_1). The matter is probably not of great significance, however, as the trend to reduce the upper hypurals is evident in both galaxioids and esocoids, both of which *Lepidogalaxias* superficially resembles in many features. But the presence of only a single long uroneural with some tendency to develop small anterodorsal

prongs and the reduction of the rudimentary or ural neural arches to one small relict on PU_1 are otherwise distinctly esocoid features.

Salmonids and osmeroids, alone among salmoniform fishes, incorporate the rudimentary neural arch posterior to the last full neural spine into the anterodorsal lamellar outgrowth of the first uroneural. This is accomplished by an articulation or fusion of the small spinose projection of the rudimentary arch with the anterior tip of the uroneural lamella so that the free rudimentary arch base forms the most
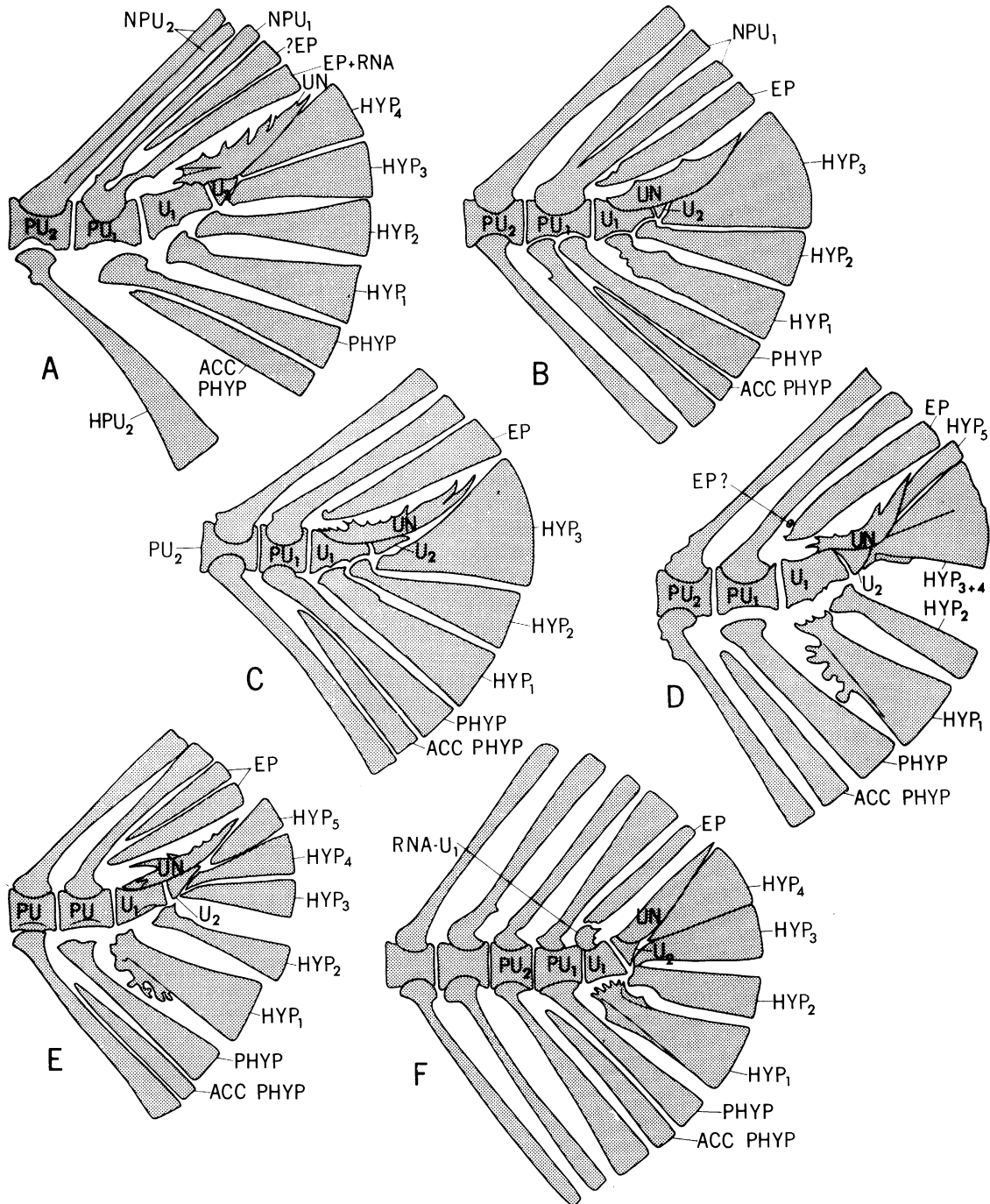
FIG. 23. Caudal skeletons in *Dallia pectoralis*. Note free rudimentary neural arch on U_1 associated with withdrawn uroneural in F. Note that uroneural never extends forward of U_1 and that a neural arch and spine (or spines) is always present on PU_1. Compare with figure 21, and contrast with figure 22.
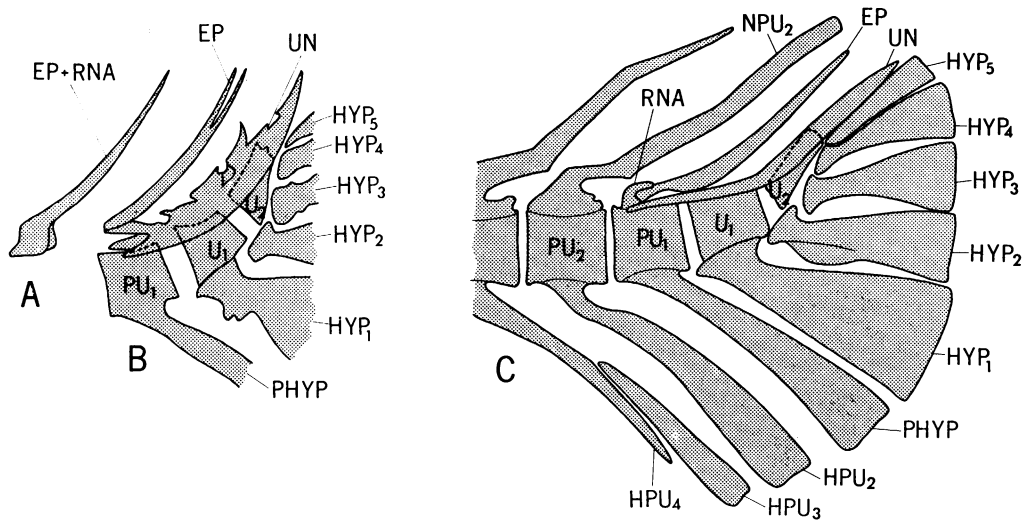
Fig. 24. Caudal skeletons in *Lepidogalaxias salamandroides*. A. Epural fused with a free rudimentary neural arch on PU$_1$. B. Bifurcate epural and a uroneural with dorsal acuminate processes. C. Complete caudal skeleton in which PU$_3$ apparently has been deleted, leaving a free hemal element (HPU$_3$). There is never more than one uroneural. Each derived condition shown here can be found in some or all esocoids (cf. figs. 20–23).

anterior part of the combined structure (figs. 25–28). It is for this specialized feature of salmonid and osmeroid caudal skeletons that Greenwood and Rosen (1971) reserved the term "stegural." In other groups there are also lamellar outgrowths of the first uroneural but these never fuse with the spines of rudimentary neural arches in the manner just described. Nevertheless, it is perhaps significant that some galaxioids have uroneural lamellae resembling those of salmonids and osmeroids (see figs. 18E, 19B).

In general, the salmonid caudal skeleton (fig. 25) is more primitive than those of osmeroids. For example, PU$_1$ and U$_1$ are unfused in salmonids, fused in osmeroids. There are invariably three uroneurals in salmonids, the first of which extends forward to PU$_2$. In osmeroids (figs. 26, 27) there are two or three uroneurals the first of which does not extend forward of a compound centrum (PU$_1$+U$_1$). The uroneurals are never fused with the centra in salmonids, but the first is fused with the compound centrum in some osmerids and salangids (fig. 26). The rudimentary neural arches in salmonids, although securely joined to the uroneural lamellae, remain distinct; in osmer-

oids evidence of separate rudimentary neural arches can be found only in very small juveniles of some species (fig. 28). As many as five upper hypurals have been found in a salmonid (*Prosopium*, fig. 25C), but never more than four in osmeroids. Salmonids show little hypural fusion (only in the first two upper hypurals of *Cristivomer*, fig. 25A), whereas osmeroids show a characteristic fusion of the first hypural with the parhypural in plecoglossids (fig. 26C), retropinnids (fig. 27), and prototroctids (McDowall, 1969, fig. 4E). Salmonids always have 17 branched caudal rays, whereas some osmeroids (retropinnids and prototroctids) have 16. Finally, salmonids retain the pegs and sockets on the bases of the first hypural, parhypural and posterior hemal spines that characterize many primitive fish groups, including "leptolepids," but this feature is present neither in osmeroids nor in any other euteleosteans except an occasional specimen of *Esox* (cf. fig. 20A and 25).

The osmeroid fishes share many advanced features and appear to be a monophyletic group, the primitive sister group of which, on the basis of uroneural and stegural structure, may be the salmonids. Together the two groups share only one advanced feature with other salmoniforms
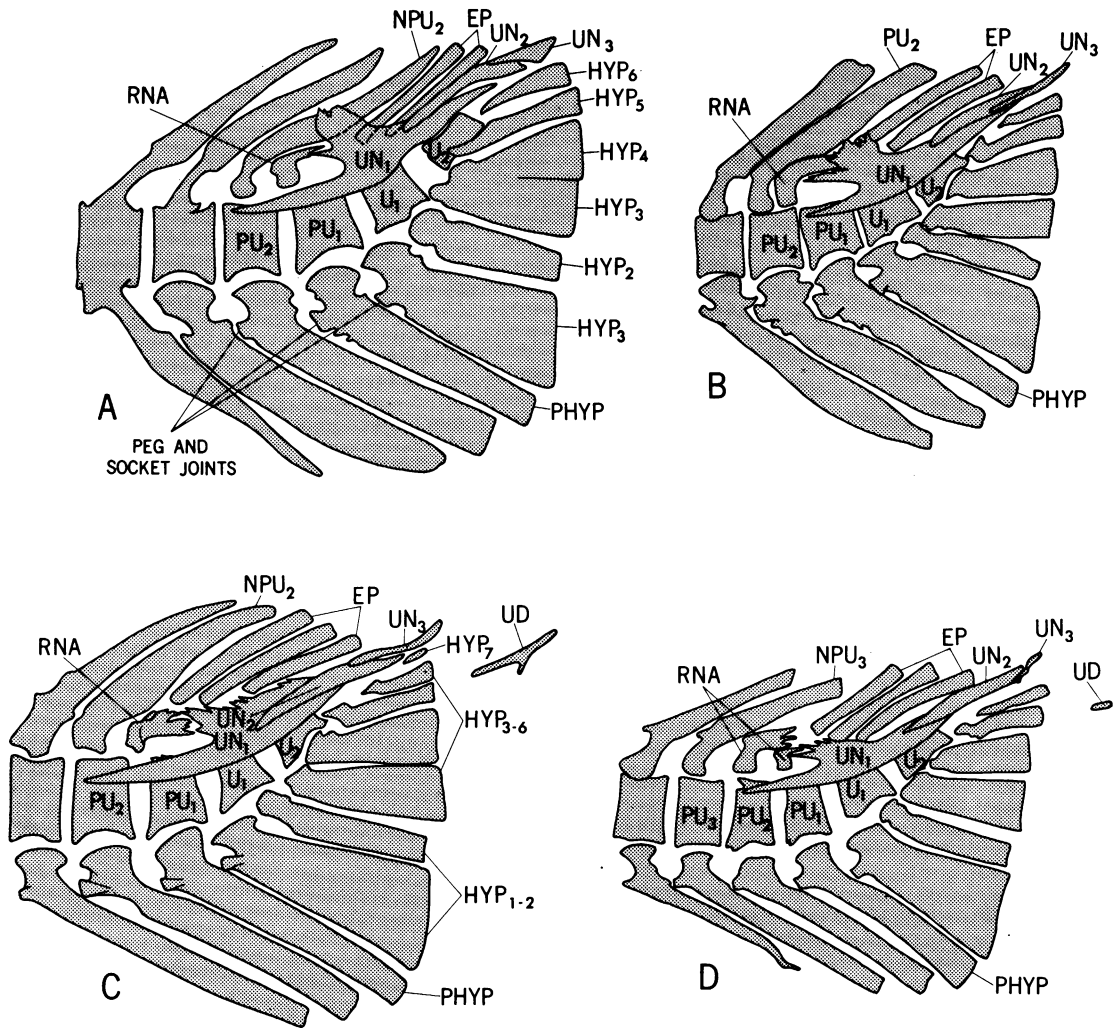
FIG. 25. Caudal skeletons of salmonids. A. *Cristivomer namaycush*. B. *Salmo trutta*. C. *Prosopium cylindraceum*. D. *Coregonus artedi*. Note presence of two rudimentary neural arches in D.

(the esocoids and *Lepidogalaxias*) other than the consolidation of ural vertebrae, and that is the tendency to reduce or lose rudimentary neural arches (character 7). Only the occasional salmonid, and no osmeroid, has more than one arch, and the arches present are always small, or they are absorbed entirely into the uroneural lamellae.

In summary, the caudal skeleton evidence indicates that there are four distinct groups of salmoniforms, the argentinoids, esocoids, galaxi-

oids, and salmonids plus osmeroids. Caudal evidence supports the alignment of plecoglossids, salangids, retropinnids, prototroctids, and osmerids as an osmeroid assemblage. *Lepidogalaxias* shares two, possibly three, advanced characters with esocoids, and one, possibly three, advanced characters with galaxioids. Galaxioids share two advanced characters with esocoids, and none with salmonids-osmeroids (unless one takes into account the small osmeroid-like uroneural lamella that has been found
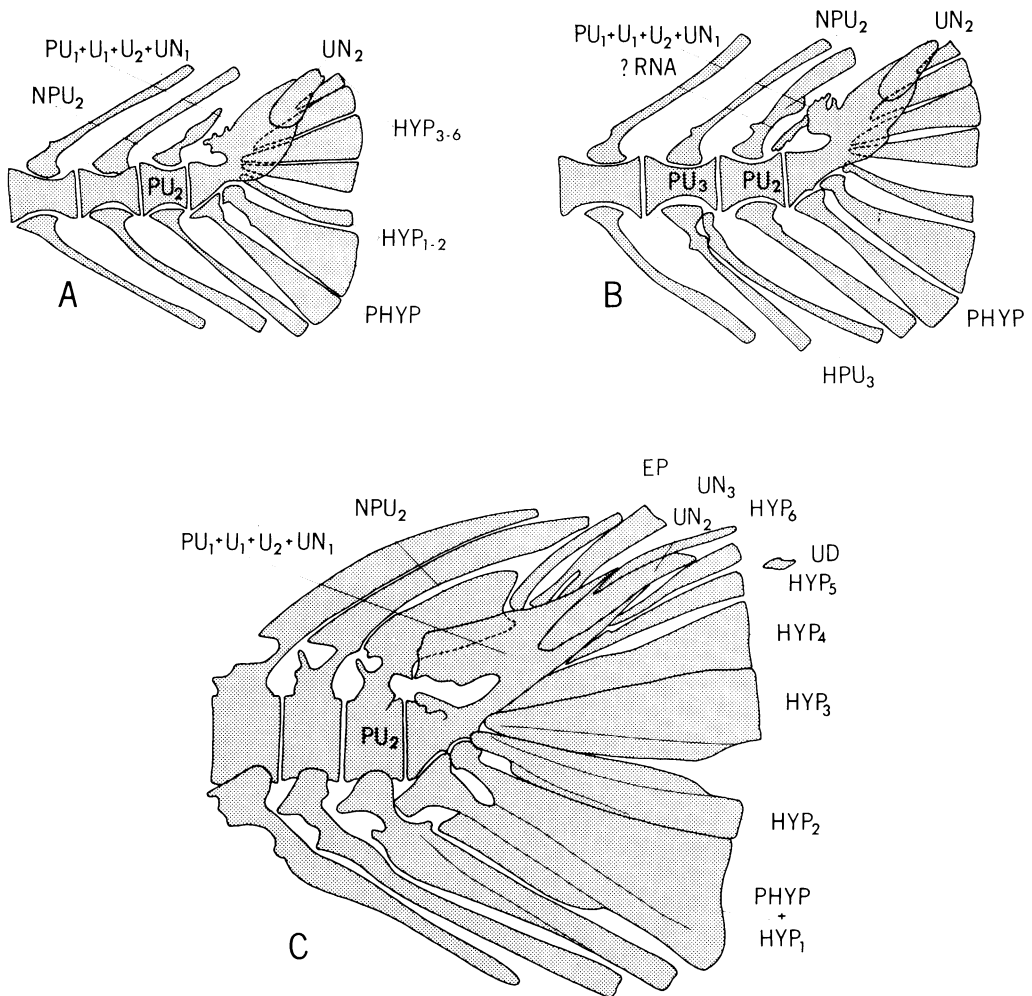
FIG. 26. Caudal skeletons in the osmeroids *Salangichthys microdon* (A, B) and *Plecoglossus altivelis* (C). Compare with figure 27, and figure 16A, B in Greenwood and Rosen (1971).

in an aplochitonid and galaxiid). Argentinoids have the most generalized caudal skeleton of all salmoniforms, sharing four advanced features with all other groups; they may be the primitive sister group of other salmoniforms.

MALE SEXUALLY DIMORPHIC STRUCTURES

Sexually dimorphic modifications in salmoniform fishes involve pigmentation, the jaws and teeth, fin size and structure, squamation, and the development of breeding tubercles. Pig-

mentary differences between males and females appear to occur in all groups except argentinoids and galaxioids. Sexual differences in coloration in the other salmoniforms were commented on by Breder and Rosen (1966). Modifications of the jaws and teeth are present in the males of many salmonines as the "kype" or simply as enlarged teeth on the dentary (Vlady-kov, 1963). Maxillary dentition is present in males and absent or reduced in females of some species of the retropinnid genus *Stokelia* (Mc-Dowall, 1969, and personal observ.) and various
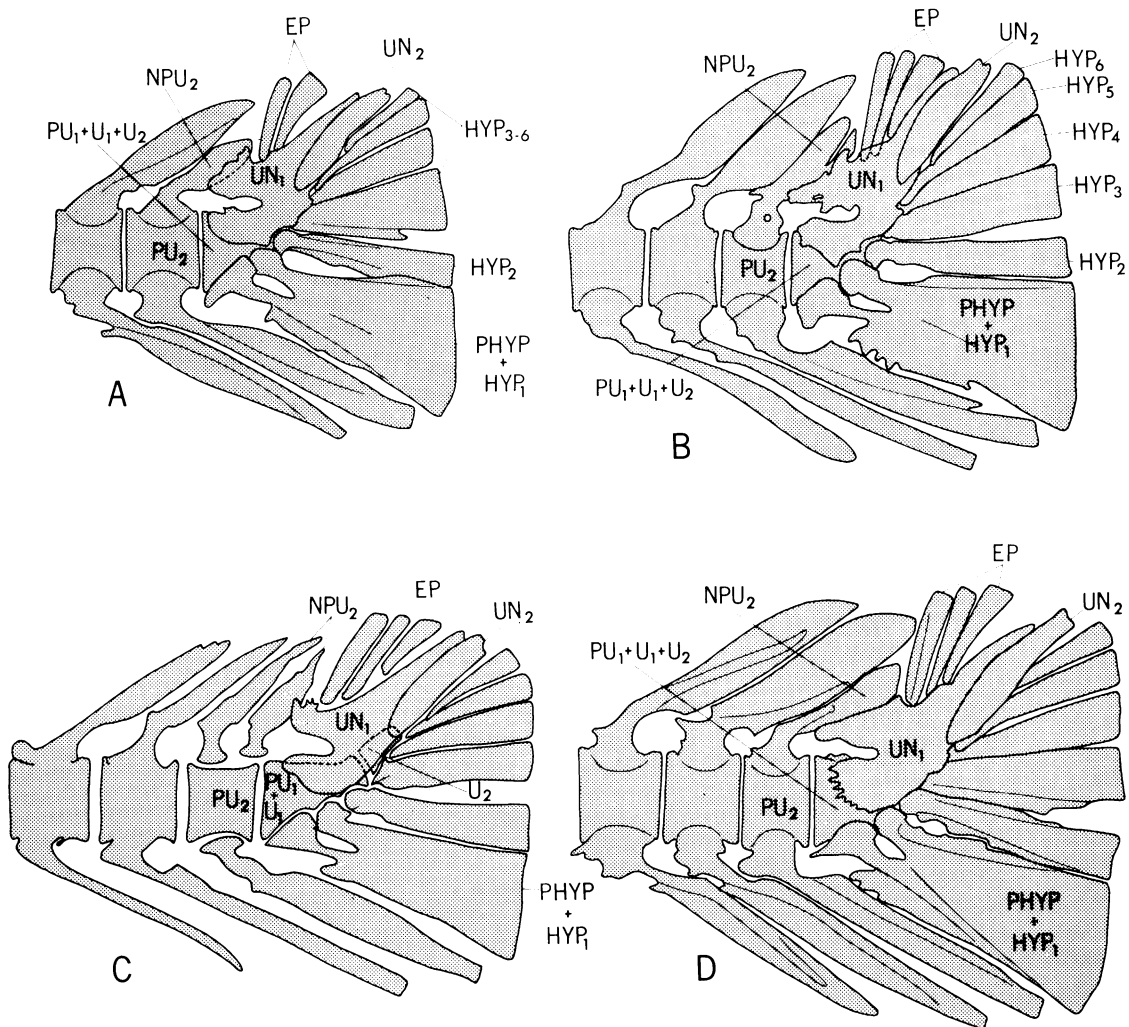
FIG. 27. Caudal skeletons in retropinnids. A, B. *Stokelia anisodon*; note difference in epural number. C. *Retropinna abbreviata*. D. *Retropinna retropinna*.

components of the orobranchial dentition of breeding male salmonids are lost, reduced, or modified. Fin height or length tends to be greater in the males of all but argentinoids and galaxioids. A distinctive type of breeding tubercle, commented on above, was described in detail from the males of plecoglossids, some osmerids, and some retropinnids by Wiley and Collette (1970). Wiley and Collette have also examined contact organs in the Coregoninae, in which females may also possess these structures, and have noted the presence of tubercles in the males

and females of *Cristivomer namaycush*. Histological study of *Cristivomer* is needed before these organs in salmonids and osmeroids can be compared meaningfully. According to Breder and Rosen (1966, p. 632), contact organs occur in males of the Argentinidae, but I have been unable to trace the source for this statement. Males of the osmerid *Mallotus villosus* have prominent ridges midlaterally and above the anal fin base formed by the elongation of rows of scales and the swelling of the underlying musculature and connective tissue. The pectoral, pelvic, dorsal, and
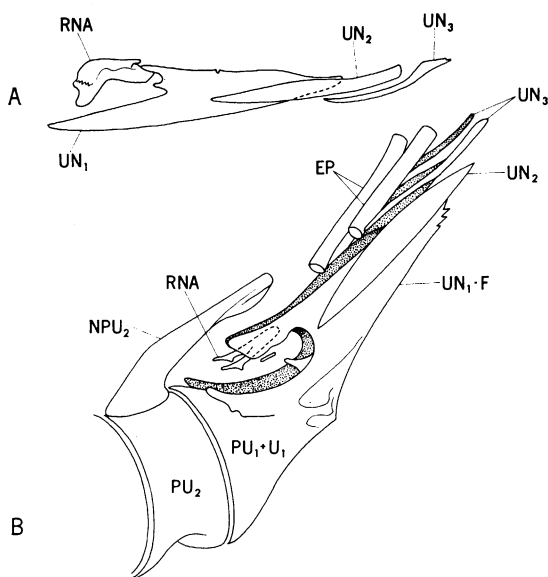
FIG. 28. Stegural anatomy in a salmonid and osmerid. A. *Prosopium cylindraceum*. B. *Spirinchus dilatus*.

anal fins are enlarged and fanlike in the males of *Mallotus* (Vladykov, 1941, fig. 1; McAllister, 1963) as they are in adult male retropinnids (McMillan, 1961, fig. 1; Woods, 1968, figs. 1, 3, 4). Male salangids and *Lepidogalaxias* possess a sheath of greatly enlarged scales above the anal fin base (figs. 29–31, and figures in Okada, 1960). The salangids are otherwise scaleless fishes, whereas *Lepidogalaxias* has small, well-separated, embedded scales. The enlarged sheath scales in both groups are seated on a thick layer of fibrous connective tissue and are surrounded peripherally and to some extent externally by a heavy layer of dermis and of epidermis with abundant mucous cells. Male salangids and *Lepidogalaxias* also have the entire anal fin skeleton modified, a feature shared with male *Mallotus villosus* (figs. 32–37). The anal fin specializations, although simpler, are most similar in salangids and *Mallotus*. In both, the anterior interhemal supports are elongate and invested with laminar bone and only the central
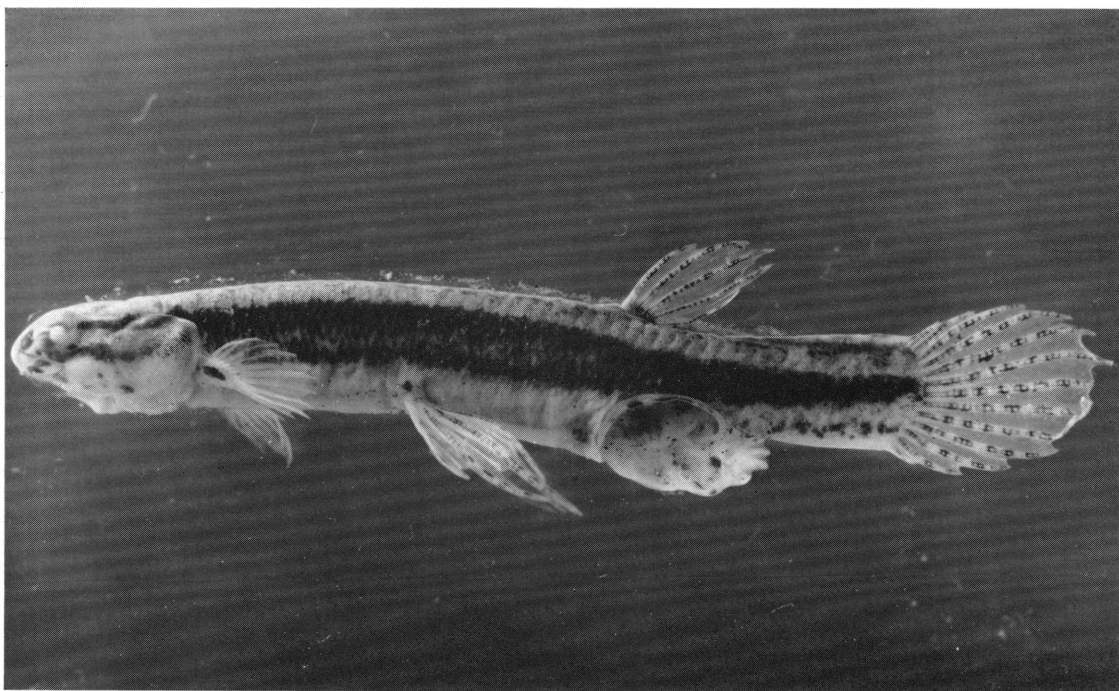
FIG. 29. Adult male *Lepidogalaxias salamandroides*, 40 mm. standard length, from Western Australia.

FIG. 30. Anal fin of adult male *Lepidogalaxias salamandroides*, as in figure 29. Semilunate structure along base of fin is a shield of enlarged and modified scales enclosed in thick envelope of goblet-cell-bearing epidermis. Compare with figure 31.

rays of the fin are much specialized. The inter-hemals of salangids are also bent and expanded distally, whereas in *Mallotus* they remain straight and are expanded proximally. The modified anal rays of salangids are twisted into an S-curve and, because of their crowding distally, tend t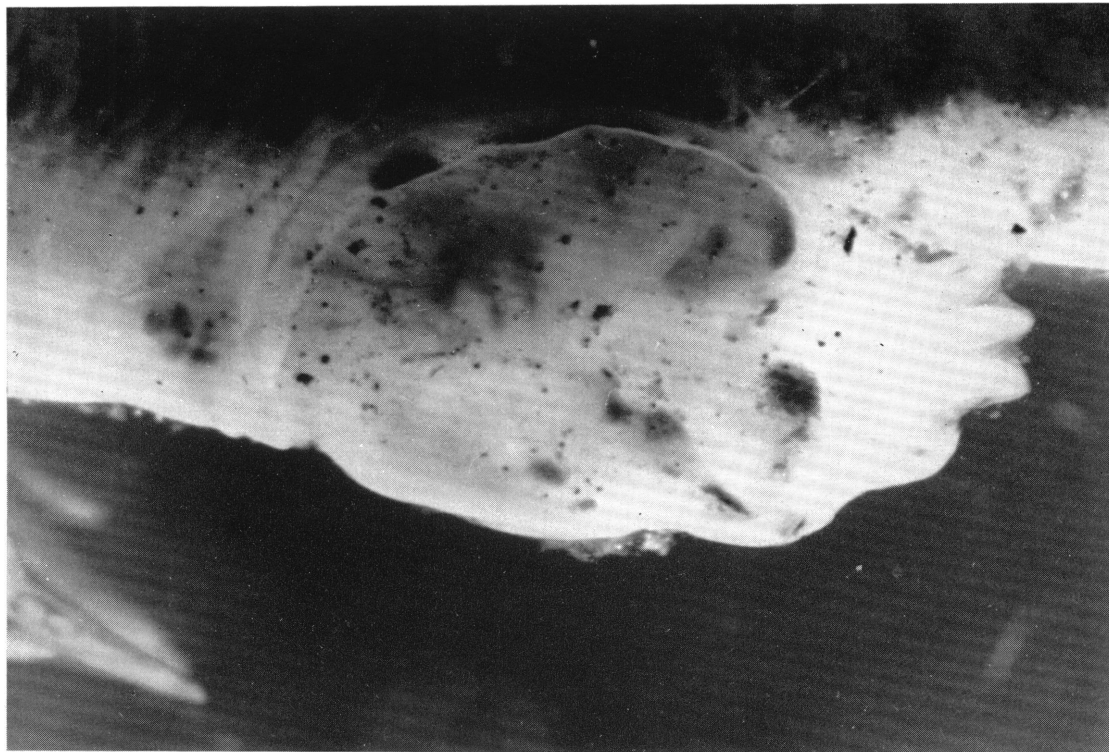o lie on one side of the fin or the other folded over adjacent less modified rays (figs. 34, 35). In *Mallotus* the central rays remain straight, but become heavily ossified; four or five of the heaviest rays ankylose distally (figs. 36, 37; see also Vladykov, 1941). In the case of *Mallotus* the anal fin also has a folded appearance, but it is the rigidity of the enlarged, ankylosed central rays that causes them to overlap adjacent elements.

Although salangids and *Mallotus* resemble one another in anal fin structure, and salangids and *Lepidogalaxias* in the anal-fin scale sheath, the anal fin rays and internal supports in *Lepido-*

galaxias are distinctive and, apparently, are of a unique type (figs. 32, 33). The anal fin rays number 15 or 16 in *Lepidogalaxias* (24 or 25 in *Salangichthys* and *Mallotus*) and all but the anterior four small lepidotrichia of the male are greatly modified over their simple and unbranched condition in the female.

Whether these three types of modified anal fins, and their associated scale structures, function in a similar way is not known. In *Lepidogalaxias* the fully differentiated male fin always occurs strongly folded to the right or left in preserved specimens, whereas in salangids and *Mallotus* the rays are merely folded upon themselves without the fin being deflected to the side. Histological study of the entire anal fin region in *Lepidogalaxias* shows that the sperm duct opens into a sinus near the anal fin origin. This sinus is bounded partly by the anterior part of the scale sheath and it is continuous with a
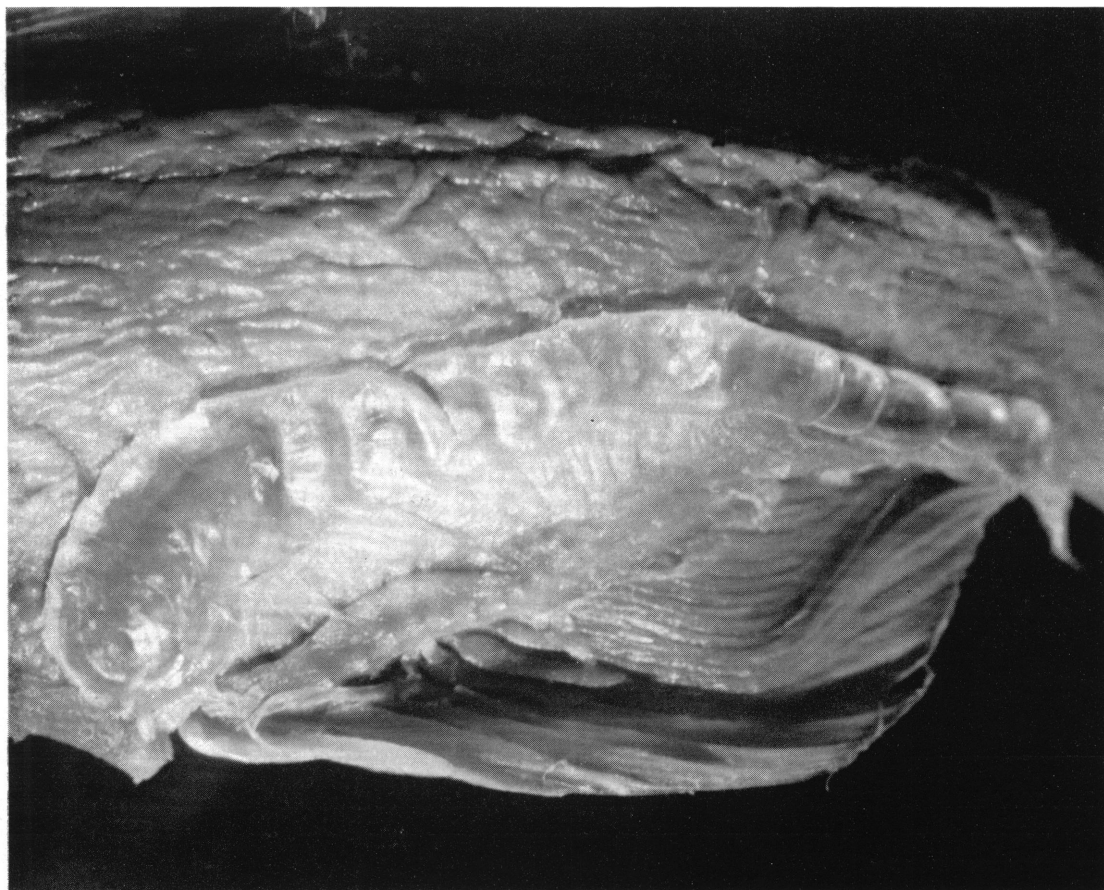
FIG. 31. Anal fin of adult male *Neosalanx hubbsi*, showing modified anal rays and basal sheath of enlarged scales.
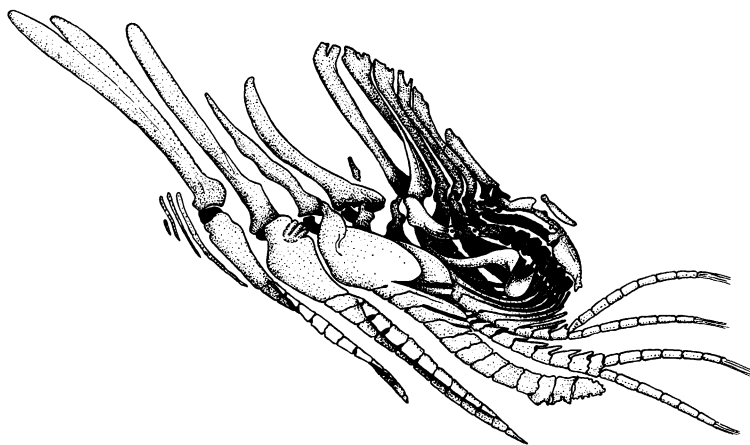
FIG. 32. Anal fin skeleton of male *Lepidogalaxias salamandroides* with unconsolidated interhemal supports.
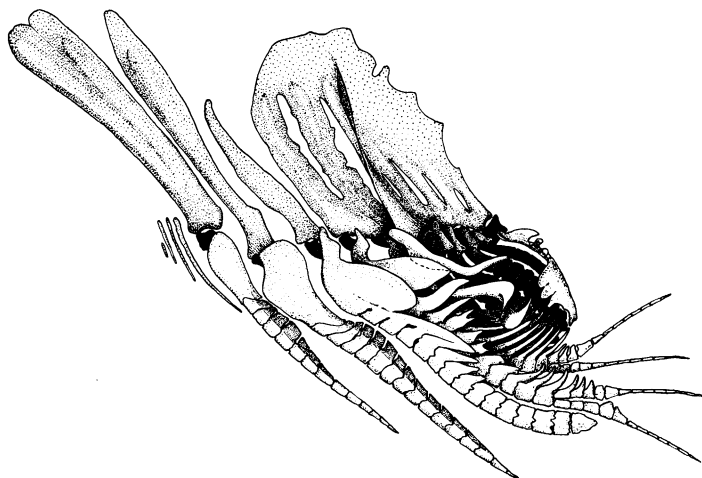
FIG. 33. Anal fin skeleton of male *Lepidogalaxias salamandroides* with consolidated interhemal supports. This may be the fully differentiated condition of the skeleton, as compared with the condition in figure 32.
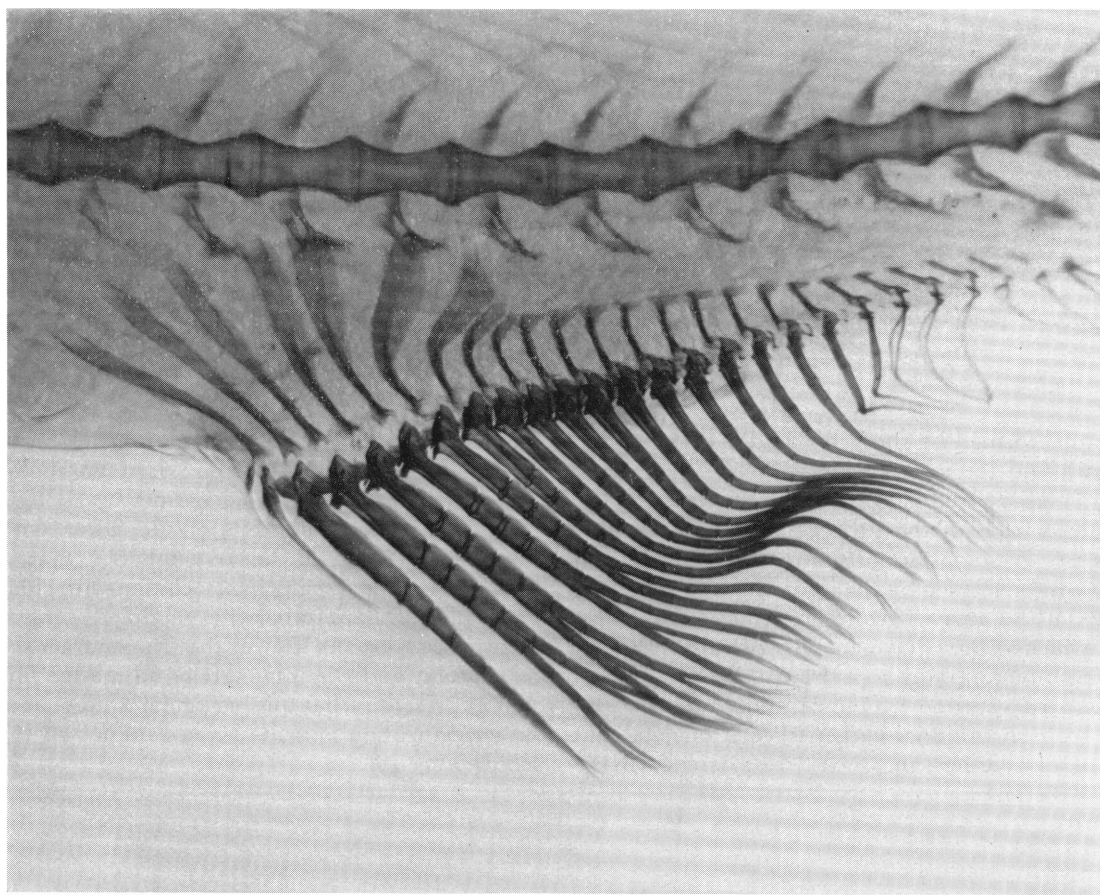
FIG. 34. Anal fin skeleton and associated vertebrae in adult male *Salangichthys microdon*. Alizarin preparation.
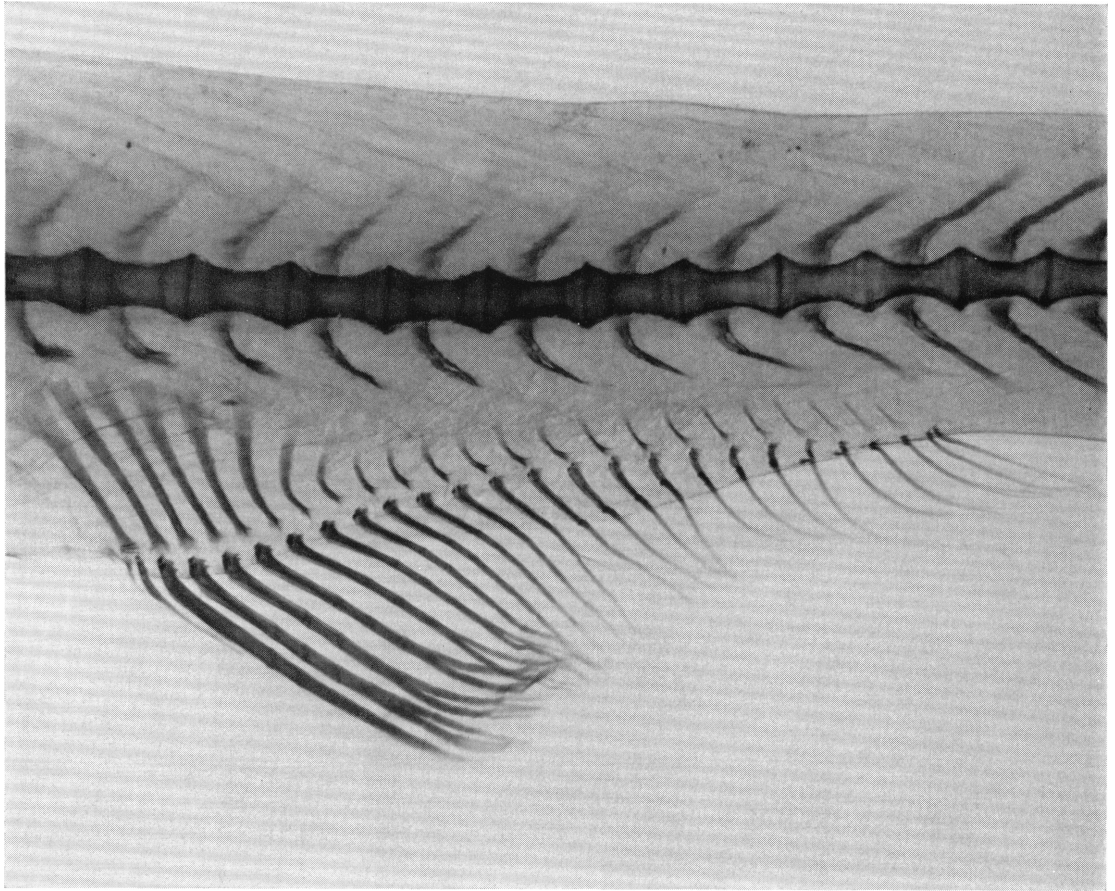
FIG. 35. Anal fin skeleton and associated vertebrae in adult female *Salangichthys microdon*. Alizarin preparation.

channel formed by the ventral edge of the scale sheath and the folded anal fin rays. This channel opens to the outside near the tip of the posterior rays of the fin, two of which are bifurcate. Presumably the channel conveys sperm and can be formed on the right or left. The functions of the array of complex structures in this fin will certainly have to be worked out with living material, and no more can be said about these structures now. One can only note that if the scale sheath does in fact serve as one wall of a sperm channel, the sheath in salangids may serve in the same way. As against the hasty conclusion that the dimorphic anal fin modifications of *Mallotus*, salangids, and *Lepidogalaxias*, indicate a relationship of the latter with osmeroids, it should be remembered that a sheath of enlarged scales in association with elongate and perhaps otherwise modified central anal fin rays occurs also in the cyprinid genera *Schizothorax* and *Diptychus*. About all that can be said at present is that this particular kind of anal fin specialization appears to be confined to the Euteleostei.

DISCUSSION

PHYLOGENETIC AND TAXONOMIC CONCLUSIONS

THE FOREGOING ANALYSIS of parts of the hyobranchial apparatus allows a rather straightforward interpretation of salmoniform relationships in which esocoids are the primitive sister group of a group including argentinoids, galaxioids (galaxiids and aplochitonids), salmonids, and osmeroids (osmerids, plecoglossids, salangids, retropinnids, and prototroctids). The caudal evidence, however, is more difficult to interpret because two of the groups (argentinoids and galaxioids) strongly resemble each other in a number of primitive features, because esocoids have a distinctive, and in some ways advanced, caudal skeleton not resembling that of other groups, and because salmonids and the osmeroids have a similar derived condition of the epaxial part of the skeleton that is just different enough to raise doubts as to whether the structure has arisen in the same way and for the same reason in the two groups. According to caudal evidence argentinoids or galaxioids could be the primitive sister group of other salmoniforms; the esocoids, on the basis of rudimentary neural arch reduction, could be related as the primitive sister group of salmonids and osmeroids; and on the basis of a similar stegural development salmonids and osmeroids might be related. The tiny Western Australian freshwater *Lepidogalaxias* shows possible relationships to esocoids and galaxioids in body and fin structure, to esocoids in caudal skeleton anatomy, and to osmeroids in the sexually dimorphic modifications of the anal fin and associated scales of the male. Somewhat similar sexual specializations of the anal fin occur in an osmerid (*Mallotus*) and salangids, but they also are to be found in two cyprinid genera. Hence, the evidence of secondary sexual characters, which are absent in argentinoids and galaxioids, suggests a possible relationship of *Lepidogalaxias* to osmeroids, says little about esocoid relationships (male esocoids have only somewhat enlarged median fins), and suggests a relationship between salmonids and osmeroids (which have breeding tubercles).

The hyobranchial evidence, however, strongly suggests that galaxioids and salmonids form a monophyletic group, and it is therefore appropriate to ask what relationships *Lepidogalaxias* has to this assemblage. After its brief history of association only with galaxiids it is somewhat surprising to find that *Lepidogalaxias* shares few traits either with galaxioids as a group or with salmonids. For example, the common ancestor of a group including galaxiids and aplochitonids must have had the dorsal fin situated well in advance of the anal fin, an adipose dorsal fin, 14 branched caudal fin rays, no scales, large paired basihyal fangs and a long, edentulous dermal plate over basibranchials 1–3, no tooth plate over basibranchial 4, the fifth epibranchial fused dorsally with the posterior cartilage of the fourth, no ectopterygoid or dermopalatine, large teeth on the endopterygoid, and in the caudal skeleton two or three epurals, three upper hypurals, two rudimentary neural arches and spines over the first preural centrum, two uroneurals, and a tendency to consolidate all the ural centra. In contrast, *Lepidogalaxias* has a posterior dorsal fin, over the anal fin, and no adipose, 9 principal, but unbranched, caudal fin rays, scales, a reduced basihyal tooth plate without teeth, no tooth plate over basibranchials 1–3, a small to moderate edentulous tooth plate over basibranchial 4, no fifth epibranchial, a well-developed ectopterygoid, a dermopalatine with strong teeth, no endopterygoid teeth, and in the caudal skeleton, one epural, possibly four upper hypurals, one or no rudimentary neural arches over the first preural centrum, one long, straplike uroneural, and consistently unconsolidated ural centra. Hence, *Lepidogalaxias* has none of the advanced characters of the galaxioids, and in having none of the advanced features shared by aplochitonids and galaxiids, that is, in being more primitive than both in these ways, cannot be a galaxiid. For many of the same reasons, *Lepidogalaxias* appears unrelated to the salmonids although more primitive traits are shared in common. The question arises, therefore, whether *Lepidogalaxias* could be a primitive sister group to salmonids plus galaxioids, and again the answer seems to be negative. The primary attributes uniting salmonids and galaxioids are features of the hyobranchial apparatus that are all absent in *Lepidogalaxias*. Nor is there evidence of its
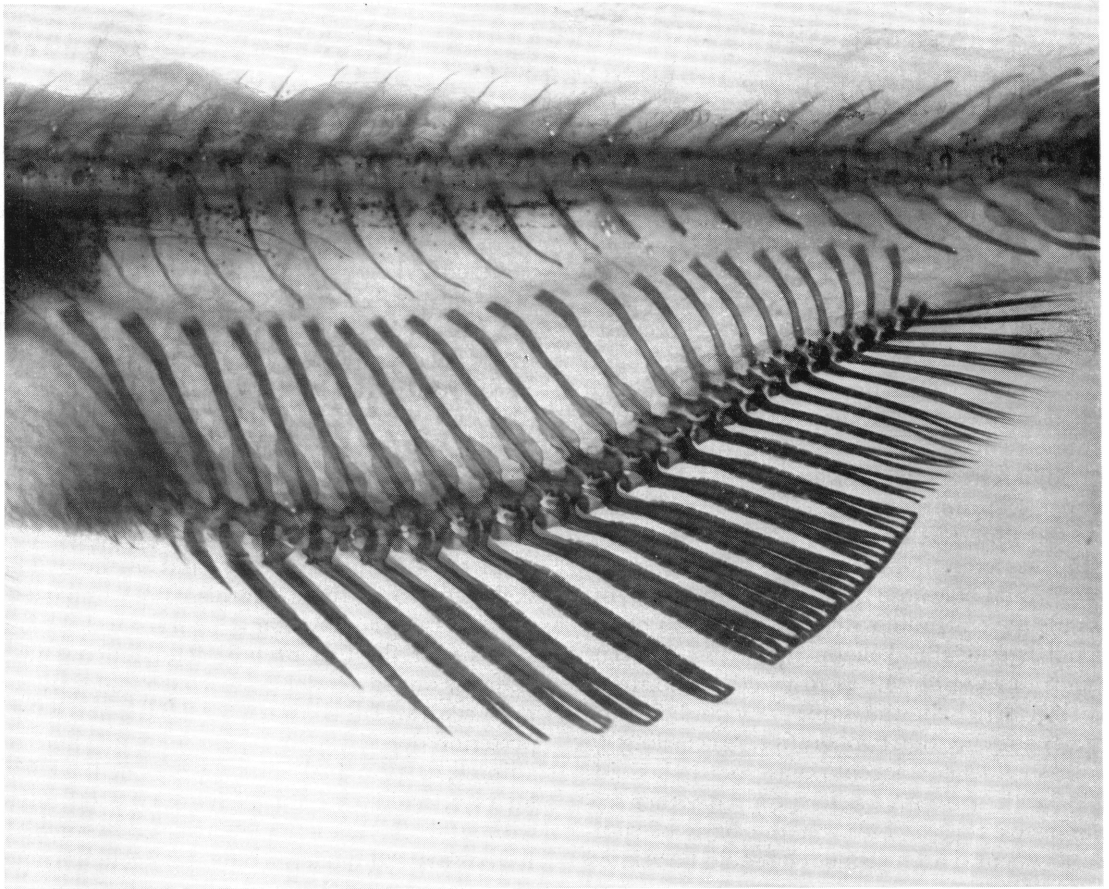
FIG. 36. Anal fin skeleton and associated vertebrae in adult male *Mallotus villosus*. Alizarin preparation.

relationship to the argentinoids, which are characterized by the presence of distinctive pharyngobranchial, and hyoid, structures. A similar conclusion must be drawn for an osmeroid-*Lepidogalaxias* linkage: although *Lepidogalaxias* shares specialized aspects of the male secondary sexual modifications of the anal fin with salangids and one osmerid, caudal and hyobranchial evidence indicates a close relationship among all salangids, osmerids, retropinnids, and *Plecoglossus*, and *Lepidogalaxias* shares none of these advanced features. In other words, *Lepidogalaxias* could scarcely be a salangid or a relative of salangids or *Mallotus* or both since it retains a primitive tooth plate over the fourth basibranchial (absent in all osmerids and therefore presumably absent in their common ancestor) and in its caudal skeleton has only one epural, one uro-

neural, and unconsolidated ural centra (versus usually three epurals, two or three uroneurals, and fused ural centra in all osmeroids, and all of which therefore must have been present in their common ancestor). We are thus left with the esocoids for comparison, a group which *Lepidogalaxias* resembles in many ways. Many of the shared advanced features are given below in the analytical key, but a few, present in *Lepidogalaxias* and all esocoids, may be stressed here (nonreductional characters in italics): an edentulous maxilla with one reduced or no supramaxilla, *the tendency to develop pitlines associated with the cephalic lateral line canals*,[1] *a posterior dorsal fin, situated over the anal*, and no

[1]The specific resemblances in pitline organization between *Lepidogalaxias* and esocoids were described by Nelson (1972).
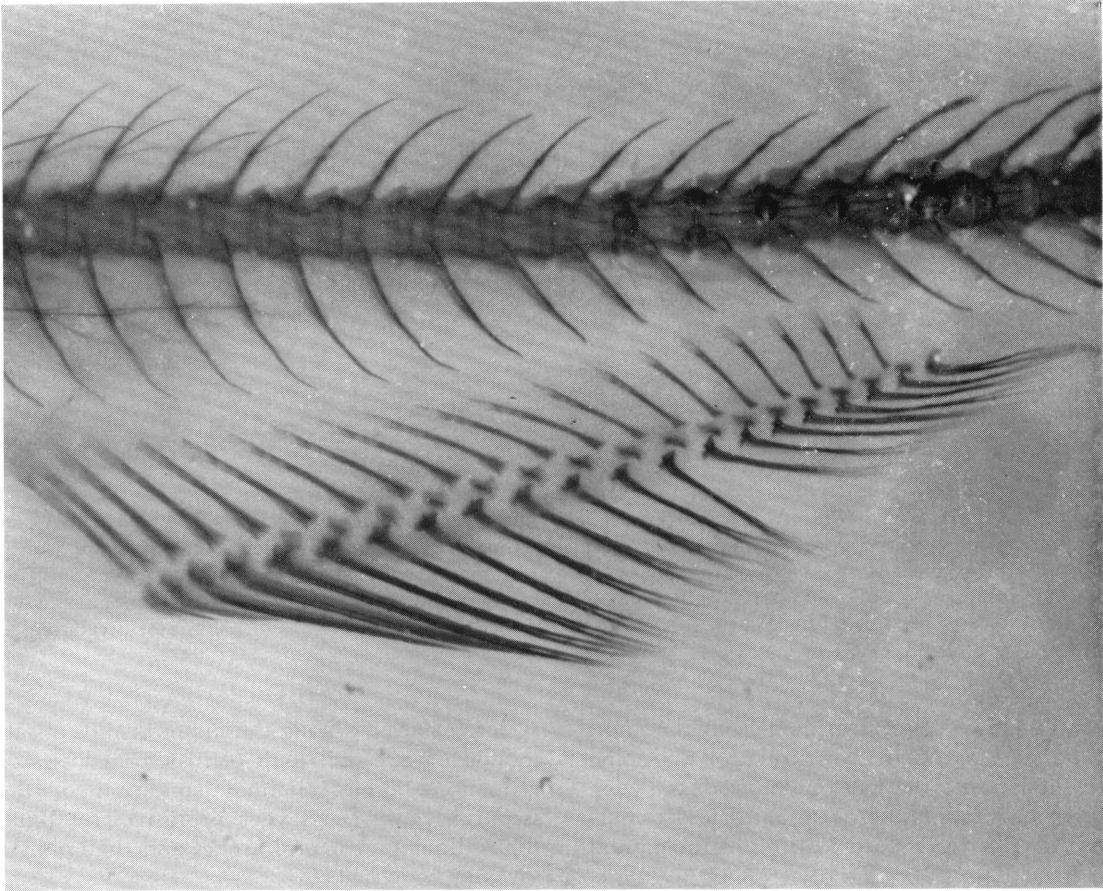
FIG. 37. Anal fin skeleton and associated vertebrae in adult female *Mallotus villosus*. Alizarin preparation.

adipose fin, and, in the caudal skeleton, no more than a single rudimentary neural arch and only *a single, long, straplike uroneural that may develop small acuminate processes on its anterodorsal margin.* Parallel derived features in both groups, that is, features present in *Lepidogalaxias* and some esocoids, include, in the caudal skeleton, a reduction in epural and hypural number, and the presence of a full neural spine on the first preural centrum, and in the branchial apparatus, the presence of a single, large, round tooth plate associated with the fourth infrapharyngobranchial, and fourth epibranchial, and the loss of the fifth epibranchial. Both groups also have some unique attributes, for example, the specialized male anal fin in *Lepidogalaxias* and the elongate, paired dermal ethmoids (proethmoids) of esocoids, as well as some features that are

primitive for teleosteans generally, but I have found no evidence to exclude the possibility of relationship between the two groups. Hence, the evidence of shared advanced features seems to point only to esocoid relationships of *Lepidogalaxias* and although this evidence is slight it is at least not in any sense contradictory. In other words, the pertinent evidence is found in *Lepidogalaxias* and all esocoids.

A comparison of salmoniform phylogenies based on caudal and hyobranchial evidence (figs. 38, 39) indicates that that involving branchial anatomy leads to the most economical hypothesis involving the fewest assumptions of independent origin of similar traits. There is but a single decisive advanced feature of caudal anatomy shared by the members of more than one major group of salmoniforms. This feature
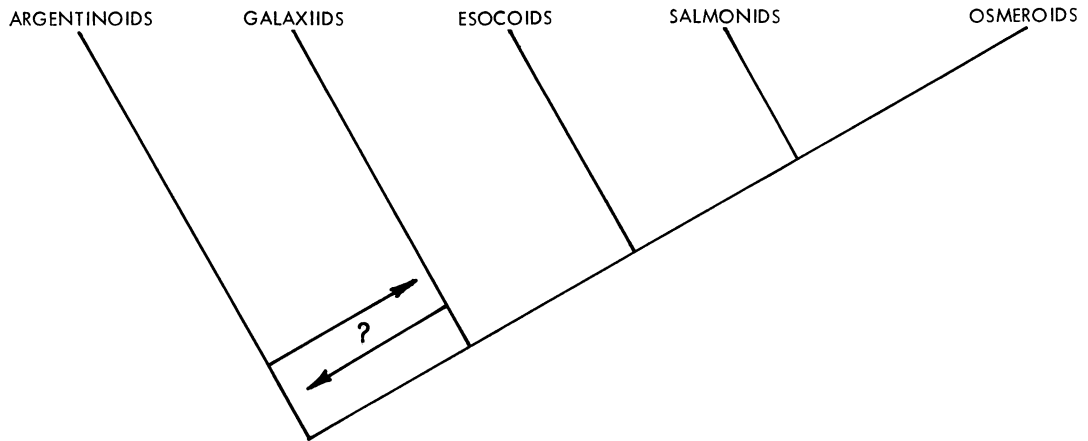
FIG. 38. A possible phylogeny of salmoniform fishes based on caudal anatomy. Argentinoids and galaxiids can occupy interchangeable positions in this hypothesis. According to this hypothesis basihyal fangs arose independently three times and a specialized fourth epibranchial associated with the dorsal edge of the fifth epibranchial twice, or alternatively esocoid basihyal and basibranchial dentition, which appears to be of primitive teleostean type, arose secondarily. The number of cases of independent evolution of comparable structures would be increased if galaxiids are the primitive sister group of other salmoniforms. Other than stegural formation and the loss of rudimentary neural arches there is little basis for arranging the groups on caudal evidence.

is the complex stegural formed from the combination of a rudimentary neural arch and spine with the laminar bone of the anterodorsal edge of the first uroneural in salmonids and osmeroids. All other advanced features of the caudal skeleton shared among the major groups of salmoniforms are the result of structural losses or reductions. The salmonid condition of the stegural, however, is very primitive, retaining the rudimentary neural arches and the laminar
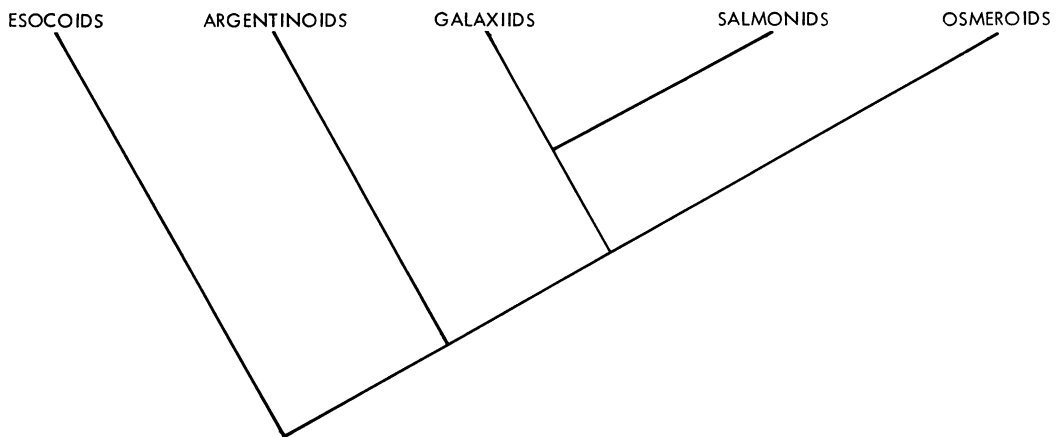
FIG. 39. A possible phylogeny of salmoniform fishes based on hyobranchial anatomy. According to this hypothesis one rudimentary neural arch has been lost independently in esocoids and in the salmonoid-osmeroid section, and stegural formation has occurred independently (or in parallel) in salmonoids and osmeroids. In this scheme argentinoids galaxiids, salmonids, and osmeroids form a well-defined group on the basis of basihyal and basibranchial anatomy, and galaxiids and salmonids a compact subgroup on the basis of basihyal and basibranchial, and on epibranchial, anatomy. This is the most parsimonious hypothesis that could be devised on present evidence, and is adopted here.

outgrowth of the uroneural as discrete and always recognizable elements. The osmeroid stegural is presumed to be an advanced version of the salmonid condition on the grounds that rudimentary neural arches are not present in the adult and that in a specimen of the osmerid, *Spirinchus dilatus*, there is evidence that a remnant of the rudimentary neural arch and spine is present in the early ontogeny of stegural formation (fig. 28B). On the presumption of this stegural homology, salmonids and osmeroids are sister groups. Esocoids might then be considered a sister group of these two on the grounds that the number of rudimentary neural arches is reduced to one, a condition advanced over that of galaxioids and argentinoids which most often have two (figs. 18, 19). The argument for esocoid placement on this basis is not impressive because the disappearance of these neural arches in osmeroids is associated with stegural formation, which does not occur in esocoids, and because some salmonids still retain two rudimentary arches (fig. 25D). Esocoids do also develop bony laminae on the first, and only, uroneural, but these outgrowths are rather different from those of salmonids and osmeroids and they are never associated with a neural arch in the salmonid manner. Not only is there slight evidence for placing esocoids on caudal evidence, but there is no rational basis for deciding on caudal anatomy whether, and how, galaxioids and argentinoids are related to the other salmoniforms. Argentinoids and galaxioids are basically so primitive in this region that they can occupy interchangeable positions in a phylogeny based on the caudal skeleton (fig. 38). Many of these points have been made previously by Patterson (1970, fig. 47 and accompanying text), although he employed the term "stegural" in a less restrictive manner than Greenwood and Rosen (1971) and the present usage. The greatest objection to a phylogeny based on the caudal skeleton, as illustrated in figure 38, is that it requires:

1. The independent origin of basihyal fangs and the loss of basibranchial dentition in argentinoids, galaxioids, and a group including salmonids and osmeroids.

2. The independent loss of uncinate and levator processes from the fourth epibranchial and the fusion of the dorsal tip of the fifth epibranchial with the posterior cartilage of the fourth in galaxioids and salmonids.

Or, alternatively, on the assumption that the attributes in 1 above are primitive for the Salmoniformes.

3. The redevelopment in esocoids of an extensive and uniform dentition of small, close-set teeth on the basihyal and basibranchials that appears to be primitive for teleosteans generally (see pp. 273–274).

In contrast, a phylogeny of the salmoniforms based on the hyobranchial apparatus only requires the assumption, concerning caudal skeleton evolution, that the salmonid and osmeroid types of stegurals were acquired independently (figs. 28, 39).

On the strength of the present study, it appears therefore, that the branchial apparatus is of considerable use in assessing higher level relationships among salmoniforms. The caudal skeleton, on the other hand, is at best difficult to apply at this level, giving an incomplete and discrepant picture of intergroup relationships. Both branchial and caudal structures, however, have proved extremely helpful in assessing the affinities of salmoniform genera and families, particularly in the identification of retropinnids, prototroctids, plecoglossids, and salangids as relatives of the Osmeridae, in confirming the relationship of the galaxiids and aplochitonids, and in suggesting a relationship of *Lepidogalaxias* with esocoids. Of the other characters analyzed here and by other workers, no one of them suggests a pattern of relationship entirely consistent with that based on a different set of criteria. Still other advanced features are characteristic of one group only (i.e., autapomorphic, as defined by Hennig, 1966). For example, secondary sexual modifications of the male anal fin seem to relate *Lepidogalaxias* and salangids on the basis of the associated scale sheath, and salangids and the osmerid *Mallotus* on the basis of the anal fin rays. A posterior position of the dorsal fin, associated with the absence of the adipose fin, can be interpreted as primarily present only in *Lepidogalaxias* and esocoids, and secondarily present in salmonoids (as in galaxiids, but not aplochitonids and salmonids) and argentinoids (as in the Alepocephaloidea, but not the Argentinoidea). The downward deflection of the anterior canal-bearing bones of an incomplete infraorbital chain seems to relate galaxioids with retropinnids and prototroctids (Nelson, 1972), but the loss of canal-bearing infraorbital bones occurs in retropinnids and prototroctids (one

bone lost), galaxioids (four bones lost), umbrids and salangids (five bones lost), and *Lepidogalaxias* (all bones lost). There are still other difficulties in applying this trait in phylogenetic analysis in view of the occurrence of the galaxioid bone pattern and number in atheriniform fishes (see Nelson, 1972, fig. 23, and discussion above). An analysis of jaw bones, squamation, and caudal fin ray number in salmoniforms gives additional contrasting results.

In short, there apparently has been a decided amount of mosaic evolution within the Salmoniformes, and only the details of the hyobranchial apparatus provide a consistent set of criteria for assembling all the groups in a single scheme. The present evidence for regarding esocoids as members of the Salmoniformes is slight, being based to a large extent on the fusion of a tooth plate to the third pharyngobranchial combined with the development of a posterior tooth plate below the fourth pharyngobranchial and fourth epibranchial in a pattern very like that of other well-toothed salmoniforms (see Rosen, 1973a). The following scheme, then, recognizes the uncertainty of esocoid relationships and, on the basis of the exceedingly primitive aspect to the basihyal and basibranchial tooth plates and dentition, includes them as the primitive sister group of other salmoniforms. Of the remaining assemblages, argentinoids are more primitive than galaxioids, salmonids, and the osmeroids in having a completely free fifth epibranchial and, in the caudal skeleton of some members, two autogenous and little modified rudimentary neural arches and spines over the first preural centrum. In advanced characters, the argentinoids share with galaxioids, salmonids, and osmeroids the presence of fanglike teeth arranged marginally on the basihyal (many forms have no basihyal dentition, however) and the loss of teeth from the basibranchial tooth plate and the development of platelike bone on the posterior neural and hemal spines. Of the remaining three groups galaxioids and salmonids appear to be more closely related to each other than either is to osmeroids on the basis of specific and detailed resemblances in the type and pattern of basihyal fangs and reduced basibranchial tooth plate, in the loss of uncinate and levator processes on the fourth epibranchial, and in the type of fusion between the cartilage of the fourth and the dorsal tip of the fifth epibranchials in connection with the formation of a canal for the fifth efferent branchial artery. Galaxioids and salmonids, as noted above, may therefore be regarded as members of a salmonoid assemblage. The osmeroid assemblage is readily defined on the basis of hyobranchial and caudal evidence and includes the Osmeridae, Plecoglossidae, Salangidae, Retropinnidae, and Prototroctidae. Both McDowall (1969) and Nelson (1972) have provided much good evidence that retropinnids and prototroctids are closest relatives to each other, and Nelson has appropriately suggested combining them in a single family-level category—here recognized as the Retropinnidae. Although there is evidence in advanced characters to relate all salangids (the Plecoglossidae is monotypic), the same cannot be said of osmerids. McAllister (1963) has provided an impressive list of characters that purports to define the Osmeridae, but of the 35 traits included only six can be considered derived in relation to their condition in other teleosteans. These derived characters are: no intermuscular bones, postterminal vertebral centra, median shaft on vomer, orbitosphenoid, or basisphenoid, and posterior neural and hemal spines with anteroposteriorly oriented blades. Not one of these six characters is peculiar to osmerids, for intermuscular bones are also absent in the other osmeroids, the vertebrae of the caudal skeleton are consolidated in all osmeroids, and the median vomerine shaft, orbitosphenoid, and basisphenoid are also lacking in some or all the other osmeroids. Bladelike outgrowths of the posterior neural and hemal spines are present not only in other osmeroids, but also in salmonoids and argentinoids. Similarities between hypomesine osmerids (e.g. *Hypomesus* and *Mallotus*) and salangids in the structure of the fourth and fifth epibranchials and the anal fin of the male, and between those same osmerids and the retropinnids in general fin development of the breeding males suggests that the Osmeridae, as recognized by McAllister and others, may be polyphyletic within the osmeroid assemblage. There is thus an evident need for an assessment of interrelationships within the osmeroid group and the four family-level categories are adopted here in a provisional, *incertae sedis* status only. A phyletic classification reflecting all the proposed relationships is:

Order Salmoniformes
  Infraorder Esocae
    Suborder Esocoidei
      Superfamily Esocoidea
        Family Esocidae
        Family Umbridae
          Subfamilies *incertae sedis*:[1]
            Dalliinae
            Novumbrinae
            Umbrinae
      Superfamily Lepidogalaxioidea
        Family Lepidogalaxiidae
  Infraorder Salmonae
    Suborder Argentinoidei
      Superfamily Argentinoidea
        Family Argentinidae
        Family Bathylagidae
          Subfamily Bathylaginae
          Subfamily Opisthoproctinae
      Superfamily Alepocephaloidea
        Families *incertae sedis*:[2]
          Alepocephalidae
          Bathyprionidae
          Searsiidae
    Suborder Salmonoidei
      Superfamily Salmonoidea
        Family Galaxiidae
          Subfamily Aplochitoninae
          Subfamily Galaxiinae
        Family Salmonidae
          Subfamilies *incertae sedis*:[3]
            Salmoninae
            Thymallinae
            Coregoninae
      Superfamily Osmeroidea
        Families *incertae sedis*:[4]
          Osmeridae
          Plecoglossidae
          Retropinnidae
          Salangidae

By way of summary, the following analytical key to the main groups of salmoniform fishes is provided (primitive or presumed primitive character states are given in italics):

a. Dorsal fin posterior in position, over anal fin, no adipose dorsal fin; maxillary edentulous, with or

[1]Evidence of relationships among *Dallia, Novumbra,* and *Umbra* is contradictory. See accounts in Cavender (1969), Nelson (1972), and in the present paper (pp. 285, 291–293).

[2]Relationship of bathyprionids to other alepocephaloids is unsettled. See Greenwood and Rosen (1971).

[3]The relationship of thymallines to other salmonids is not clear, according to Norden (1961).

[4]Relationships among osmeroid families and possibly between some osmerid genera and members of other osmeroid families need review according to evidence presented here.

without a supramaxilla; endopterygoid edentulous; *a tooth plate with or without teeth over fourth endoskeletal basibranchial,* with only a single large, oval, strongly dentigerous tooth plate supported by the fourth infrapharyngobranchial and fourth epibranchial, the fourth epibranchial always somewhat reduced and without a distinct posterodorsal process for the external branchial levator muscle; no mesocoracoid in the shoulder girdle; no pyloric caeca; in the caudal skeleton, *the first and second ural* (U_1, U_2) *and first preural* (PU_1) *centra unfused,* with never more than a single rudimentary neural arch and spine over PU_1, with only a single, long, straplike uroneural; freshwater . . . . Infraorder Esocae

b. Elongate paired dermal ethmoids (=proethmoids) attached anteriorly to premaxillae and posteriorly to frontals; *frontals separate; cephalic sensory canals subdivided into mandibular, preopercular, supraorbital, infraorbital, temporal, extrascapular,* and *posttemporal components* sometimes represented by pitlines; ethmoidal and antorbital canals represented by pitlines; mandibulopreopercular, subnasal, and opercular pitlines present (Nelson, 1972); infraorbital bones, when reduced, represented by at least the first (=preorbital or lacrimal); *tooth plates of basihyal-basibranchial chain dentigerous,* with a basihyal and three basibranchial plates; with a single perichondral ossification surrounding the basal two-thirds of the endoskeletal basihyal; *fin rays bifurcate; scales normal, overlapping;* male sexual dimorphism consisting mainly of somewhat enlarged median fins . . . . Suborder Esocoidei

bb. Ethmoidal ossification confined to capsular perichondral ossification of mesethmoid; frontal bones united (fig. 40); cephalic lateral line system reduced to three preopercular pores and a series of pitlines representing the mandibular, preopercular, supraorbital, infraorbital, temporal, and extrascapular components; ethmoidal canal represented by a pitline; with a subnasal pitline; no infraorbital bones; edentulous tooth plates present only on the basihyal and fourth endoskeletal basibranchial; with a double perichondral ossification surrounding the entire endoskeletal basihyal, the proximal one covering its basal two-thirds; fin rays unbranched; scales mostly small, nonoverlapping, and embedded; male sexual dimorphism consisting of an elaborate sheath of enlarged scales over the anal fin base and elaborately differentiated anal fin rays . . . . Suborder Lepidogalaxioidei

aa. *Dorsal fin in mid* or posterior position, *adipose dorsal fin present* or absent; maxillary edentulous or not; with a single supramaxillary (*rarely with a*
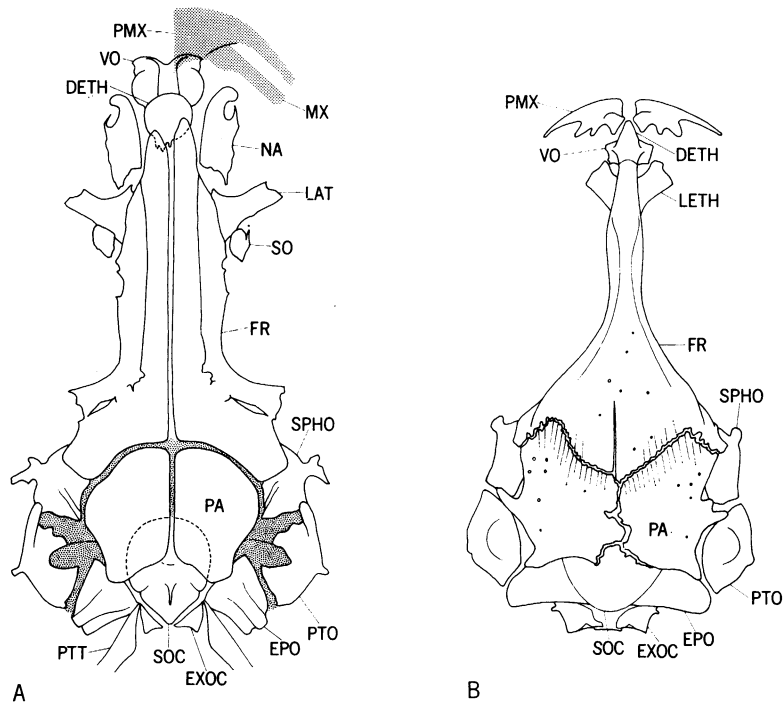
FIG. 40. Dorsicrania in *Nesogalaxias neocaledonicus* (A) and *Lepidogalaxias salamandroides* (B). Frontal bones are separate in A, united in B. In A, premaxilla (shown in shaded silhouette) lies dorsal to ethmovomer block; in B, premaxilla articulates with the lateral surface of the dermethmoid.

small additional anterior supramaxillary in some alepocephaloids) or supramaxillae absent; *endopterygoid dentigerous* or not; *endoskeletal basihyal with a small, proximal, perichondral ossification*; without a tooth plate over the fourth endoskeletal basibranchial; with a single, large, oval, strongly dentigerous tooth plate supported by the fourth infrapharyngobranchial and fourth epibranchial *or with a separate tooth plate* on each; the fourth epibranchial reduced *or not; mesocoracoid present* or absent; *pyloric caeca present*; in the caudal skeleton, *the first and second ural* (U$_1$, U$_2$) *and first preural* (PU$_1$) *centra fused* or not, *with two*, one, or no rudimentary neural arches on PU$_1$, with two, often *three uroneurals*, the second sometimes fusing with the first; marine, anadromous, or freshwater . . . . Infraorder Salmonae

c. Jaws edentulous *or not*, with or without a supramaxilla; dermal basihyal, when dentigerous, with fanglike teeth arranged along distal tip or marginally; basibranchial tooth plate edentulous and with a sharp median ridge of bone and membrane that divides orobranchial chamber into right and

left halves; with a complex posterior pharyngobranchial organ, the crumenal organ (see Greenwood and Rosen, 1971) containing an accessory cartilage on the posterior end of the fifth ceratobranchial *and an unfused fifth epibranchial; fourth epibranchial with* or without uncinate or levator processes, *never with an enclosed canal for the fifth efferent branchial artery*; in caudal skeleton, centra U$_1$, U$_2$, and PU$_1$ consolidated *or not with two rudimentary neural arches and spines above* PU$_1$; *dorsal fin in mid* or posterior position, *adipose dorsal fin present* or absent; marine. Suborder Argentinoidei (See Greenwood and Rosen, 1971, for distinctions between argentinoids and alepocephaloids.)

cc. Jaws edentulous *or not*, with or without a supramaxilla; dermal basihyal dentigerous with marginal fanglike teeth, except in forms with general reduction in dentition (Thymallini, Coregoninae, Salangidae); basibranchial tooth plate edentulous *or not, without a sharp median ridge dividing orobranchial chamber; without a posterior pharyngobranchial*

organ or accessory cartilage; fifth epibranchial fused *or not* with cartilage of fourth; *fourth epibranchial with* or without uncinate and levator processes, frequently with a closed canal for fifth efferent branchial artery; in caudal skeleton, centra U_1, U_2, and PU_1 consolidated *or not, with two* to no rudimentary neural arches on PU_1; *dorsal fin in mid* or posterior position, *adipose dorsal fin present* or absent; freshwater or anadromous (one marine species) . . Suborder Salmonoidei

d. Basihyal fangs in forms with unreduced dentition large, arranged in right and left pairs and forming a distinct terminal pair; basibranchial edentulous or with a few scattered teeth, never with enlarged marginal dentition or with a blunt, somewhat elevated median ridge; fourth epibranchial without uncinate or levator processes; *fifth epibranchial unfused,* or with a probable primary fusion between its dorsal tip and the midpoint of the posterior cartilage on the fourth and a secondary fusion ventrally to form a closed canal for the fifth efferent branchial artery; in caudal skeleton, centra U_1, U_2, and PU_1 consolidated *or not,* with two or *three uroneurals,* with one or *two rudimentary neural arches and spines over* PU_1, the tip of the posterior arch in some cases (salmonids) joining but not fusing with a dorsal outgrowth of the first uroneural to form a primitive type of stegural; *dorsal fin in mid* or posterior position, *adipose dorsal fin present* or absent; freshwater or anadromous . . . . Superfamily Salmonoidea

dd. Basihyal fangs in forms with unreduced dentition large, arranged in alternating positions on right and left side, and tending to form a single large terminal tooth; basibranchial dentigerous, with small sparse teeth medially and enlarged marginal teeth in most cases, with a blunt, somewhat elevated median ridge except when tooth plate is greatly expanded; fourth epibranchial without uncinate or levator processes in a few cases, but never without both in any species; *fifth epibranchial unfused* or fused ventrally to the posteroventral end of the fourth, with a closed canal for the fifth efferent branchial artery in one case (*Plecoglossus,* in which the fifth epibranchial that bounds the canal posteriorly remains unfused); in caudal skeleton, centra U_1, U_2, and PU_1 consolidated, or only U_1 and PU_1 consolidated, with two *or three* uroneurals, without rudimentary neural arches on

PU_1, these arches having become fused into a dorsal outgrowth of the first uroneural to form a stegural; *dorsal fin in mid* or somewhat posterior position, *adipose dorsal fin present*; freshwater and anadromous (one species marine) . . . . Superfamily Osmeroidea

REMARKS ON SALMONIFORM ZOOGEOGRAPHY

Except for the argentinoid fishes, salmoniforms are mainly freshwater or anadromous. On the basis of the proposed phylogeny (fig. 39), salmoniforms are therefore primitively freshwater fishes that have twice become secondarily marine (the suborder Argentinoidei and *Osmerus eperlanus*). All other forms live permanently or breed in freshwater. It should be noted, however, that if esocoids are incorrectly associated in this order and the sister group of the Salmonae should prove to be marine instead of freshwater, then the Salmonoidei may be secondarily anadromous, leaving the sea only to breed, and tertiarily in freshwater (as landlocked forms). In any event, the common ancestor of the Salmonoidea and Osmeroidea evidently either lived or bred in fresh water. Apart from the pandemic, entirely marine, bathypelagic argentinoids, salmoniforms are amphitropical, panboreal, and panaustral in distribution. Only a few forms, some salangids and a galaxiid (*Nesogalaxias*), occur in tropical regions (figs. 41–43).

The recent geophysical evidence pertaining to world continental plate tectonics provides a time scale to which salmoniform distributions, and phylogeny, may be referred. According to current geologic concepts all the continents were once joined in a single great land mass, Pangaea, which initially divided to form Laurasia (Eurasia and North America) and Gondwanaland (Antarctica, the southern continents, the Indian subcontinent, and Australia). Gondwanaland subsequently subdivided by Africa and India breaking away, then east Antarctica and Australia, followed by New Zealand, and lastly west Antarctica and South America (fig. 44). According to most recent estimates, as compiled by McKenna (1973), the final disruption of land continuity of Pangaea occurred about 180 million years ago and the final breakup of Africa from other southern landmasses about 90 million years ago. If the present
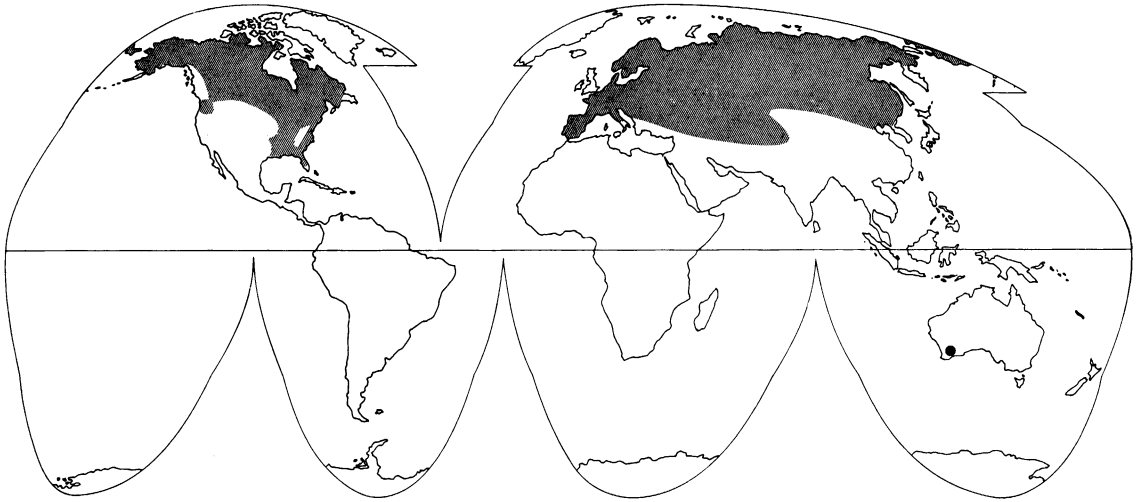
FIG. 41. World distribution of the esocoid fishes. The single black spot in southwestern Australia represents the known occurrence of *Lepidogalaxias*, here interpreted as a southern esocoid.

phylogenetic concepts of the Salmoniformes are correct, or even if the esocoids are not a sister group of the Salmonoidei, the amphitropical distributions within each of the main groups of fishes concerned may indicate that the salmoniforms are at least as old as Pangaea, that is, 180 million years. Myers (1967), on other grounds, had previously suggested a comparable age for the main fish groups. The amphitropical distributions of the nonmarine assemblages are: esocoids in Laurasia (pikes and mudminnows) and southwestern Australia (*Lepidogalaxias*); salmonoids in Laurasia (salmonids) and southern South America, New Zealand, Australia, and South Africa (galaxiids); osmeroids in Laurasia (osmerids, plecoglossids, salangids)

FIG. 42. World distribution of the fishes of the superfamily Salmonoidea, the northern Salmonidae and the southern Galaxiidae (including *Aplochiton* and *Lovettia*). See text for distributional details. Note North African occurrence of salmonids in a region entirely north of the South Atlas Fault (see text).

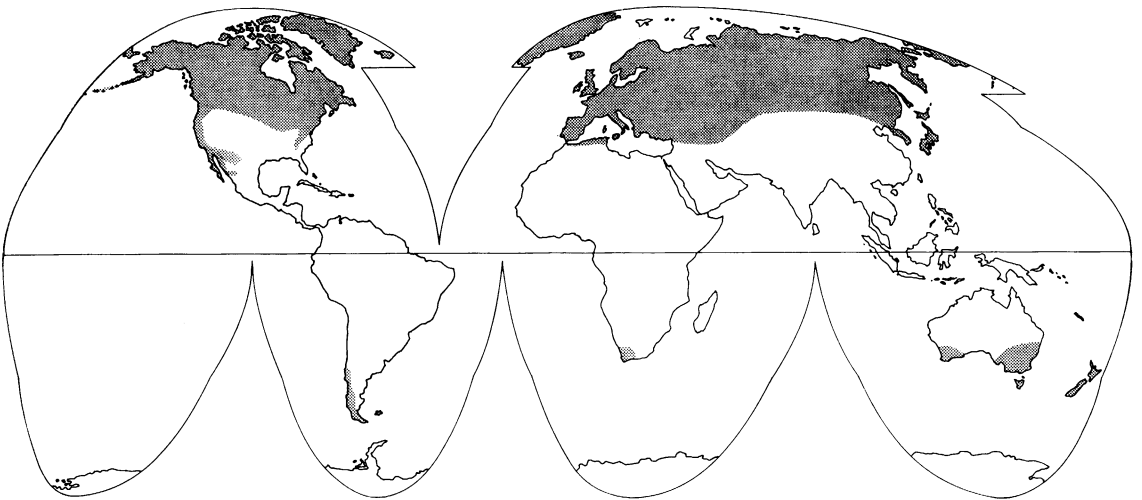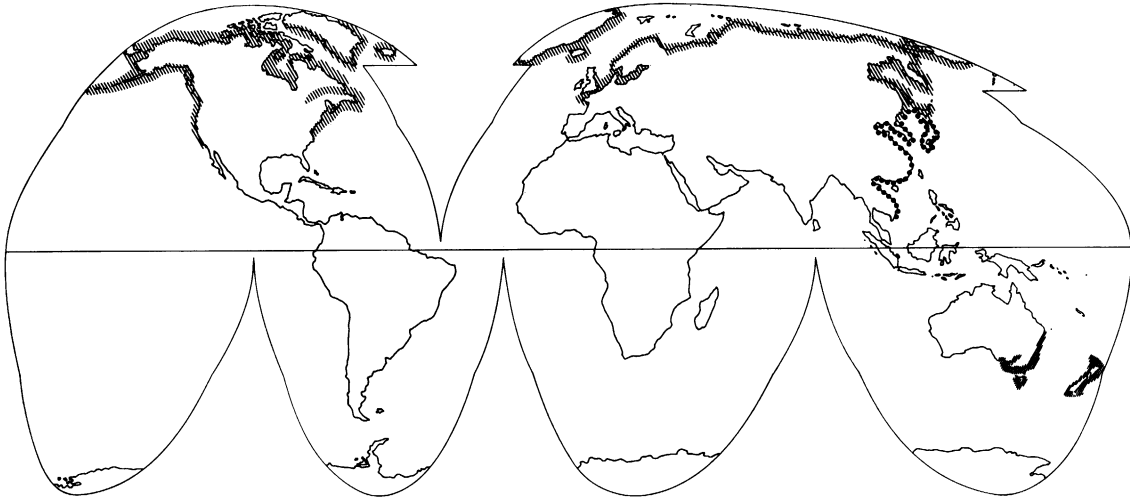FIG. 43. World distribution of the fishes of the superfamily Osmeroidea, the northern Osmeridae (hatched) and Salangidae and Plecoglossidae (within dotted area of eastern Asia), and the southern Retropinnidae (including *Prototroctes*).

and New Zealand and Australia (retropinnids). Moreover, the galaxiid distribution occupies all the major components of the original Gondwana land mass except Antarctica and India, and may therefore be at least 90 million years old.

McDowall (1964, 1966, 1970, 1973) has accounted for the austral distribution of galaxiids largely from an ecological standpoint. A central part of his argument is that *Galaxias maculatus* (*G. attenuatus* of older publications) is widely distributed in South America, New Zealand, and the Australian region, and that being an anadromous form, and therefore marine during part of its life history, it could easily have dispersed from one continental mass to another. However, there is as yet no evidence that any galaxiid does undertake, or is capable of undertaking major, transoceanic migrations. Indeed, no such evidence exists even in the case of the many species that occur in New Zealand which, except for *G. maculatus*, are confined to New Zealand and the islands less than 10 degrees of latitude south and 10 degrees of longitude east. The only other groups of salmoniforms in this region (retropinnids) are confined to the area between New Zealand and southeastern Australia. Nevertheless, McDowall (1966) stated

that, "The fact that *G. attenuatus* [=*G. maculatus*] is present in three widely separated land masses . . . shows that its larvae and juveniles are capable of oceanic dispersal . . ." and then, neglecting the possibility of low evolutionary rates, ". . . and that this dispersal could have taken place quite recently." McDowall seemed quite definite about temporal events when, in the next paragraph he continued, "Apart from the comparatively recent dispersal of *G. attenuatus* [=*G. maculatus*] . . ." and ". . . one of the five [salt-tolerant New Zealand] species is known to have crossed the South Pacific . . ." thus clearly indicating his belief that a low evolutionary rate is out of the question. Hence, two views based on surmise have reenforced each other to exclude the possibility of former land connections as suggested long ago by Gill (1893) and more recently by Stokell (1950). Curiously, in one of the papers just cited, McDowall (1966, pp. 14–15) observed that "Ogilby (1899) drew attention to the distinctness of *G. attenuatus* [=*G. maculatus*] when he removed it to the new genus *Austrocobitis*. The validity of using *G. attenuatus* [=*G. maculatus*] to explain the dispersal of the ancestral Galaxiidae is thus doubtful, but the knowledge that other 'more typical' Galaxiidae have marine stages in their
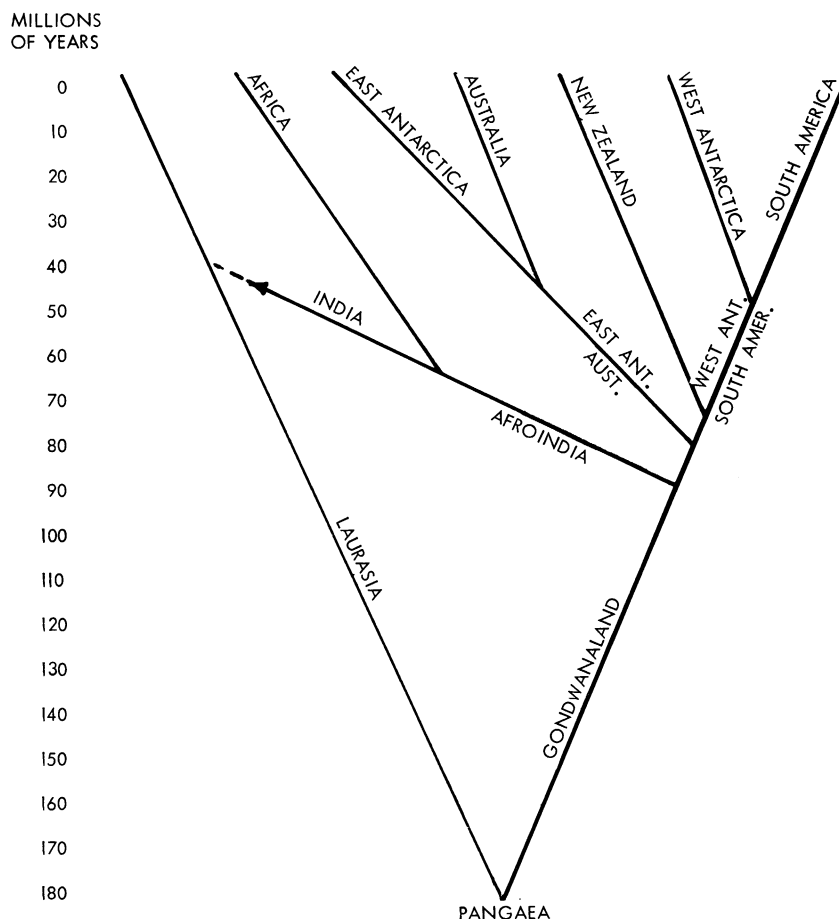
FIG. 44. Diagrammatic representation of the sequential disruptions of the super-continent Pangaea through time, according to data from McKenna (1973, and personal commun.). The beginning of disruption of the Gondwanaland fragment is located at minus 90 million years.

life cycles renders it unnecessary to depend exclusively on *G. attenuatus* [=*G. maculatus*] as a pointer to *Galaxias* distribution patterns and means of dispersal." McDowall had a strong prior commitment to his views when he concluded (1964) that "It seems fairly certain that the New Zealand fresh-water fishes must have arrived in New Zealand since its isolation from other land masses." The second part of McDowall's argument concerns the means of oceanic transport in relation to the number of species present in a given area. Hence, he concludes that Africa (with only one species; McDowall, 1973) was the last continent to be colonized by galaxiids circumnavigating the

South Pole ". . . in the west wind drift from Australia to New Zealand, South America, and South Africa." Again, regarding *G. maculatus* there is ". . . little chance that this species was transported by other than ocean currents. Further support for transoceanic dispersal of fresh-water fish to New Zealand is the faunal relationship between south-east Australia (Tasmania) and New Zealand . . . and the presence of the warm east-Australian (Notonectian) sea current which impinges on much of the west coast of New Zealand." How many invasions of the sea are required to account for the widely distributed galaxiids? One, two, or a hundred? Taxonomists working with galaxiids

seem to be agreed that the species of New Zealand or South America are not descended from a single ancestral form, but rather that there are many cross-relationships among the species of different land masses. The South African form is one of the most distinct and derived members of the group. As the last arrival of the postulated circumpolar migration, should it not be relatively little differentiated? Or must we also assume for it a more rapid evolutionary rate? In a recent account of the zoogeography of the Aplochitonidae (=Aplochitoninae, as used here), McDowall (1971b) further extended himself. He argued that the present distribution of the group (two species of *Aplochiton* in southern South America and one of *Lovettia* in Tasmania) should be accounted for by recent transoceanic dispersal because marine life history stages are known for *Lovettia* and suspected for *Aplochiton* and because the members of the two genera, although related, are rather different. Yet, in the same account, he invoked the occurrence of the taxonomically inseparable populations of *Galaxias maculatus* and the lamprey, *Geotria australis*, in South America, New Zealand, and Australia as evidence that continental disruptions ". . . must have been far too early in time to permit us to use continental drift to explain the range of these species." Apart from the inconsistency in the argument, it is clear that here again there is no *evidence* of marine dispersal for aplochitonines, and this group includes forms that are brought together entirely on the basis of primitive characters (McDowall, 1971b, p. 32). Hence, the relationships of *Lovettia* to *Aplochiton* or to the species of *Galaxias* is still in doubt. Moreover, lamprey evolution is suspected of being at least conservative when one considers that a modern type of lamprey occurred in Pennsylvanian deposits about 280 million years old (Bardack and Zangerl, 1971). But the most arbitrary part of the argument concerns the distribution of *Lovettia*. It is confined to Tasmania, not even reaching the nearby Flinders and Cape Barren Islands. An odd behavior for a type of fish that, according to McDowall, goes so readily to sea. He dismissed its absence from the Australian mainland by invoking temperature limitations and its unknown ". . . inability to compete with species in the more diverse fauna of mainland Australia." He attempted no explanation of its absence from the Cape Barren and Flinders Islands or from New Zealand,

which, concerning galaxiine distributions, had been regarded by McDowall as a major way station for hypothetical ocean-going *Galaxias* (see below, p. 316). It seems to me that the number and types of historical events that must be assumed to account for McDowall's hypotheses of galaxiid distributions render the hypotheses untestable, and invite serious consideration of the concept that 1) galaxiids are where they have been for a very long time, 2) that some of the principal lineages of galaxiids have been evolving in parallel on the different land masses (Stokell, 1950, for example, suggested assignment of an Australian and the South African forms to a genus *Paragalaxias*, and McDowall, 1973, pointed to similarities between the African species and the South American *Brachygalaxias bullocki*), and 3) that a Gondwanaland hypothesis, based on a growing body of geophysical evidence, simply accounts for the now disparate galaxiid population centers. It is still, of course, possible to discover in which parts of the Gondwana land mass galaxiids might have originated by identifying the primitive sister group of a well-established galaxiid phylogeny. Within the Aplochitoninae, the South American trout-like *Aplochiton* may represent a primitive sister group to the very specialized and peculiar Tasmanian *Lovettia*, perhaps indicating that the Aplochitoninae originated in the South American fragment of Gondwanaland. The Aplochitoninae is also the primitive sister group to the Galaxiinae, so that the entire family may have had its origin in South America, spreading eastward overland in fresh water, rather than eastward transoceanically, to colonize Africa, and eastward via the Antarctic continent to Australia and New Zealand. But such conclusions will have to await agreement among taxonomists on what constitutes an acceptable phylogeny of the many species of galaxiids. Agreement seems far off, however. Not only do Scott (1936, 1966), Stokell (1950), and McDowall (1968b, 1970, 1971a) disagree on galaxiid interrelationships, but also there is no consensus on the number of species to be recognized (McDowall, 1972a), the relationships of some of them have been regarded as so remote that they are considered not closely related to any others, and only the relationships of three New Zealand forms (*postvectis, fasciatus, argenteus*) with one Australian form (*truttaceus*) remain undisputed.

The contrasting zoogeographic conceptions

of salmoniform, and in particular, galaxiid distributions are paralleled exactly by the contrasting interpretations given to chironomid and plant distributions in the southern hemisphere. In a monograph on the transantarctic relationships of chironomid midge distributions, Brundin (1966) has shown that the cold-adapted midges have a southern distribution in fresh water which is very similar to that of galaxiids. Of the regions occupied by galaxiids, the midges are not known from southwestern Australia and New Caledonia, and midges occupy one additional region in the Chilean and Argentinian Andes. Moreover, the two main groups of midges analyzed by Brundin have boreal relatives in Laurasia. Brundin concluded from carefully documented and detailed phylogenies that the austral groups arose in South America and spread to New Zealand, Australia, and Africa across the eastern and western segments of Antarctica, although he recognized the probability of some return dispersals from all but Australia. In other words, Australia was mainly or entirely a "receiver land" in midge distributions. Another similarity between midge and galaxiid distributions is the depauperate African fauna consisting of one to a few species. Brundin has given a Gondwanaland interpretation to his data: "The theory of continental drift provides a background fitting all demands raised by the nature of the transantarctic relationships, as displayed by the chironomid midges. Indeed, the fit between the history told by the distribution patterns and reconstructed phylogenies on one hand, and the latest opinions concerning the geological nature and mutual connections of the Gondwana fragments, and the time-table affixed to the disruption of Gondwanaland on the other, is so close that there is agreement even in details." The timetable referred to by Brundin is, of course, the sequence of continental separations in relation to the positions of branching points in his phylogenies.[1]

In the way that McDowall would have the galaxiids undertaking passive circumpolar journeys under the influence of a west wind drift in ocean currents of appropriate direction, speed,

[1]Darlington (1970, p.13) obviously misunderstood this point when he thought that Brundin had referred to actual rather than "relative phylogenetic time." The correlation of branching sequences with presumed known geologic sequential continental separations is a matter of record for those wishing to make such comparisons.

and temperature, Darlington (1970) has argued for a transantarctic (and perhaps worldwide?) distribution of midges based on their chance dispersal through the air, as "aereal plankton" resulting in a "very orderly" geographic pattern of occurrence over vast distances. Darlington appears to object to a Gondwanaland hypothesis on the grounds that it is simple and straightforward ("This . . . is surely biogeography made easy.") and to prefer the vagaries of waif dispersal for formulating correspondingly vague and untestable—and therefore unrejectable! —hypotheses. The point is that, of course, insects can be carried away by winds and fishes by ocean currents, but we have no evidence if or how galaxiids (or midges) are being so moved, if they could even survive such a journey in terms of what their biology, their ontogenetic requirements, or (in the case of fishes) the oceanic ecology would permit, if the physical details of the ocean currents or winds can be correlated precisely with galaxiid or midge population centers, and if waif transport has occured the number of times necessary to account for the number of distinct lineages in each population center. Finally, even if present distributions are relatively recent, can we assume that wind and current patterns have not been different during the entire evolutionary histories of the groups? The number of separate events that must be assumed in such chance dispersal hypotheses is unknowably large, as against the more manageable framework of a changing continental landscape that is being provided by a growing and consistent body of geophysical evidence.

The fact that both galaxiids and the chironomid midges have an amphitropical distribution in temperate and subarctic and subantarctic waters raises the question not only of their points of origin, whether austral or boreal, but whether the ancestors might in fact have been cold-adapted animals. With regard to the midges, Brundin concluded from comparative study of larval and pupal ecology and of various structural systems of the young stages, that the family Chironomidae originated in cool running waters. He further pointed out that because the abundant ". . . tropical groups of all altitudinal zones stand out as apomorph in relation to their cold-adapted austral and boreal sister groups, . . . the main pattern of chironomid evolution has been of the bipolar type." It is

noteworthy that, although we are far from the degree of phylogenetic understanding achieved by Brundin for midges, the ostariophysan fishes stand much in the same relation to the bipolar Salmoniformes, both in their great success in the tropics and in their seemingly relative apomorph character, that the tropical midges do to their austral and boreal plesiomorph relatives. There is some slight evidence that the Ostariophysi are related at least to the nonesocoid salmoniforms in the structure of the upper pharyngeal dentition, the nature of the fourth

epibranchial, and the presence of similar breeding tubercles, but much study obviously is needed exactly to determine ostariophysan relationships. One might note at this time, however, that the primitive sister group of other ostariophysans, the gonorynchiforms, are presently distributed in the freshwaters of Africa, and in Australia, southeast Asia, and the west coast of North America in fresh, brackish, and salt water, that the characoid fishes are freshwater African and South American, that the cyprinoids have a freshwater African and Tethyan
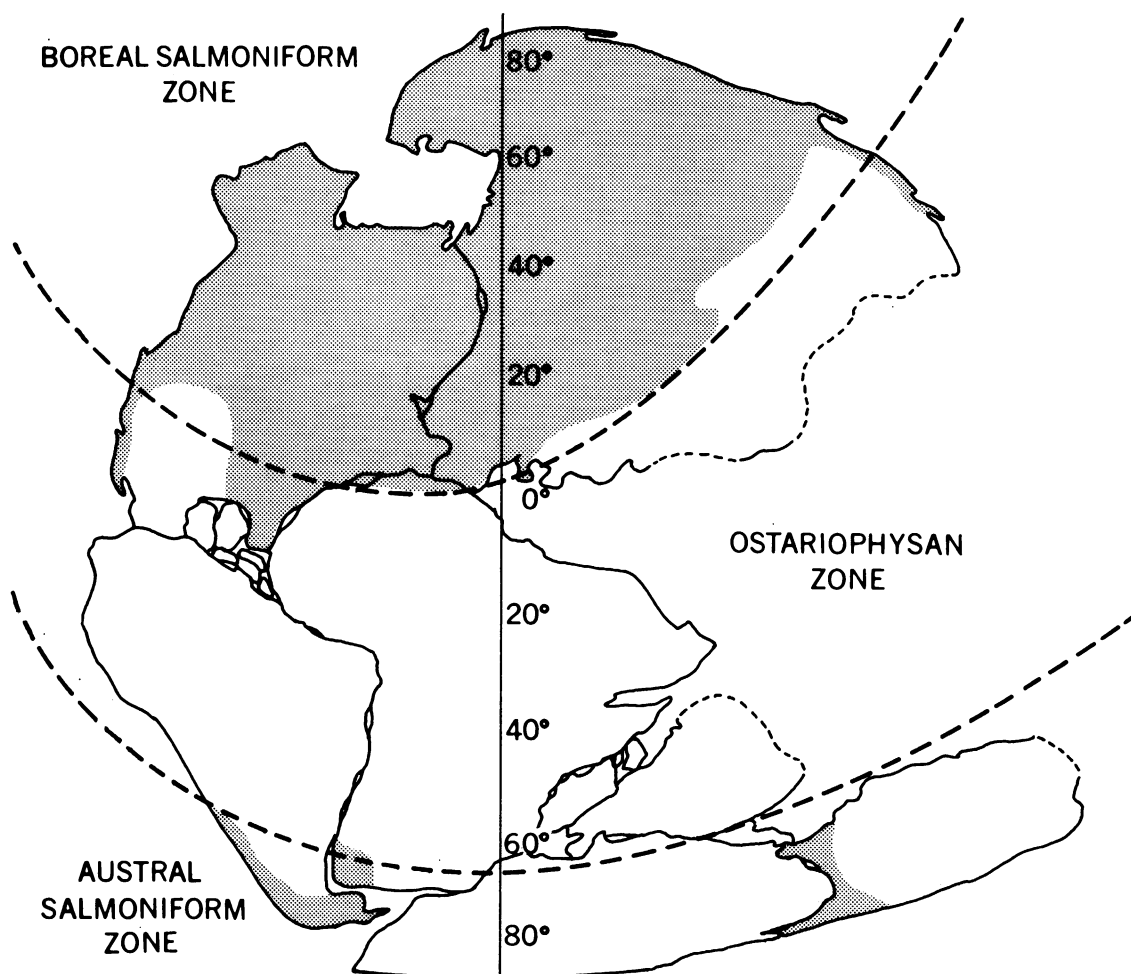
FIG. 45. Present-day world distribution of salmoniform fishes, exclusive of the marine argentinoids, superimposed on a map of Pangaea. Vertical line shows Pangaean latitudes. Dashed lines show smoothed contours of boreal and austral salmoniform zones which also approximately delimit an ostariophysal zone. There is, however, considerable marginal overlap between the salmoniform and ostariophysan sectors. Base map from Dietz and Holden (1970).

distribution, and that the catfishes are found in Africa, South America, the Tethyan region, and perhaps secondarily as the marine and freshwater plotosids in southeast Asia and Australia. Clearly, ostariophysans occupy most of the globe not inhabited by salmoniforms, although there is some overlap especially in Laurasia, but it is clear from a view of present salmoniform and ostariophysan distributions superimposed in a simplified manner on a map of Pangaea (fig. 45), that ostariophysan history may also partly have been involved with the history of Gondwanian disruptions rather than simply with migrations across boreal land bridges in a supposedly stable world.

Of the many animal and plant distributions in the southern hemisphere similar to those of galaxiids and the chironomid midges, one other, that of the southern beeches of the genus *Nothofagus*, has particular relevance here because this distribution has also been interpreted in very different ways. Darlington (1965) referred to *Nothofagus* as a probable ". . . key to the history of terrestrial life in the far south . . ." These trees are presently distributed in New Zealand and New Caledonia, New Guinea, southeastern Australia, and southwestern South America. The distribution of fossilized pollen remains indicates that *Nothofagus* was once more widely distributed in east and west Antarctica. The dating of this fossil pollen forms the bulwark of Darlington's argument that *Nothofagus* has been distributed by means of chance dispersal since the Late Cretaceous. Simply stated the issue is: if the pollen is Late Cretaceous in New Zealand and the Antarctic Peninsula, early Tertiary in Australia and Tasmania, Upper Eocene in South America, Pliocene in New Guinea, and nonexistent as fossils in New Caledonia, then *Nothofagus* was not only too late to be affected by continental drift but shows a pattern of gradual dispersal through time from New Zealand and the Antarctic Peninsula outward as far as Australia to the west, South America to the east, and New Guinea and New Caledonia to the north. Of course, Darlington, at that time, disputed the former existence of a Gondwana land mass as currently envisioned by geophysicists and therefore required that animal and plant distributions had to be arrived at by the crossing of barriers of some sort via surface ocean currents or prevailing winds. One must assume that, in the case of *Nothofagus*, Darlington

was also postulating a changing wind pattern, from west to east to north, in order to account for seed dispersal or appropriate winds at one time and ocean currents at another for the rafting of entire fruit- or seed-laden (and salt-impervious) trees. Two observations are relevant here: although pollen can be carried great distances (as many as 3000 miles), long-distance dispersal of the seeds is doubted (according to botanical opinions cited by Darlington), and recent paleontological sampling indicates that pollen remains of *Nothofagus* are of comparably great age in New Zealand, Antarctica, Australia, and South America and sampling in New Guinea and New Caledonia has been inadequate (Dettman and Playford, 1969; Menendez, 1971; Tedford, *in litt.*).

Darlington's views on the significance of southern plant distributions are strongly at odds with those of phytogeographers. In a monograph on the geography of flowering plants, Good (1947) had this to say: "Unanimity in scientific questions is very unusual, but it is probably no exaggeration to say that the opinion of plant geographers is almost unanimous that the present distribution of plants cannot be explained without allowing for some kind of alteration in the distribution of land and sea— that is to say, without assuming that the now severed continents have been joined to one another at some time in the past." And Croizat (1952), in his manual of phytogeography, offered the following opinion: "All in all, there is no risk in affirming that about 40% . . . of the major angiospermous families reveal wellmarked 'antarctic' migrations in their ranks. This given, we readily understand why Darwin and Wallace forsook any instrument of dispersal but straight landbridges when facing the problem of migration in the southern hemisphere, and why Darwin freely advocated radiations of vegetable progenitors from Antarctica. The traffic taking place in this hemisphere is so massive, and involves so many groups of all sorts, that it would be nonsense to insist that, after all, landconnections have nothing to do with it, but [that it is all due instead to] certain mysterious, unexplained and unexplainable agencies blowing seeds right and left." Croizat (p. 362) listed 49 families of seed plants involving congeneric species that have a transantarctic distribution.

Darlington in fact had dismissed three of the most outstanding examples of correspondence of

transantarctic biological distributions with a Gondwana hypothesis (the galaxiids, midges, and the southern beeches) simply by invoking any and all conceivable means of dispersal. Croizat (1958) has termed this ecological-dispersive approach "zoogeography by apriorisms," a view with which I entirely concur.

Whitley (1956) explained galaxiid distributions by advocating a pre-Tertiary Antarctic continent, the parts of which separated and ". . . shifted their positions to some extent." His reasons for this advocacy are that many other animal and plant groups have similar distributions and that the members of these different groups have very different kinds of, and capabilities for, dispersal. The animal groups mentioned are earthworms, freshwater crustaceans and their parasites, molluscs, non-galaxiid fishes, and birds. Whitley's reasoning is basically the same as that presented more precisely and in great detail by Croizat (1958) who considered these multiple, corresponding distributions of diverse organisms to delineate average biogeographic 'tracks.' It is my view that Croizat's concept of 'tracks' forms the only existing scientific basis for biogeographic analysis because it allows an interpretation of the history of the distribution of one group to be tested by those of others without resort to surmise. Within such a framework of 'tracks,' cladistic phylogenies provide the input for interpreting points of origin and direction of dispersal in an individual group.

My purpose is not so much to support or reject the general concepts of a Gondwanian distribution or of persisting long-range waif transport as it is to emphasize that conclusions concerning the distribution, dispersal, and phylogeny of galaxiid fishes need not exceed the evidence presently available. Part of Darlington's original conception of these fishes is that some of them can and do breed in salt water and that they distribute themselves via pelagic larvae: "One species, Galaxias attenuatus [=G. maculatus] which breeds in the sea, occurs in fresh water with only slight differentiation of races in southern Australia, New Zealand, and southern South America" (Darlington, 1957, p. 107). ". . . some of these fishes enter or breed in the sea and may have dispersed through it, or their ancestors may have done so" (Darlington, 1965, p. 38). To an extent, Darlington had derived such ideas from ichthyologists dealing with

galaxiid distributions. He cited Regan (1905) who offered a set of unsupported statements that galaxiids freely enter and can live indefinitely in salt water, that they are probably of marine ancestry, and that they give no evidence of land connections,[1] and Myers (1949), who had this to say: ". . . these fishes are, as a group, salt-tolerant and possibly either anadromous or catadromous, and . . . they are not really strong evidence for continental connections simply because it seems possible that they may cross ocean barriers." Of G. maculatus, McDowall (1968a) wrote that it ". . . spawns in tidal estuaries, either in salty or fresh water, but usually in areas affected by upstream tidal push." None of the specific spawning habitats cited by McDowall in that report could be called marine; some occurred as far as 12 miles upstream and others in lakes. The hatched young fish are presumed to be washed out to sea during their early life history for a period of growth before returning to freshwater to breed (as in the northern salmonids), but the distribution, occurrence, or habits of the young of anadromous galaxiids are not well known and have been little studied. According to McDowall (1968a), the ". . . larvae and juveniles of G. maculatus have not been recorded from the sea and nothing is known of their growth during the marine existence except their total growth at that time." More recently, and not surprisingly, the young of a galaxiid have been reported from the sea off New Zealand (McDowall, 1972b): "They have been caught up to 60 miles off the coast, but it is not known whether the juveniles travel great distances, or whether a small part of the population is swept away from the coast by ocean currents." The recent statements of Stokell

[1]Simpson (1940) had earlier also cited Regan (1905) in the same context and with the same objective: the support of an aprioristic zoogeography to be superimposed on a supposedly stable continental landscape. Referring to Regan's unsupported remarks about galaxiids, Simpson wrote: "This is excellent authority and this opinion has been shared by a clear consensus of ichthyologists ever since. Nevertheless, Galaxias is usually cited by adherents of Antarctic bridges as evidence for their view. So far as any reason can be given for this disregard of authority and consensus, it is to be found in the fact that there is a partially conflicting authority, that of Eigenmann (1909) . . ." Simpson's inability to comprehend a disregard of authority and consensus in science is perhaps the best measure of the quality of his zoogeographic considerations, just as his eagerness to accept Regan's pronouncements is a stern warning to rid science of authority and consensus.

(1972), regarding *G. maculatus*, conflict with those of other authors: "This is the only galaxiid known to the writer to have a marine stage in its existence, but it is not catadromous as is sometimes stated. The conception of a catadromous species and even a catadromous genus has resulted from the colorful accounts of the spawning habits of this fish and the obscurity surrounding the life history of most other species." Regarding the reproductive habitat, Stokell remarked that the ". . . movement of maturing fish from their customary habitat at low and moderate altitudes to tidal water is a true reproductive migration but it does not come within the meaning of the term catadromous. It is a reproductive movement within fresh water . . ." McDowall (1972c), on the other hand, concluded that there are five species of galaxiids with marine growth stages, *G. maculatus*, *G. brevipinnis*, *G. fasciatus*, *G. postvectis*, and *G. argenteus* as determined by rearing river-running young stages to maturity. McDowall's account seems to indicate that all the reared young were from rivers and not from the sea so that it is still a question as to what exactly occurs in the sea and where. In another paper, McDowall (1972a), referring to the widespread populations of *Galaxias maculatus*, clearly stated the problem: "Whether the uniformity of phenotype is due to persistent gene flow, recency of dispersal, or great phenotypic and genotypic stability is not known . . ." It is *assumed*, in other words, based on incomplete knowledge of *G. maculatus*, that larval galaxiids are to be found periodically in the stretches of ocean between Australia and New Zealand, New Zealand and South America, and South America and Africa, or that larvae could have been there in the past. It is also *assumed* that whatever accounts for the "uniformity of phenotype" of *G. maculatus*, even if this should prove to be ultimately attributable to transoceanic dispersal, applies now and has always applied to other galaxiids.

As a consequence of such *assumptions* of larval dispersal and some knowledge of the *actual* salt tolerance of a species, it has been conventional for ichthyologists and zoogeographers to divide freshwater fishes into primary (restricted to freshwater) and secondary (salt tolerant) divisions as suggested by Myers (1938). Hence the primary division ostariophysans and a few other fishes are to be "trusted" in zoogeographic analysis, but the secondary ones are

not. There seem to me to be two things basically wrong with this notion. One minor problem is that when coastal ostariophysan habitats were studied, for example, in the Chesapeake and Delaware Bays (Schwartz, 1964), it was found that minnows, suckers, and catfishes are all tolerant of some salt. Of the twelve species analyzed, four minnows, a sucker, and two catfishes were found to occur in salinities between 10.7 and 17.6 parts per thousand (ppt.). One catfish, *Ictalurus catus*, lives year-round in salinities to 14.5 ppt. but returns to freshwater to spawn, and Schwartz reported that most species tolerate these salinites for extended periods of time. There are, in addition, marine catfishes, anadromous Asiatic and eastern European cyprinids (Berg, 1949; Okada, 1960), and salt tolerant Middle American and African characoids (Miller, 1966; Chardon, 1967). The major difficulty with the concept is that various secondary division groups, such as cichlids and atheriniforms, have worldwide distributions closely resembling those of the ostariophysans, suggesting therefore that whatever factors have been involved in the distribution of primary division fishes have been equally effective in determining those of secondary division groups.[1] Myers (1949) has put the matter thus: "Secondary fresh-water fishes show, by similarity of their distributional patterns that they usually employ the same methods of dispersion as do primary ones. They are seldom or never present on true oceanic islands, except for a few semimarine members of some of the component families . . . The distributional pattern indicates plainly that most secondary fresh-water fishes are not regularly distributed by sea, but that narrow sea barriers can be crossed." There is, of course, no reason to doubt that freshwater fishes have extended and are now extending their ranges by crossing relatively short distances between nearby islands in areas of island chains or archipelagos as may be the case with the cyprinodontids *Rivulus marmoratus* and *Cyprinodon variegatus* in the Caribbean (Rosen, 1973b), but the evidence so far does not show that the species of *Rivulus* and *Cyprinodon* are more closely related to some Old World forms

[1]And one might note that, among salmoniforms, the anadromous salmonids of North Africa occur entirely north of the South Atlas Fault which demarcates a region originally part of Europe and only later broken away and joined to Africa.

than to those of the New World. An acceptable and detailed phylogeny of all the cyprinodontoids has yet to be produced, but they are still a significant segment of the fish distributions of the world. They may, after all, show us as much, and more, than the ostariophysans, about the history of the earth. Instead of primary and secondary fishes, there seem to me to be only continental and oceanic groups of fishes, as long ago suggested by Boulenger, Pellegrin, and Regan (see Myers, 1949), the assignment to which is determined not by what we imagine to be the habits of the fishes and their possible dispersal mechanisms but by their distribution in relation to phylogeny and in relation to the distributions of other organisms.

LITERATURE CITED

BARDACK, D., AND R. ZANGERL
1971. Lampreys in the fossil record. *In* The biology of lampreys, vol. 1, pp. 67–84.
BERG, L. S.
1949. Fresh water fish of USSR and surrounding country. Vol. II, pp. 467–925. Zool. Inst. Akad. Nauk SSSR, vols. 27, 30.
BREDER, C. M., JR., AND D. E. ROSEN
1966. Modes of reproduction in fishes. Garden City, New York, The Natural History Press, 941 pp.
BRUNDIN, L.
1966. Transantarctic relationships and their significance, as evidenced by chironomid midges. K. Svenska Vetenskaps-akad. Handl., ser. 4, vol. 11, no. 1, pp. 1–472.
CAVENDER, T. M.
1969. An Oligocene mudminnow (family Umbridae) from Oregon with remarks on relationships within the Esocoidei. Occas. Papers Mus. Zool., Univ. Michigan, no. 660, 33 pp.
1970. A comparison of coregonines and other salmonids with the earliest known teleostean fishes. *In* Lindsey, C. C., and C. S. Woods (eds.), Biology of coregonid fishes. Winnipeg, Canada, Univ. Manitoba Press, 560 pp.
CHARDON, M.
1967. Réflexions sur la dispersion des Ostariophysi à la lumière de recherches morphologiques nouvelles. Ann. Soc. Roy. Zool. Belgique, vol. 97, pt. 3, pp. 175–186.
CROIZAT, L.
1952. Manual of phytogeography. The Hague, Netherlands, Uitgeverij Dr. W. Junk, 587 pp.
1958. Pan-biogeography. Vol. 1. The New World. Caracas, pub. by the author, 1018 pp.
DARLINGTON, P. J., JR.
1957. Zoogeography, the geographical distribution of animals. New York, John Wiley and Sons, Inc., 675 pp.
1965. Biogeography of the southern end of the world. Cambridge, Mass., Harvard Univ. Press, 236 pp.
1970. A practical criticism of Hennig-Brundin "Phylogenetic Systematics" and Antarctic biogeography. Syst. Zool., vol. 19, no. 1, pp. 1–18.
DETTMAN, M. E., AND G. PLAYFORD
1969. Palynology of the Australian Cretaceous: a review. *In* Stratigraphy and paleontology. Essays in honor of Dorothy Hill. Australian Natl. Univ. Press, pp. 174–210.
DIETZ, R. S., AND J. C. HOLDEN
1970. The breakup of Pangaea. *In* Continents adrift: readings from Scientific American, publ. 1972, 172 pp.
GILL, T.
1893. A comparison of antipodal faunas. Mem. Nat. Acad. Sci., vol. 6, pp. 91–124.
GOOD, R.
1947. The geography of the flowering plants. London, New York, Toronto, Longmans, Green and Co., 403 pp.
GOSLINE, W. A.
1960. Contributions toward a classification of modern isospondylous fishes. Bull. Brit. Mus. (Nat. Hist.), zool., vol. 6, no. 6, pp. 325–365.
GREENWOOD, P. H., AND D. E. ROSEN
1971. Notes on the structure and relationships of the alepocephaloid fishes. Amer. Mus. Novitates, no. 2473, 41 pp.
GREENWOOD, P. H., D. E. ROSEN, S. H. WEITZMAN, AND G. S. MYERS
1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms. Bull. Amer. Mus. Nat. Hist., vol. 131, art. 4, pp. 339–456.
HENNIG, W.
1966. Phylogenetic systematics. Urbana, Chicago, London, Univ. Illinois Press, 263 pp.
McALLISTER, D. E.
1963. A revision of the smelt family, Osmeridae. Bull. Natl. Mus. Canada, no. 191, biol. ser. no. 71, 53 pp.

McDowALL, R. M.
1964. The affinities and derivation of the New Zealand fresh-water fish fauna. Tuatara, vol. 12, no. 2, pp. 59–67.
1966. Further observations on *Galaxias* whitebait and their relation to the distribution of the Galaxiidae. *Ibid.*, vol. 14, no. 1, pp. 12–18.
1968a. *Galaxias maculatus* (Jenyns), the New Zealand whitebait. Fish. Res. Bull., no. 2, new ser., Fish. Res. Div., New Zealand Marine Dept., 84 pp.
1968b. The status of *Nesogalaxias neocaledonicus* (Weber and de Beaufort) (Pisces, Galaxiidae). Breviora, no. 286, 8 pp.
1969. Relationships of galaxioid fishes with a further discussion of salmoniform classification. Copeia, no. 4, pp. 796–824.
1970. The galaxiid fishes of New Zealand. Bull. Mus. Comp. Zool., vol. 139, no. 7, pp. 341–431.
1971a. The galaxiid fishes of South America. Zool. Jour. Linnean Soc., vol. 50, no. 1, pp. 33–73.
1971b. Fishes of the family Aplochitonidae. Jour. Roy. Soc. New Zealand, vol. 1, no. 1, pp. 31–52.
1972a. The species problem in freshwater fishes and the taxonomy of diadromous and lacustrine populations of *Galaxias maculatus* (Jenyns). *Ibid.*, vol. 2, no. 3, pp. 325–367.
1972b. Are you positive those were whitebait you saw out at sea? Commercial Fishing, August, 2 pp.
1972c. What's in that whitebait net? Fish. Res. Div. Inform. Leaflet, no. 3, 9 pp.
1973. The status of the South African galaxiid (Pisces, Galaxiidae). Ann. Cape Prov. Mus. (Nat. Hist.), vol. 9, pt. 5, pp. 91–101.
McKENNA, M. C.
1973. Sweepstakes, filters, corridors, Noah's arks, and beached Viking funeral ships in paleogeography. *In* Tarling, D. H., and S. K. Runcorn (eds.), Implications of continental drift to the earth sciences. London and New York, Academic Press, vol. 1, pp. 295–308.
McMILLAN, H. M.
1961. An addition to the knowledge of the fish, *Retropinna anisodon* Stokell (Retropinnidae). Trans. Roy. Soc. New Zealand, zool., vol. 1, no. 10, pp. 139–144.
MEES, G. F.
1961. Description of a new fish of the family Galaxiidae from Western Australia. Jour. Roy. Soc. Western Australia, vol. 44, pt. 2, pp. 33–38.
MENENDEZ, C. A.
1971. Floras tererarias de la Argentina. Ameghiniana, vol. 8, nos. 3–4, pp. 357–371.

MILLER, R. R.
1966. Geographical distribution of Central American freshwater fishes. Copeia, no. 4, pp. 773–802.
MYERS, G. S.
1938. Fresh-water fishes and West Indian zoogeography. Ann. Rept. Smithsonian Inst. for 1937, pp. 339–364.
1949. Salt-tolerance of fresh-water fish groups in relation to zoogeographical problems. Bijd. Tot Dierk., vol. 28, pp. 315–322.
1967. Zoogeographical evidence of the age of the South Atlantic Ocean. Studies Trop. Oceanogr., Miami, no. 5, pp. 614–621.
NELSON, G. J.
1967a. Epibranchial organs in lower teleostean fishes. Jour. Zool., London, vol. 153, pp. 71–89
1967b. Branchial arteries of the teleostean fish *Elops hawaiiensis*. Zool. Beitr., new ser., vol. 13, no. 1, pp. 137–148.
1969a. Infraorbital bones and their bearing on the phylogeny and geography of osteoglossomorph fishes. Amer. Mus. Novitates, no. 2394, 37 pp.
1969b. Gill arches and the phylogeny of fishes, with notes on the classification of vertebrates. Bull. Amer. Mus. Nat. Hist., vol. 141, art. 4, pp. 475–552.
1970. Gill arches of some teleostean fishes of the families Salangidae and Argentinidae. Japanese Jour. Ichthyol., vol. 17, no. 2, pp. 61–66.
1972. Cephalic sensory canals, pitlines, and the classification of esocoid fishes, with notes on galaxiids and other teleosts. Amer. Mus. Novitates, no. 2492, 49 pp.
NORDEN, C. R.
1961. Comparative osteology of representative salmonid fishes, with particular reference to the grayling (*Thymallus arcticus*) and its phylogeny. Jour. Fish. Res. Board Canada, vol. 18, no. 5, pp. 679–791.
OKADA, Y.
1960. Studies on the freshwater fishes of Japan. II. Special part. Jour. Fac. Fish., Prefectural Univ. Mie, vol. 4, no. 2, pp. 267–579.
PATTERSON, C.
1970. Two Upper Cretaceous salmoniform fishes from the Lebanon. Bull. Brit. Mus. (Nat. Hist.), geol., vol. 19, no. 5, pp. 205–296.
REGAN, C. T.
1905. A revision of the fishes of the family Galaxiidae. Proc. Zool. Soc. London, pt. 2, pp. 363–384.
ROSEN, D. E.
1973a. Interrelationships of higher euteleostean fishes. *In* Interrelationships of fishes. Jour.

Linnean Soc. London, Zool., vol. 153, suppl. no. 1, 578 pp.

1973b. Cyprinodontoidea. *In* Fishes of the western North Atlantic. Mem. Sears Found. Marine Res., no. 1, pt. 6, pp. 229–262.

ROSEN, D. E., AND P. H. GREENWOOD

1970. Origin of the Weberian apparatus and the relationships of the ostariophysan and gonorynchiform fishes. Amer. Mus. Novitates, no. 2428, 25 pp.

SCHWARTZ, F. J.

1964. Natural salinity tolerances of some freshwater fishes. Underwater Nat., vol. 2, no. 2, pp. 13–15.

SCOTT, E. O. G.

1936. Observations on fishes of the family Galaxiidae: Pt. 1. Papers Proc. Roy. Soc. Tasmania (1935), pp. 85–112.

1966. The genera of the Galaxiidae. Australian Zool., vol. 13, pt. 3, pp. 244–258.

SIMPSON, G. G.

1940. Antarctica as a faunal migration route. Proc. Sixth Pacific Sci. Congr. Vol. 2. Berkeley and Los Angeles, Univ. California Press, pp. 755–768.

STOKELL, G.

1950. A revision of the genus *Paragalaxias*. Rec. Queen Victoria Mus., Launceston, vol. 3, no. 1, pp. 1–4.

1972. Freshwater and diadromous fishes of New Zealand. Canterbury Mus., bull. no. 5, 48 pp.

VLADYKOV, V. D.

1941. The structure of the anal fin in the capelin, *Mallotus*, Osmeridae. Nat. Canadien, vol. 68, nos. 8, 9, pp. 193–207

1963. A review of salmonid genera and their broad geographical distribution. Trans. Roy. Soc. Canada, vol. 1, ser. 4, sect. 3, pp. 459–504.

WEITZMAN, S. H.

1962. The osteology of *Brycon meeki*, a generalized characid fish, with an osteological definition of the family. Stanford Ichthyol. Bull., vol. 8, no. 1, pp. 1–77.

WHITLEY, G. P.

1956. The story of *Galaxias*. The Australian Mus. Mag., March 15, 1956, pp. 30–34.

WILEY, M. L., AND B. B. COLLETTE

1970. Breeding tubercles and contact organs in fishes: their occurrence, structure, and significance. Bull. Amer. Mus. Nat. Hist., vol. 143, art. 3, pp. 143–216.

WOODS, C. S.

1968. Variation and taxonomic changes in the family Retropinnidae (Salmonoidea). New Zealand Jour. Marine Freshwater Res., vol. 2, no. 3, pp. 398–425.