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On Müller's and Cuvier's Concepts of Pharyngognath and Labyrinth Fishes and the Classification of Percomorph Fishes, with an Atlas of Percomorph Dorsal Gill Arches

DONN E. ROSEN¹ AND COLIN PATTERSON²

Foreword (Colin Patterson)

Donn Rosen's ambition, during the last decade and more of his life, was to crack the problem of the Perciformes, by far the largest and most diverse "order" of fishes. Humphry Greenwood and I first asked him to tackle the job back in 1970, for the "Interrelationships of Fishes" meeting held in London in 1972. Donn took some persuading, but at length agreed ("from now on, it's spines in the chowder"—letter, 1971). The work for that paper led him for the first time into the anatomy of the dorsal part of the pharynx, and of the dorsal gill arches in particular. As might have been predicted, the problem of the Acanthopterygii, and the Perciformes in particular, turned out to involve all or most of the Euteleostei. So Donn's paper on acanthopterygians became a study of higher

euteleosts whose objective was "to lay a foundation for future analysis of the Acanthopterygii" (Rosen, 1973: 398); and its conclusion was that acanthopterygians may be defined by two features of the dorsal gill arches, but that Perciformes possess no known synapomorphies, and so may not be monophyletic.

During the rest of the 1970s, Donn was occupied with other things, notably the revolution in biogeography (Rosen, 1975, 1978, 1979; Nelson and Rosen, 1981), but by early 1981 he was ready for another frontal assault on the perciforms, and had an NSF grant "to convert my office into a percomorph factory" (letter, April 1981). Within a year, "the percomorph problem has re-expanded into the neoteleost problem once again, so I'm looking at all paracanthopts, beryciforms, and myctophids in addition" (letter, March 1982).

¹ Curator, deceased 1986, Department of Ichthyology, American Museum of Natural History.

² Research Associate, Department of Ichthyology, American Museum of Natural History; Department of Palaeontology, British Museum (Natural History), London SW7 5BD.

Out of this grew another review of higher euteleosteans (Rosen, 1985), a revision of paracanthopts (Patterson and Rosen, 1989), and one effort to tackle the perciforms by attrition rather than frontal assault (Rosen, 1984).

In the spring of 1983, he underwent his first bout of brain surgery. His recovery from that seemed excellent, and within a year he visited London to continue our joint work on paracanthopts. But he did not fully recover the use of his left hand, which meant that he could no longer easily carry out the microdissections of cleared-and-stained fishes in the glycerin dish which for him "was the crucible in which truth had to leave its residues" (Nelson et al., 1987). He was not short of material, however, for in the "percomorph factory" in the two years before his illness he had assembled a large collection of pencil drawings, of dorsal gill arches in particular, and as Nelson et al. (1987) said, "Typically, he would accumulate the drawings and then write the manuscript to fit them." The following paper was begun in that way in summer 1985, after his recovery from the first surgery, and was taken up again after the second operation, which occurred in the fall of 1985, a year before his death. In those circumstances, it is not surprising that he felt the need for the other characteristic of his working method noted in Nelson and other's obituary: "by nature he preferred collaboration." He turned to two of his oldest collaborators, Humphry Greenwood and myself, and to one of his youngest, Melanie Stiassny, now his successor at the AMNH; each of us was shown drafts of the work in progress, and was asked to join him. Working with Donn in those days, in late 1985 and 1986, was no picnic, and perhaps we may each be forgiven for not accepting Donn's request for help with the total commitment that he gave to this project during what remained of his life. I spent two periods with him in early 1986, in February and in April, and it was clear that he held on to the project as his lifeline back to scientific well-being during those last difficult months.

The manuscript, as Donn left it, consisted of about 80 pages of typescript and almost 150 drawings, arranged in 47, mostly com-

pound, figures. There seemed to me to have been two principal impulses behind the work. The first is an idea characteristic of the development of pattern cladism: that preevolutionary systematists such as Müller and Cuvier, unrestricted by theory, might have had a better insight into broad patterns of relationship than Donn's contemporaries. The second is the belief that those contemporaries, particularly recent contributors on Labroidei \approx Müller's Pharyngognathi acanthopterygii), tended to be too narrowly focused in their view of a problem and not ready enough to cast the net of investigation more widely. But Donn would have been ready to admit that his own approach to the problems was limited in different ways, principally by his physical handicap, which made not only dissections but his character and literature surveys more casual than they would once have been.

Since Donn died, there have been a number of important contributions to the perciform problem, and to pharyngognaths in particular. Most notable is Stiassny and Jensen's (1987) review of labroid interrelationships, which was dedicated to Donn's memory and in which his manuscript was acknowledged as a thought-provoking impetus. Sadly, I found that this work had removed much of the stuffing from Donn's manuscript, for one of his principal conclusions, in turn the stepping-stone for further speculation, was that the Labroidei of Kaufman and Liem (1982) and Stiassny and Jensen (1987) (Cichlidae, Embiotocidae, Pomacentridae, Labridae, Odacidae, Scaridae) might not be monophyletic. In particular, Donn argued that certain "percoid" groups (Girellidae, Kyphosidae, Scorpididae) are more closely related to embiotocids than to other labroids, and he also suspected that the Sparoidea and Haemuloidae of Johnson (1980), together with the Gerreidae, might be more closely related to the Labridae, Odacidae, and Scaridae than are cichlids, embiotocids, and pomacentrids. As he would surely have acknowledged, his potential apomorphies favoring those views are thin on the ground and I was unable further to substantiate them, whereas Stiassny and Jensen's (1987) survey of labroid characters, although it does not close the book on the

matter, leaves little room for Donn's hypotheses. With them removed, the substance of his manuscript was much reduced, but I have included his accounts of the character complexes which he thought bore on the problem. The paper also included a general cladogram covering the Acanthomorpha. This incorporated a number of novel ideas, most notably that myctophids, polymixiids, paracanthopts, and atherinomorphs are more closely related to higher perciforms than are holocentrids and basal percoids. These ideas were not convincingly supported by characters, whereas they are contradicted by characters cited by Johnson (1984), Stiassny (1986), and others. I therefore omitted the cladogram and the text referring to it, but have deposited it, together with a copy of the manuscript as Donn left it, in the Dean Library of the Department of Ichthyology in the American Museum of Natural History.

In reworking the manuscript for publication, I have incorporated references to more recent work, have rewritten the historical surveys, rewritten, reorganized or omitted major parts of the main text, and added a few figures and observations based on my work. In the original manuscript there was no mention of *Pholidichthys leucotaenia* Bleeker, the only member of the Pholidichthyidae. *Pholidichthys* is a superficially blennylike fish which is remarkably similar to the labroids in a number of features of gill-arch structure (Springer and Freyhof, 1976; Stiassny and Jensen, 1987: 294); I do not know whether it was omitted by intention or accident, but since I have no access to material and can add nothing to Springer and Freyhof's (1976) description and discussion or Stiassny and Jen-

sen's (1987) comment, I have not added any reference to it. In a revision of this sort, there is a problem with the first person singular in statements like "I have found," "I conclude," or "my own studies": these are left as written, with the implication that the "I" or "me" concerned in the main text is Donn Rosen. I have also left the bulk of the figures as they were, in the belief that the paper will have lasting value as an atlas of osteology, particularly of the dorsal gill arches, in a wide range of perciforms. As it now stands, the paper is less the radical reorganization that Donn planned, and more a critique of recent work on various perciform groups; it points out incongruent or questionable characters, rather than presenting a new synapomorphy scheme. Nevertheless, I believe it deserves a place in the literature.

For help and hospitality during the work, I am grateful to all the members of the Department of Ichthyology in the American Museum of Natural History, in particular to Gareth Nelson and Melanie Stiassny, also to Stan Blum in the Department of Vertebrate Paleontology, and above all to Donn's widow, Mel Rosen, whose fortitude and dedication are beyond my praise. In London, Humphry Greenwood and Gordon Howes have been generous with time and advice. Finally, I thank Dave Johnson for a most thorough and sensitive review of the manuscript. I regret that I have been unable to come up with rational responses to several of his comments; yet I found myself unable to respond by further excision, which would have removed too much of the flavor of what Donn, with such effort, was striving toward.

ABSTRACT

A review of the anatomy of the buccal and pharyngeal jaws, basicranial specializations associated with the pharyngeal jaws, and palatal musculature attaching to the prootic and parasphenoid bones has led to a reevaluation of some percomorph relationships that extends and supports the recent work of Johnson (1984), G. Nelson (1967, 1969), Stiassny (1986, Stiassny and Jensen, 1987), Lauder and Liem (1983), and some older taxonomic concepts of Müller, Günther, Gill, and Cuvier.

The concept of a Pharyngognathi, in particular,

is supported to include the labroids, and the sparoids and haemuloids, and also the gerreids, kypopsids, scorpidids, and girellids.

The problem of the Labyrinthici is also reviewed because certain aspects of their anatomy, especially in anabantoids, have been considered pharyngognathous. The group is considered correctly to include the Anabantidae, Nandidae, Badidae, Osphronemidae, Belontiidae, Helostomidae, Channidae, Synbranchidae and Luciocephalidae, and perhaps the Mastacembelidae.

The Acanthomorpha as redefined by Stiassny (1986) are reduced to 10 branches with a few polychotomies that need to be tied to each other and to the percoid residue discussed by Johnson (1984).

Recent predictions that these large problems are beyond the scope of present investigation and resolution appear overly pessimistic.

INTRODUCTION

Merely corroborative detail, intended to give artistic verisimilitude to an otherwise bald and unconvincing narrative (Pooh-Bah to Pitti-Sing).

[From the complete libretto of *The Mikado*, p. 152 of *The Best Known Works of W. S. Gilbert*; Arden Book Co., J. J. Little and Ives Co., New York.]

The above quotation captures the spirit of what has been written more recently as elaborations on Müller's (1844, 1845, 1846) and Cuvier's (1828, 1831, in Cuvier and Valenciennes, 1828–1849) casually formulated concepts of pharyngognath and labyrinth fishes, and captures also the spirit of what I have to say below about those recent elaborations. It seems that, although Cuvier's and Müller's narratives were bald by modern standards, they were far from unconvincing since ichthyologists have found these group concepts apt, at least in part.

For more than a century percoid fishes have posed a taxonomic challenge to ichthyologists concerned with producing a resolved hierarchical classification of monophyletic taxa. As understood by Regan (1913), the percoids constitute a suborder that includes 12 form-groups encompassing 82 families. One of Regan's form-groups is the division Perciformes, recognized today as the suborder Percoidae, which contained 49 of his 82 percoid families. Regan's concept of this group was based only on symplesiomorphy since he referred to the percoids as a whole as "the most generalized suborder, defined by the absence of the special peculiarities which characterize the other suborders of the Percomorpha," thus appealing openly to the absence of information. Regan's percoid classification was a retrogressive step in our understanding of fish relationships, since some of the taxa in his basal Perciformes have long been grouped in such subsequently corroborated assemblages as the Pharyngognathi of Johannes Müller (1844, 1845, 1846), who was explicit about his intent in producing a natural system.

Even though Müller's classification had been supported, in part, and enlarged upon

by subsequent investigations, many taxonomists continued to use Regan's system almost unchanged (e.g., Berg, 1940; Greenwood et al., 1966; Gosline, 1971; McAllister, 1968). In contrast, Jordan (1923) used a modified version of the Pharyngognathi, and such recent studies as those by G. Nelson (1967), Stiassny (1981, 1982; Stiassny and Jensen, 1987), Liem and Greenwood (1981), and Lauder and Liem (1983) have illustrated the general usefulness of Müller's conceptions.

The work reported here started with a study of the dorsal gill arches and supports, in part, Müller's original notions. Müller's (1844, 1845, 1846) Pharyngognathi comprised two suborders, Ph. acanthopterygii, and Ph. malacopterygii: the first contained three families, Labroidei cycloidei, Labroidei ctenoidei, and Chromides; the second contained the family Scomberesoces. The gill arch character cited as uniting them was "the lower hyoid bones united" (p. 533 in Griffith's 1846 translation). Commenting on this arrangement, Günther (1862: iii) wrote "I fully share the opinion of those who do not consider the coalesced pharyngeal bones as a character of sufficient importance to unite acanthopterous and malacopterous fishes into one Order, I have changed the name of Pharyngognathi acanthopteri into Acanthopterygii pharyngognathi." Within that order, Günther placed five families: Pomacentridae (= Müller's Ph. ctenoidei), Labridae (= Müller's Ph. cycloidei), Embiotocidae, Gerr[e]idae (placed "near the Embiotocidae"), and Chromides. Gill (1872: xiii) commented that Müller's pharyngognath character, united pharyngeal bones, "would violently divorce forms from their natural allies, and . . . was one liable to recur in very dissimilar groups, and not . . . a tech-

nical expression of a natural group." Gill's Pharyngognathi (1872: 6) differed from Günther's in only two minor details; Chromides were renamed Cichlidae, and Labridae were split into three families, Labridae, Scaridae, and Gill's own (1863) monotypic Siphonognathidae. Günther (1880) later modified the content of his Pharyngognathi by removing Gerreidae (*Gerres* only) to the Percidae.

In Boulenger's classification (1904a, 1904b), the Pharyngognathi were no longer maintained as a separate group. Günther's and Gill's pharyngognath families were placed in the division Perciformes, first of nine subgroups in the Acanthopterygii. Within the Perciformes, Boulenger separated the Pomacentridae, Labridae, and Scaridae from the remainder by their possession of 3½ gills instead of four. Among the four-gilled Perciformes, he listed Embiotocidae and Cichlidae next to the last three families, but put the Gerreidae close to the Percidae. Goodrich (1909) returned to a more explicit system in retaining Pharyngognathi (as a "sub-tribe" within the Perciformes). His five pharyngognath families were divided into three groups, Pomacentridae + Cichlidae, Embiotocidae alone, and Labridae + Scaridae. Jordan's (1905, 1923) arrangement was akin to Goodrich's: his Chromides included Pomacentridae and Cichlidae, with (1923) a third family for the Eocene †*Priscacara*; his Pharyngognathi contained the Labridae and Scaridae, with (1923) the †Phyllodontidae and five other families split from among the labrids and scarids of which only the Odacidae are still recognized; and his Holconoti contained the Embiotocidae alone. Jordan's Chromides, Pharyngognathi, and Holconoti were placed as three neighboring suborders in 1905, and raised to ordinal rank in 1923.

Regan's (1913) influential classification of percoids resembled those of Goodrich and Jordan in two respects. First, he isolated the Labridae, Scaridae, and Odacidae in a division Labriformes; and second, he isolated the Embiotocidae in a division Embiotociformes. However, Regan separated the Pomacentridae from the Cichlidae, maintaining a division Pomacentriformes for pomacentrids alone, and leaving cichlids in his basal division Perciformes. Regan's treatment of embiotocids is inconsistent in his synopsis (p.

112) and his main text (p. 131): in the former they are called Embiotociformes and placed after the Labriformes, whereas in the latter they are separated from Labriformes by the Pomacentriformes and are named Ditremiiformes. Regan wrote (p. 131) that "The 'pharyngognathous' fishes . . . form three well-marked and probably not specially related groups, which resemble each other in the ankylosis of the lower pharyngeals. . . . Were it not for this all three would be included in the division Perciformes, since their external and anatomical characters are those of typical perciform fishes." Regan made a similar comment—"three distinct and apparently unrelated groups" in his 1929 classification. Berg (1940) repeated Regan's classification, ranking the three pharyngognath groups as superfamilies.

The next major classification of teleosts, Bertin and Arambourg's (1958), recognized the Pharyngognathi as a suborder Labroidei, containing the four families Pomacentridae, Embiotocidae, Labridae, and Scaridae. The first of these families was called "un terme de passage" between Cichlidae and the last two. Greenwood et al. (1966) wrote the first major classification entirely to omit any pharyngognathous grouping: the suborder Labroidei was maintained, but it contained only the Labridae, Odacidae, and Scaridae; the pharyngognathous embiotocids and pomacentrids were relegated to the Percoidei, where they are placed on either side of the Cichlidae. McAllister (1968) retained a more Regan-or Berg-like classification, with three pharyngognathous suborders, Embiotocoidi, Pomacentroidei, and Labroidei. Perhaps in recognition of Regan's comments on lack of relationship between the three, the third is separated from the first two by several other groups. Gosline (1971) used a classification much like Regan's and Berg's, with adjacent superfamilies Embiotocoidae, Pomacentroidae, and Labroidae placed at the end of his Percoidei. J. Nelson (1984) adopted a scheme like that of Greenwood et al., recognizing a suborder Labroidei (Labridae, Odacidae, Scaridae), but leaving Embiotocidae and Pomacentridae in the basal Percoidei, where they are placed next to Cichlidae.

The modern works summarized in the last paragraph express the precladistic phase of

TABLE 1
Historical Summary of Classifications of Pharyngognath Fishes

Müller, 1846	Suborder Pharyngognathi acanthopterygii Families Labroidei cycloidei, Labroidei ctenoidei, Chromides
Günther, 1862	Order Acanthopterygii pharyngognathi Families Pomacentridae (= Müller's Ph. ctenoidei), Labridae (= Müller's Ph. cycloidei), Embiotocidae, Gerreidae, Chrom- ides
Gill, 1872	Superfamily Pharyngognathi Families Pomacentridae, Embiotocidae, Gerreidae, Cichlidae (= Müller's Chromides), Labridae, Scaridae, Siphonognath- idae
Goodrich, 1909	Sub-tribe Pharyngognathi Families Pomacentridae, Cichlidae, Embiotocidae, Labridae, Scaridae
Jordan, 1923	Order Holconoti Families Embiotocidae, Hysterocarpidae Order Chromides Families Pomacentridae, †Priscacaridae, Cichlidae Order Pharyngognathi Families †Phyllodontidae, Labridae, Coridae, Neolabridae, Spar- isomidae, Scaridae, Odacidae, Siphonognathidae
Regan, 1929	Division Embiotociformes Family Embiotocidae Division Pomacentriformes Family Pomacentridae Division Labriformes Families Labridae, Odacidae, Scaridae
Berg, 1940	Superfamily Embiotocoidae Family Embiotocidae Superfamily Pomacentroidae Family Pomacentridae Superfamily Labroidae Families Labridae, Odacidae, Scaridae
Bertin and Arambourg, 1958	Suborder Labroidei Families Pomacentridae, Embiotocidae, Labridae, Scaridae
Greenwood et al., 1966, J. Nelson, 1984	Suborder Percoidei Families Embiotocidae, Cichlidae, Pomacentridae [and many others] Suborder Labroidei Families Labridae, Odacidae, Scaridae

fish systematics. The trend, in the 140 years summarized in table 1, has been to play down the pharyngeal jaw character first recognized by Müller, as convergence or parallelism, and to dissociate the fishes that he and Günther grouped by means of that character. The Labroidei (Müller's Pharyngognathi cycloidei; Günther's Labridae) survived, but the Pomacentridae (Müller's Pharyngognathi ctenoidei), Cichlidae (Müller's Chromides),

Embiotocidae, and Gerreidae were not grouped with them.

The first attempt to apply cladistic principles, or grouping by synapomorphy, among pharyngognaths was G. Nelson's (1967) study of gill arches. He found no support for Tarp's (1952) proposal that the closest relatives of embiotocids are Girellidae, but did find dorsal gill-arch features, additional to the fused fifth ceratobranchials, relating pomacentrids

and embiotocids (in that sequence) to labroids. Stiassny (1981) found further gill-arch apomorphies relating the other members of Müller's and Günther's pharyngognaths—Gerreidae and Cichlidae—to Nelson's assemblage. Stiassny found that these apomorphic features showed a mosaic distribution, with certain characters relating cichlids more closely to embiotocids and labroids, others relating cichlids to embiotocids, and at least one other (microbranchiospines) relating gerreids and cichlids. She also found indications that the Sparidae might be related to pharyngognaths.

Liem and Greenwood (1981) provided the first justified phylogenetic hypothesis of pharyngognath fishes. They proposed that labroids are monophyletic, that their sister group is Cichlidae + Embiotocidae, and that each of those families is monophyletic. Liem and Greenwood considered pharyngognathy in pomacentrids, girellids, sciaenids, and also in anabantoids, concluding (p. 98) "we reject the hypothesis that any of the other pharyngognathous acanthopterygians are related" to their group. Kaufman and Liem (1982) revised this conclusion and proposed a new hypothesis, summarized in a cladogram in which embiotocids are the sister group of labroids (rather than of cichlids), cichlids are the sister group of embiotocids + labroids, and pomacentrids are the sister group of that assemblage. They named the whole group Labroidei [it is in fact Günther's (1862) Pharyngognathi, minus gerreids], renaming the old Labroidei by lumping Labridae, Odacidae, and Scaridae in Labridae. Accepting that, in the rest of his paper the expanded Labridae of Kaufman and Liem is called the Labridae KL to distinguish it from the restricted Labridae of previous authors. Only two incongruent characters are mentioned in Kaufman and Liem's paper: the unification of the lower pharyngeals and their dentition in pomacentrids, a feature that must be homoplastic in their scheme since cichlids retain unfused lower pharyngeals without symphysial teeth; and pharyngocleithral joints in pomacentrids and Labridae KL. As possible relatives of their labroid assemblage ("one of which may represent the primitive sister group of the Labroidei") Kaufman and Liem mentioned

kyphosids, sciaenids, gerreids, and pomadasysids, and certain anabantoids, centrarchids, and carangids.

Stiassny and Jensen (1987) reexamined the implications of pharyngognathy in acanthomorphs, and produced a better supported and more carefully argued scheme than did their predecessors. A PAUP analysis of 15 characters in the four families comprising Kaufman and Liem's (1982) Labroidei (Cichlidae, Embiotocidae, Pomacentridae, Labridae KL) generated a single most parsimonious tree differing from its predecessors in placing cichlids as the sister group of other labroids, and embiotocids as the sister of Pomacentridae + Labridae KL. Eight out of the 15 characters are homoplastic on this tree. The tree requires 23 steps, whereas Liem and Greenwood's (1981) and Kaufman and Liem's (1982) schemes require, respectively, 29 and 26 steps with Stiassny and Jensen's characters. A tree differing from Stiassny and Jensen's by reversing the position of pomacentrids and embiotocids requires 24 steps.

Stiassny and Jensen (1987), like Liem and Greenwood (1981) and Kaufman and Liem (1982), were interested primarily in labroid monophyly and intrarelationships, but they mentioned previous conjectures of relationship between various labroids and other teleosts. These include Tarp's (1952: 16) proposition that the Girellidae are "the closest living relatives of the Embiotocidae"; Morris's (1982) suggestion that pomacentrids and embiotocids are sister groups with the Scorpididae as possible ancestors (implying that all or some scorpidids might be the sister group of the two pharyngognath families); Stiassny's (1981) note of labroidlike upper pharyngeal features in Sparidae and Gerreidae; and Stiassny and Jensen's (1987) reported of united fifth ceratobranchials in some leiognathids.

Thus recent cladistic studies have reemphasized the reality of the Pharyngognathi of Müller and Günther, and the search for the sister group of that assemblage, though hardly undertaken yet, might be directed toward the nonpharyngognath families mentioned in the work summarized above: Carangidae, Centrarchidae, Gerreidae, Girellidae, Kyphosidae, Leiognathidae, Pomadasysidae,

Sciaenidae, Scorpididae, Sparidae, and some anabantoids. The various percoid families named bring in one of the great unsolved problems in systematic ichthyology, interrelationships among Regan's Percoidei; and some of these percoids and the anabantoids bring in two other ancient groups, Cuvier's Squamipinnes and Labyrinthici. Concerning the first of these three groups, the Percoidei, recent studies, notably those of Johnson (1980, 1984, 1986; Tyler et al., 1989), have begun to impose some order on chaos. Johnson (1980) argued that the Sparidae are related to Centranchidae, Lethrinidae, and Nemipteridae in a monophyletic Sparoidea. In 1984 Johnson proposed (p. 496) that Carangidae form a monophyletic Carangoidea with the Coryphaenidae, Echeneidae, Nematistiidae, and Rachycentridae; and (p. 469) that the Scorpididae and Girellidae may be sister groups. Mok and Shen (1983) proposed that the Kyphosidae (in which they included Scorpididae and Girellidae) are the sister group of Toxotidae, and that those two families are related successively to the Enoplosidae and Monodactylidae. For Mok and Shen these four families are members of Cuvier's (1828, in Cuvier and Valenciennes, 1828–1849) Squamipinnes, and are the sister group of the remainder of this group. However, Tyler et al. (1989) have criticized both the descriptive work and the conclusions of Mok and Shen (1983) (see further below on Squamipinnes).

Concerning the anabantoids, some of which might be nonpercoid relatives of the Pharyngognathi, Liem and Greenwood (1981) used the concept of pharyngognathy in a purely descriptive sense to include all cases in which powerful pharyngeal jaws are present (e.g., sciaenids); they thus brought labyrinth fishes into the discussion because of the branchial-parasphenoid bite. Not all labyrinth fishes have parasphenoid teeth or a single (median) lower pharyngeal jaw. But anabantoids form a monophyletic group defined, in part, on the dorsal gill arch specializations discussed below. Liem and Greenwood (1981) presented an analysis of teleosts with a bite involving the parasphenoid dentition, and concluded that the anabantoid condition is derived, differing from the primitive teleost condition and from that in other acanthomorphs with

parasphenoid teeth (*Pristolepis*, *Nandus*, *Badis*, *Channa*) in "muscular, neuronal and biomechanical" features so that "pharyngognathy in the Anabantoidei represents a uniquely specialized character complex both functionally and morphologically."

Among workers previously concerned with the problem of what pharyngognathy might mean taxonomically, there is significant disagreement about which taxa should be included in a larger group with labrids and with anabantoids. Within a labroid clade, questions about including pomacentrids, girellids, sciaenids, sparids, and gerreids have been raised. And, based on my own studies, I would include haemulids on that list. Johnson's (1980) concepts of Sparoidea and Haemuloidea suggest that centranchids, nemipterids, lethrinids, and inermiids might also be implicated in the pharyngognath problem.

So far as labyrinth fishes are concerned, previous work has dealt with comparisons among such family-level groups as luciocephalids, channids (= ophicephalids), helostomatids, osphronemids, belontiids, synbranchids, pristolepids, nandids, badids, anabantids, and mastacembelids. Travers (1984) has written extensively on the anatomy and relationships of the last family, but, in my view, the position of mastacembelids is still problematical.

In addition to the 22 nominal families discussed above, I have examined representatives of the Leiognathidae and the two species of †*Priscacara* from the Green River Eocene, the latter genus primarily because it had been included by Jordan (1923) in his Chromides next to cichlids and pomacentrids [however, Cavender (1986) referred *Priscacara* to the Percichthyidae]. The position of †*Priscacara* remains uncertain, but of the two known species, one (†*P. serrata*) has a well-developed lower pharyngeal jaw (LPJ) with molariform teeth, which is, perhaps, why Jordan included it. The LPJ and UPJ of the other species is not known.

I do not know if some of the above 24 higher taxa are monophyletic. In consequence, I have tried to examine species belonging to type genera for the family group names. By so doing, I hope to minimize future taxonomic confusion resulting from the cladistic arrangement of families that later

prove to be nonmonophyletic. For example, assignment of the Cichlidae based on *Cichla*, Pomacentridae on *Pomacentrus*, Haemulidae on *Haemulon*, etc. might be less troublesome nomenclaturally if the family groups are shown to be unnatural. I have also assumed that previous authors considered certain family-group taxa because they foresaw the possibility of a relationship among them. Some of these hypotheses of relationship were advanced confidently, others tentatively, but here they all were treated with equal regard during a search for characters amongst the entire AMNH collection of acanthomorph skeletons.

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ABBREVIATIONS

For materials examined, see figure captions.

Institutional

AMNH	American Museum of Natural History
ANSP	Academy of Natural Sciences, Philadelphia
BMNH	British Museum (Natural History)
UMMZ	Museum of Zoology, University of Michigan
USNM	United States National Museum

Illustrations

ACC	accessory cartilage of unknown significance in dorsal gill arches
ACH	anterior ceratohyal
ACL	area on LPJ for articulation with cleithrum

AP	adductor arcus palatini process on parasphenoid
APP	anterior part of autopalatine
ARPR	articular process on UPJ (PB3)
BB1-3	(ossified) basibranchials
BH	basihyal
BRR	branchiostegal rays
C1-5	ceratobranchials
DHH	dorsal hypohyal
E1-4	epibranchials
FM	foramen magnum
FSB	fenestra in wall of otic bulla contacting swimbladder
GR	modified gill-raker
H1-4	hypobranchials
IAB	interarcual bone (ossified IAC)
IAC	interarcual cartilage
LIG	ligament
MC	mental cirrus
MDC	dorsal crest on maxilla
MDP	dorsal maxillary process
NA	nasal
PAD	pad of soft connective tissue
PB1-4	pharyngobranchials
PCH	posterior ceratohyal
PHA	pharyngeal apophysis on basicranium
PMPR	combined articular and ascending premaxillary processes
PSP	parasphenoid
PTF	posttemporal fossa
TP3,4	dermal toothplate of third or fourth pharyngobranchial
TPE2,3	dermal toothplate of second or third epibranchial
VHH	ventral hypohyal

PHARYNGOGNATH RELATIONSHIPS

LOWER AND UPPER PHARYNGEAL JAWS: Pharyngognath in its original usage by Müller (1844, 1845) derived from the observation that the fifth ceratobranchials in some fishes were enlarged, strongly dentigerous, and joined in the midline to form a single triangular bone (figs. 1–3) opposed by toothplates fused to the pharyngobranchials (figs. 4, 5). In later studies by Stiassny (1981, 1982; Stiassny and Jensen, 1987), Liem and Greenwood (1981), and Kaufman and Liem (1982) these two features were referred to, respectively, as the lower pharyngeal jaws (LPJ) and upper pharyngeal jaws (UPJ). These workers noted also that the UPJ bears a dorsal articulating process (ARPR) on the third pharyngobranchial (PB3) which directly contacts a

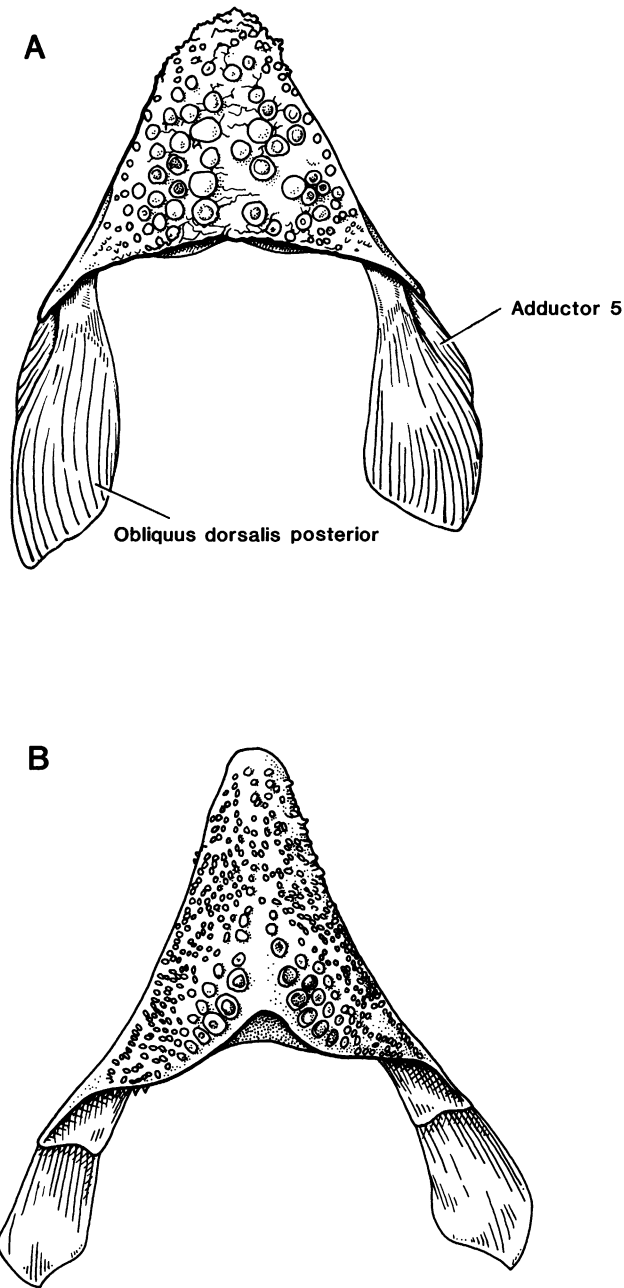


Fig. 1. Lower pharyngeal jaws (united fifth ceratobranchials) of two gerreids; A, *Gerres cinereus* (Walbaum), AMNH 21732, B, *Gerres lineatus* (Cuvier and Valenciennes), AMNH 12020, in dorsal view.

corresponding basicranial apophysis on the parasphenoid or parasphenoid and basioccipital (Greenwood, 1978); this condition is defined as a diarthrosis. In addition the LPJ is functionally a single structure that is slung

from the basicranium by modified dorsal gill arch muscles (variably developed in pomacentrids: Stiassny and Jensen, 1987: 284), and has a characteristic median ventral keel that is continuous with a pair of lateral struts or

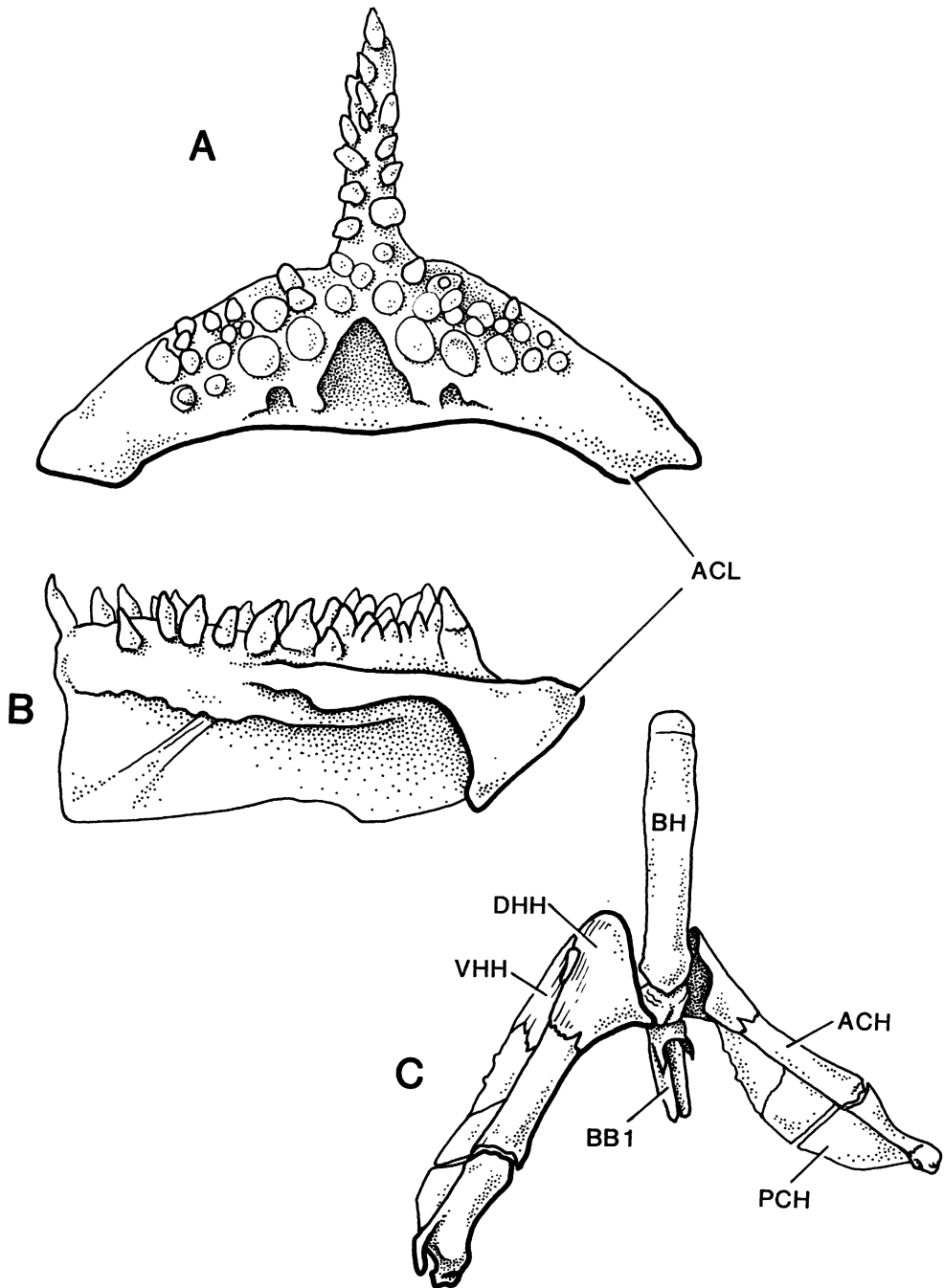


Fig. 2. Lower pharyngeal jaws (fused fifth ceratobranchials) and hyoid skeleton in the labrid *Hali-choeres bivittatus* (Bloch), AMNH 23598. A, B, LPJ in dorsal view, anterior up, and left lateral view; C, ventral hyoid skeleton in dorsolateral view, anterior up.

“horns” (figs. 1, 3; Stiassny and Jensen, 1987: figs. 1, 3). As a consequence of the studies by Stiassny and Liem and their co-workers, and

G. Nelson (1967), it now is clear that the characteristic features of the LPJ and UPJ mentioned above define a group including

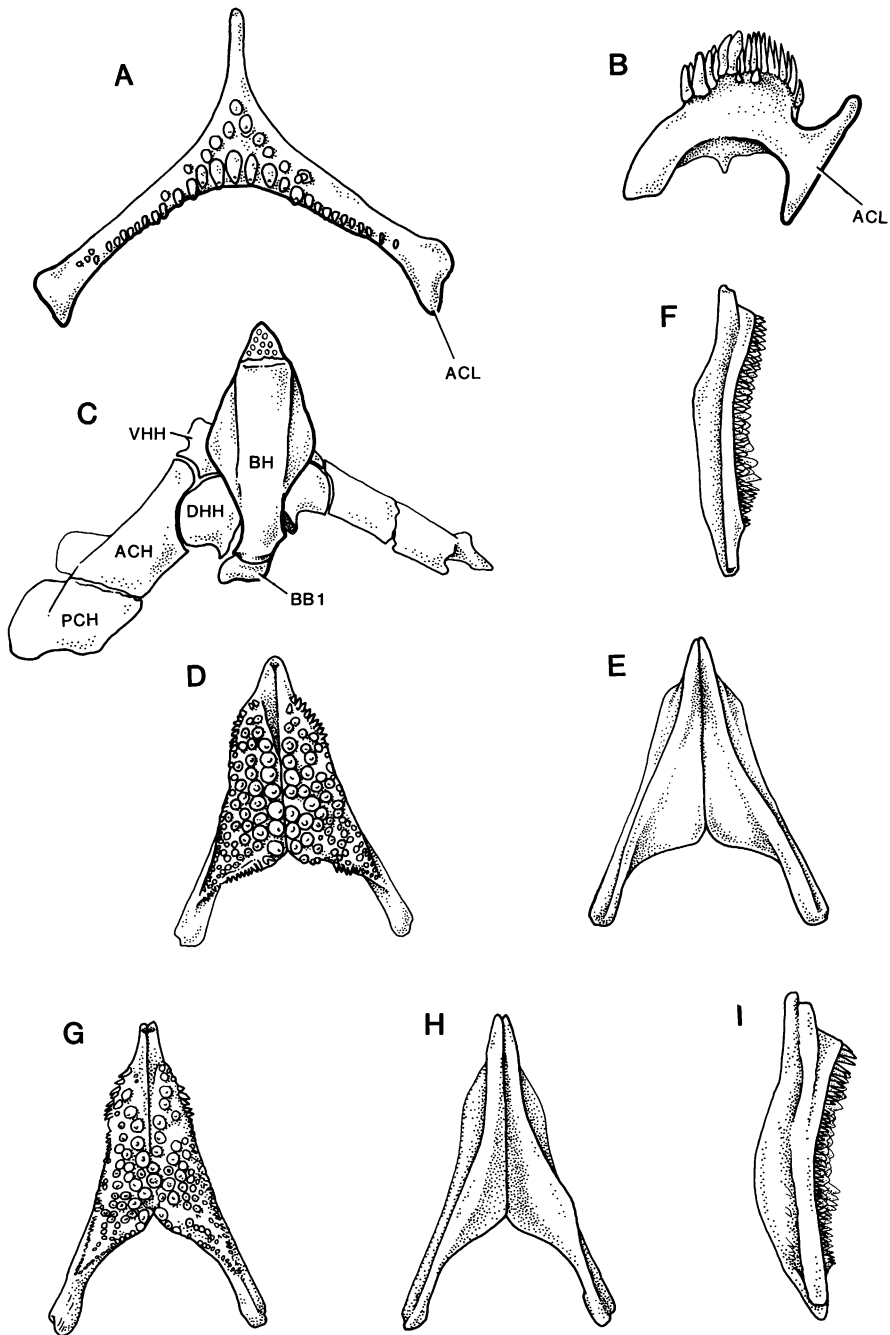


Fig. 3. Lower pharyngeal jaws (LPJ) in a pomacentrid (A–C) and two haemulids (D–I). A–C, *Pomacentrus planifrons* Cuvier, AMNH 23632, A, dorsal view of fused fifth ceratobranchials, anterior up, B, left lateral view of same, C, ventral hyoid skeleton in dorsolateral view, anterior up. D–F, LPJ of *Haemulon carbonarium* Poey, AMNH 30825, in D, dorsal, E, ventral, and F, left lateral view, anterior up in each. G–I, LPJ of *Haemulon album* Cuvier and Valenciennes, AMNH 30827, views as in D–F.

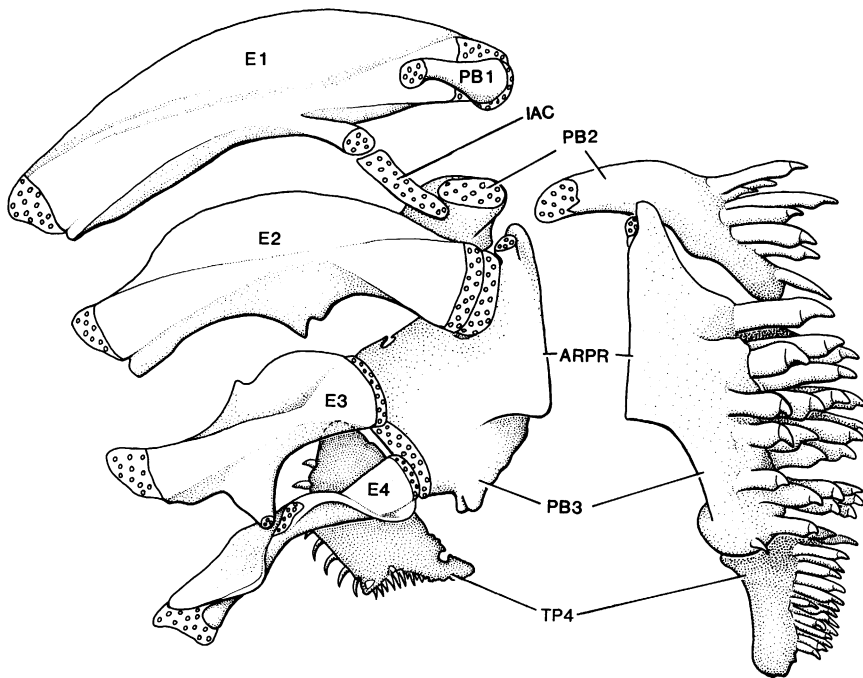


Fig. 4. Left dorsal gill arches of the gerreid *Eucinostomus gula* (Quoy and Gaimard), AMNH 17764. Dorsal view (left) and medial view of PB2-4 (right). Note the platelike flanges along the anterior margin of E1 and E2, a possible precursor of the anterior extension of these bones in cichlids and pomacentrids (fig. 18), and the typical pharyngognath teeth with concave tips and constricted bases.

Labridae KL, embiotocids, pomacentrids, and cichlids. Other groups of teleosts also have LPJ of pharyngognath type (e.g., Belontiiformes, which Müller included in his Pharyngognathi as Pharyngognathi malacopterygii). In general, these lack the muscular sling and characteristic median ventral keel and lateral struts mentioned above, but among belontiiforms Stiassny and Jensen (1987) reported a median keel in exocoetoids, and in hemiramphids and exocoetids a muscular sling "simulating the labroid configuration in remarkable detail" (p. 284). Not all cichlid fishes show these ventral LPJ features. Machado-Allison (1973) and Stiassny (1982) illustrated the LPJ of *Cichla*, showing that a single median keel is not present as a simple consequence of the failure of the right and left ceratobranchials to suture posteriorly, where the two bones are not in contact. Among adult labroid fishes only cichlids retain anatomical evidence of the paired origin of the LPJ, either because the two halves are incompletely joined (as in *Cichla*), or because

a suture between them is visible. The LPJ of other labroids shows no such signs of a bilateral origin, and suggests, therefore, that derived characteristics of LPJ are a synapomorphy uniting embiotocids, pomacentrids, and Labridae KL, as Stiassny and Jensen (1987) concluded.

In the dorsal gill arches a separate, cartilaginous fourth pharyngobranchial (PB4) is absent in all labroids and in gerreids (fig. 4), but is (primitively) present in some sparoids (fig. 6B), all haemuloids (fig. 7A, C), and in kyphosids (fig. 6A). A separate toothplate in the PB4 position is present in all but Labridae KL. Pharyngeal dentition, when represented by separate teeth, is distinctive in labroids, sparoids, haemuloids, and some squamipinnans. Each tooth is constricted proximally, and distally is capped by a conical, decurved tip of brown or umber colored enameloid (acrodin) (figs. 4-10). This characterizes juvenile teeth, and teeth along the margins of the pharyngeal jaws. Medially, and especially in larger individuals, these teeth may be mo-

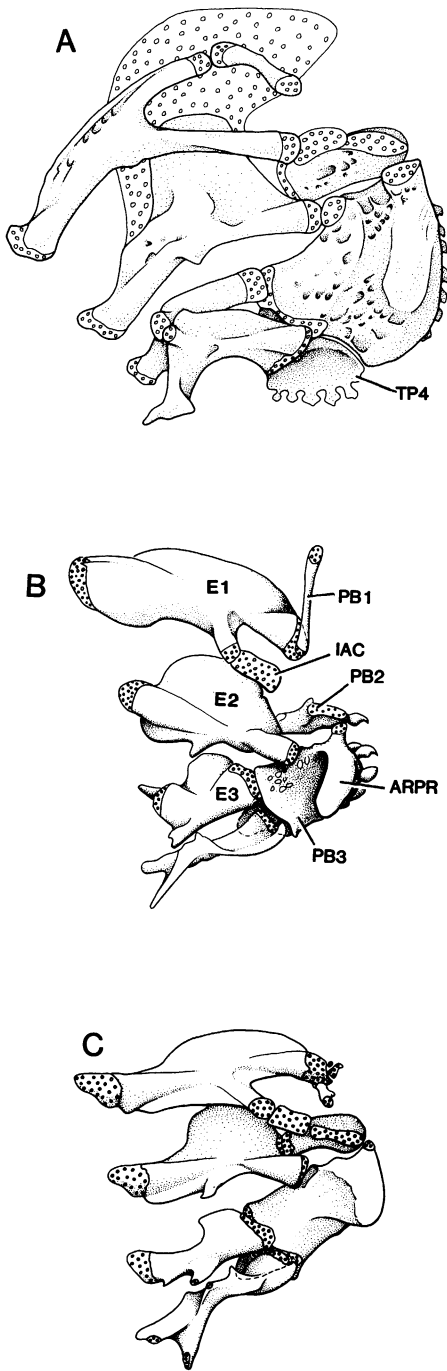


Fig. 5. Left dorsal gill arches of a cichlid (A) and two pomacentrids (B, C), dorsal views. A, *Cyrtocara leuciscus* (Regan), AMNH 11712, B, *Pomacentrus planifrons* Cuvier, AMNH 23632, C, *Chromis cyaneus* (Poey), AMNH 38143. Note the apomorphous enlargement of the anterior surface

lariform or mammiform distally, retaining the proximal constriction.

Cichlids are unusual among pharyngognaths in having the oral margin of the second epibranchial greatly enlarged, extending forward under the first epibranchial, and tipped with a platelike cartilaginous extension (fig. 5A; Stiassny, 1981). Pomacentrids and embiotocids also possess an expansion of the second epibranchial in the same position, with a small cartilage cap in embiotocids but without cartilage in pomacentrids (fig. 5B, C; Stiassny, 1981). Stiassny and Jensen (1987: 292) concluded that the cartilage cap on the second epibranchial is nonhomologous in cichlids and embiotocids.

Embiotocids and labrids (figs. 8, 11B; G. Nelson, 1967: figs. 2, 3; Stiassny, 1981: fig. 8; Stiassny and Jensen, 1987: fig. 13) have slightly expanded second epibranchials, although nothing exactly comparable with the cichlid-pomacentrid condition, but share other features with each other, and with odocids (fig. 11A) and scarids (fig. 9), namely: (1) the second pharyngobranchial (PB2) reduced to a slender edentulous rod, bent slightly at its midpoint and oriented posteriorly, and (2) the absence of direct contact (or an interarcual cartilage) between the first epibranchial and PB2. Those are two of the five modifications used by Nelson (1967) to hypothesize an evolutionary series from pomacentrids through embiotocids to Labridae KL, the other three being: (3) the first basibranchial situated ventral to the axis of the basibranchial series (Emery, 1980: 227; Greenwood, 1985: fig. 14; Stiassny and Jensen, 1987: fig. 10); (4) loss of PB1; and (5) loss of the PB4 toothplate.

Nelson did not consider the Cichlidae in his comparisons, but like pomacentrids they possess only feature (3) (fig. 5; Stiassny 1981, 1982; Stiassny and Jensen, 1987).

UPPER JAW: Another recent effort to assemble percoids into natural subdivisions (Johnson, 1980) recognized three monophyletic superfamilies including eight families: Lutja-

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of the second epibranchial, tipped with cartilage in A, and the raised articular surface on PB3 (ARPR) for contact with the pharyngeal apophysis on the parasphenoid.

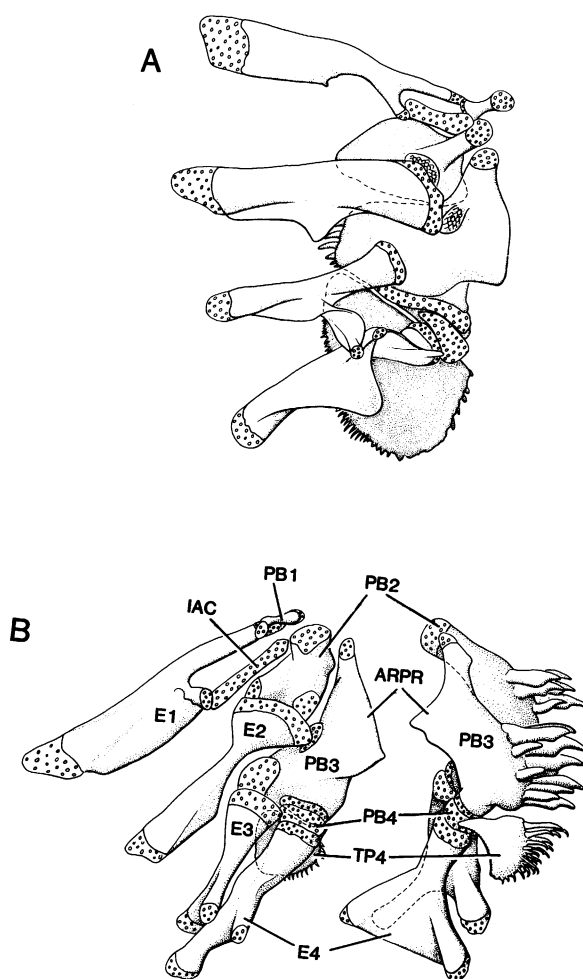


Fig. 6. Left dorsal gill arches of a kyphosid (A) and a lethrinid (B). A, *Kyphosus sectatrix* (L.), AMNH 20855, dorsal view, B, *Lethrinus ornatus* Cuvier and Valenciennes, AMNH 14916, dorsal (left) and medial views. Both have a primitive interarcual cartilage and a well-developed cartilaginous PB4. Only B shows a well-developed articular surface for the pharyngeal apophysis on the parasphenoid (fig. 14), but both show the pharyngeal teeth characteristic of pharyngognaths: large, decurved teeth, posteriorly concave at the tip and slightly constricted at the base.

noidea (Lutjanidae, Caesionidae), Sparoidea (Sparidae, Centracanthidae, Lethrinidae, Nemipteridae), and Haemuloidea (Haemulidae, Inermiidae). Johnson was careful to point out that he found no satisfactory evidence to relate lutjanoids, sparoids, and haemuloids (or even the fishes contained within his Lutjanioidea; see also Johnson, 1984: 491), although an implication of such relationship might be drawn from his classification (pp. 9–12) in which the three superfamilies are listed in the above order, rather than alpha-

betically. J. Nelson (1984: 298–303) refers to Johnson in associating the eight families in a similar though not identical way (reversing the order of the haemuloids and sparoids and inserting the gerreids before them). I find indications in Johnson's paper that his Sparoidea and Haemuloidea may be related to the Pharyngognathi as construed here (including Gerreidae).

The maxilla of pharyngognath fishes (figs. 12–15) has a high posterolateral crest (MDC) just below and lateral to a large dorsal process

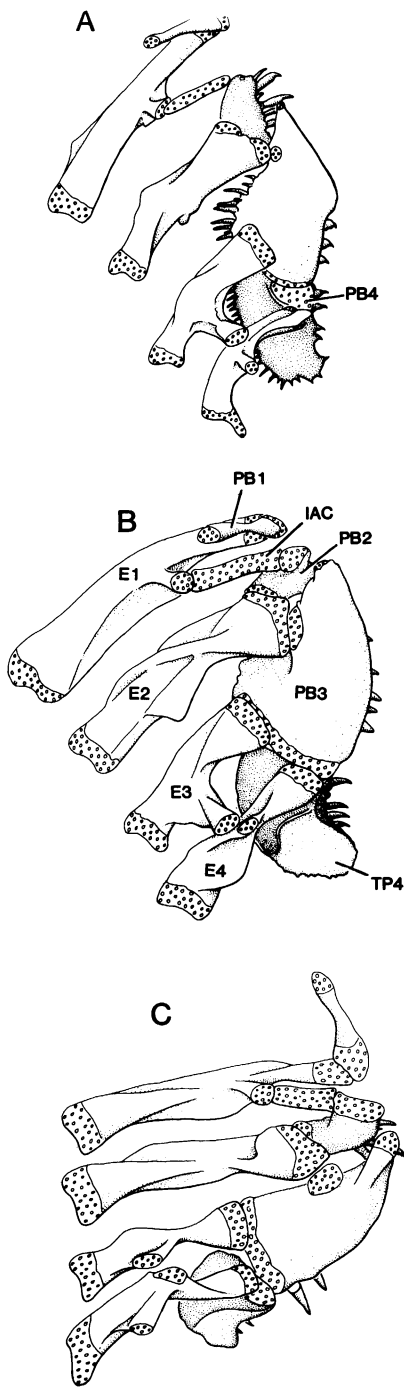


Fig. 7. Left dorsal gill arches of three haemuloids, dorsal views. **A**, the inermiid *Emme-lichthyops atlanticus* Schultz, USNM 188198, **B**, the haemulid *Anisotremus virginicus* (L.), AMNH 21910, and *Pomadasys* sp., AMNH 14388.

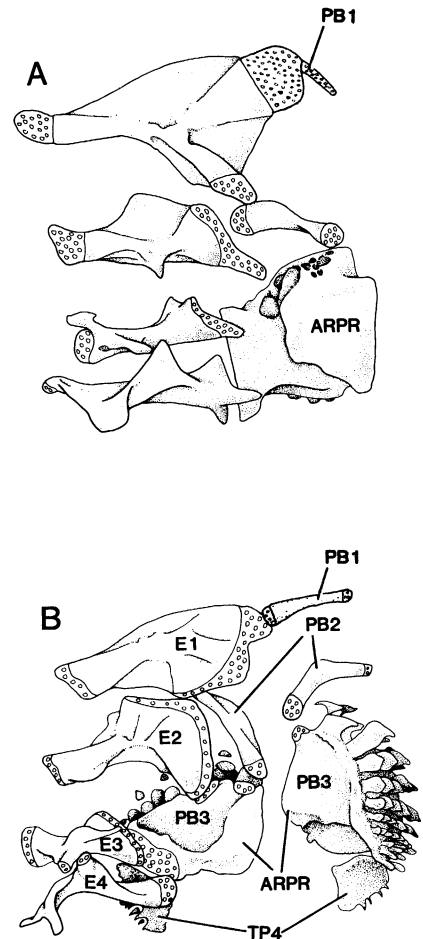


Fig. 8. Left dorsal gill arches of a labrid (**A**) and an embiotocid (**B**). **A**, *Halichoeres bivittatus* (Bloch), AMNH 23598, dorsal view, **B**, *Cymatogaster aggregata* Gibbons, AMNH 1973, dorsal (left) and medial views. The articular process for the pharyngeal apophysis on the parasphenoid is well-developed in both and the marginal teeth on PB3 have the shape noted in figure 6. **A** also shows platelike expansions on the anterior margins of the first and second epibranchials, as in cichlids and some pomacentrids (fig. 5). We agree with Stiassny and Jensen (1987: 292) that the anterolateral expansion of the articular head of EB2 in embiotocids (**B**) is nonhomologous with the cartilage-capped anterior expansion of EB2 in cichlids.

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These taxa have some relatively primitive traits: poorly developed PB3 articular surfaces, primitive interarcual cartilages and a cartilaginous PB4 in **A** and **C**.

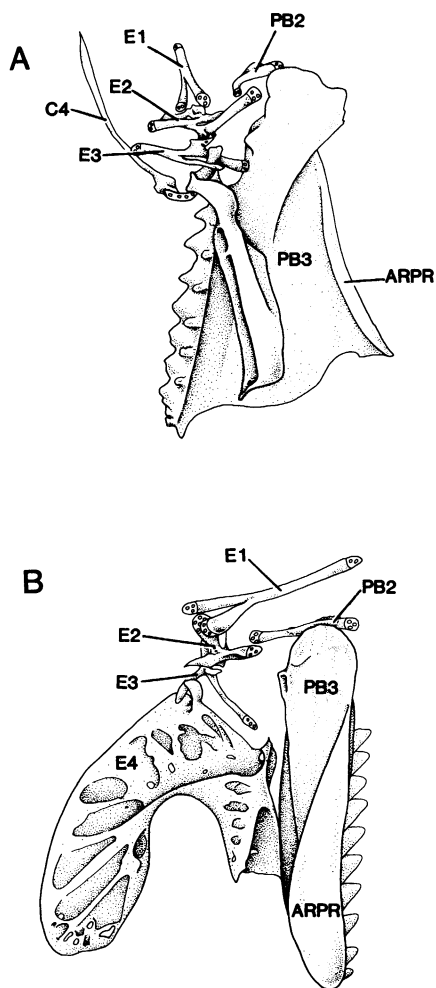


Fig. 9. Left dorsal gill arches of the scarid *Scarus bowersi* (Snyder), AMNH 38114, showing the maximum development of the articular process on PB3 for contact with pharyngeal apophysis on the parasphenoid. A, lateral view, anterior end up, B, dorsal view. The characteristic pharyngognath PB3 teeth are small and just visible in a reduced form in A.

(MDP); the posterolateral crest is named the dorsal wing, with its anterior border called the shank ridge, in cichlids (Barel et al., 1976). Between the crest and the dorsal process is a deep, oblique groove in which the anterior process of the autopalatine (APP) fits and is attached by connective tissue. The ascending processes of the premaxillae slide in and out of a rostral fossa (Rognes, 1973: figs. 6–10, “ascending process fossa”) floored by the der-

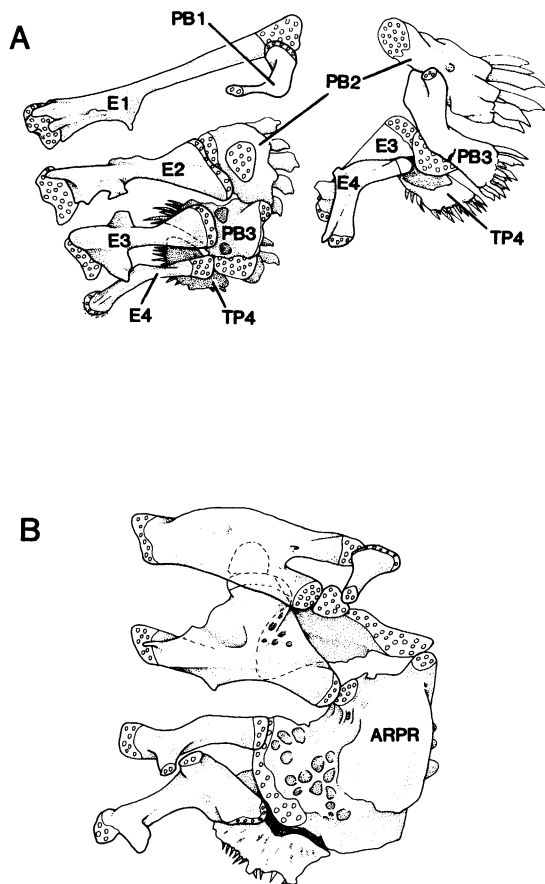


Fig. 10. Left dorsal gill arches in a leiognathid (A) and a cichlid (B). A, *Leiognathus equulus* (Forskål), AMNH 27027, dorsal (left) and dorsomedial views, B, *Cichlasoma centrarchus* (Gill and Bransford), AMNH 22096, dorsal view. Pharyngognathous PB3 tooth form can be seen in A. The articular process on PB3 is particularly obvious in B, but present in a reduced state in A.

mal ethmoid and roofed by the long, flat nasal bones which are sutured or tightly attached to the frontals and lateral ethmoid. Rognes (1973: 100) commented that the labrid nasal “is a relatively long bone movably connected at its posterior end with the anterior edge of the frontal by strong connective tissue and at its anterior end to the dorsal process of the maxillary by a ligament, the nasal-maxillary ligament.” In some cichlids (e.g., Stiassny and Jensen, 1987: fig. 18C), pomacentrids (e.g., Emery, 1980: fig. 12), and embiotocids (e.g., fig. 12B; Morris, 1982: fig. 29), the maxillary

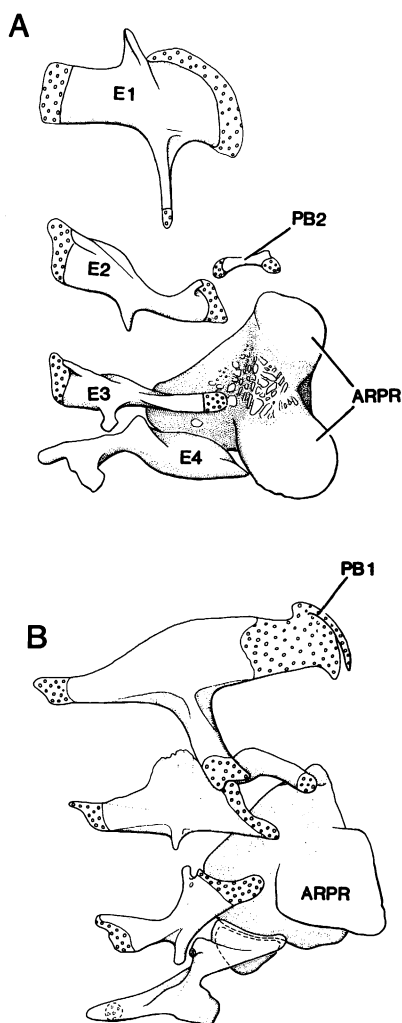


Fig. 11. Left dorsal gill arches in an odacid (A) and a labrid (B), dorsal views. A, *Olisthops cyanomelas* Richardson, AMNH 31319, B, *Coris gaimard* (Quoy and Gaimard), AMNH 38142. The articular surfaces for the pharyngeal apophysis on the parasphenoid are very well developed. B shows an anterior expansion of E2, as in cichlids and pomacentrids (fig. 5).

crest and dorsal process (and therefore, the intervening groove for the autopalatine) are relatively small, but still differ in these features from serranids, centropomids, and centrarchids, among more generalized percoids. In the gerreids (fig. 13D) and the taxa included by Johnson (1980) in the Haemuloidae (fig. 14A, B, D; Johnson, 1980: figs. 13–18) and Sparoidea (fig. 15; Johnson, 1980:

figs. 7–12) the maxillary crest and palatine groove are both well developed except in the haemuloids *Xenocys jessiae* and *Inermia vittata* (Johnson's figs. 16, 17). The dorsal processes of the maxillae in gerreids form an arch over the ascending premaxillary processes when the maxilla is rotated outward during opening of the mouth (Schaeffer and Rosen, 1961: fig. 7, although that illustration of the maxilla fails to show the posterolateral crest). The more primitive percomorph maxilla has a straight dorsal margin and the posterolateral crest is represented by a knoblike process lateral to a dorsal process which clasps the articular process on the premaxilla. That primitive maxillary anatomy occurs in serranids (Morone; Stiassny, 1986: fig. 10), the centrarchid *Micropterus*, and in the lutjanids, caesionids, and inermiids illustrated by Johnson (1980: figs. 2–6, 17, 18).

The maxillary anatomy described above is also very well developed in the squamipinnans *Chaetodon xanthurus* (fig. 14E), *Pomacanthus paru*, AMNH 38130, *Scatophagus* sp., AMNH 20329, and among ephippidids, in *Drepane punctata* (fig. 14C), but not in *Chaetodipterus* or *Platax* which have a simple, primitive maxilla, as in *Monodactylus* and lutjanids. The derived maxillary structures appear to be present in some zeoids and plectognaths (Rosen, 1984: figs. 27–29; *Antigonia*, triacanthoids), but not in *Capros* or acanthuroids. Tyler et al. (1989) concluded that acanthuroids (including siganids, luvarids, zanolids, and acanthurids) are most closely related successively to scatophagids and ephippidids.

Another feature of the upper jaw is also of some interest. In Labridae KL (fig. 13B, C) the articular process is coalesced with the ascending process of the premaxilla (Rognes, 1973); the long, slender articulo-ascending process is able to slide in and out under the intermaxillary ligament within the rostral fossa and fills the fossa when the mouth is closed. The alveolar process of the premaxilla is only about half the length of the articulo-ascending process. Coalescence and elongation of the articular and ascending processes is also present in gerreids (fig. 13D), and many cichlids (fig. 12D), haemuloids (fig. 14), and sparoids (fig. 15) but not in pomacentrids (fig. 13A) or embiotocids (fig. 12A–C). These two

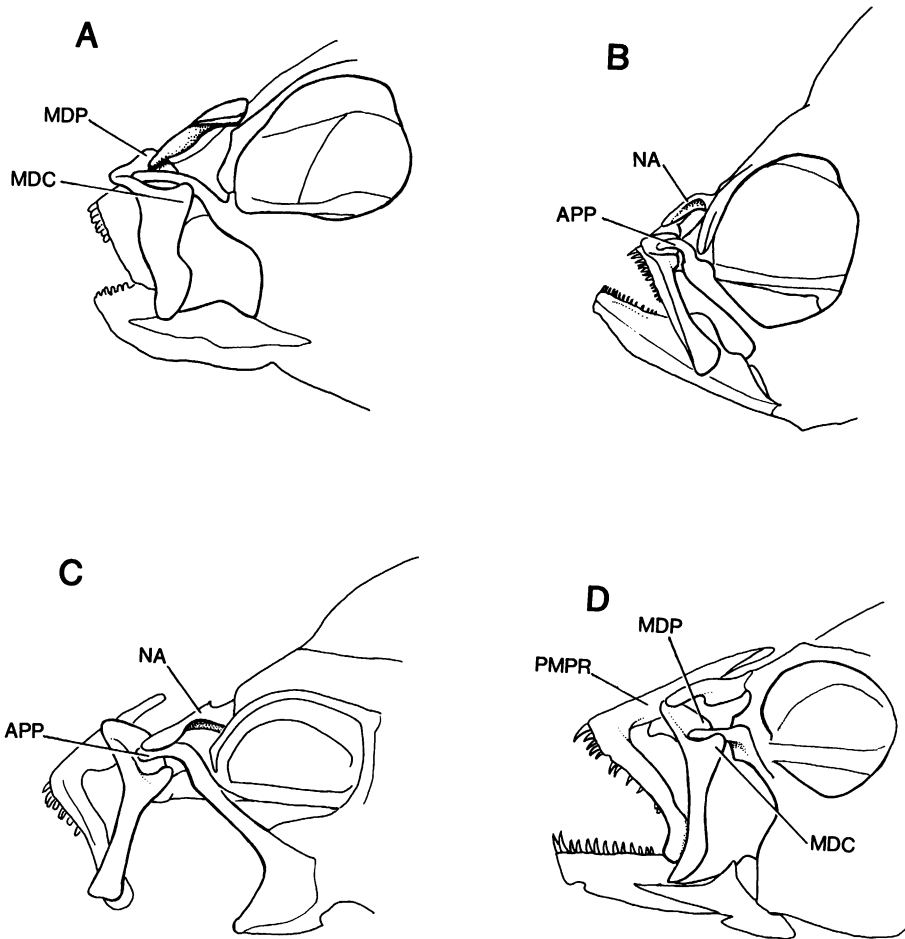


Fig. 12. Buccal jaws of embiotocids (A–C) and a cichlid (D) showing the long nasals sutured to frontals covering a rostral fossa for the premaxillary ascending processes. A, *Cymatogaster aggregata* Gibbons, AMNH 2739; B, *Hyperprosopon argenteum* Gibbons, AMNH 27947; C, *Rhachochilus* sp., AMNH 27943; D, *Cichlasoma friedrichsthali* Steindachner, AMNH 27822.

features contrast with the more primitive conditions in serranids and lutjanids (Johnson, 1980), among other percoids, in which the relatively short ascending process is separated from the articular process by a deep notch. In this primitive configuration the articular process also is set off from a relatively long alveolar process (twice or more the length of the ascending process) which bears a broad, triangular, postmaxillary process on its dorsal margin. Various sparoids and haemuloids are figured by Johnson (1980) as having a thumblike postmaxillary process on a short alveolar arm, a feature not seen in any of the squamipinnate material examined. The lat-

ter also have ascending and alveolar premaxillary segments that are subequal in length [except *Drepane* (fig. 14C) which has a rather long ascending process].

Both pomacentrids (fig. 13A) and embiotocids (fig. 12A–C) have relatively short premaxillary ascending processes. Among pomacentrids this process is most elongate and most closely coalesced with the articular process in *Chromis* (Emery, 1973: fig. 38). In embiotocids (Morris, 1982) the ascending process is short and separated from the articular process by a notch in *Amphistichus* and *Hyperprosopon*, but is about equal in length to the alveolar process and coalesced

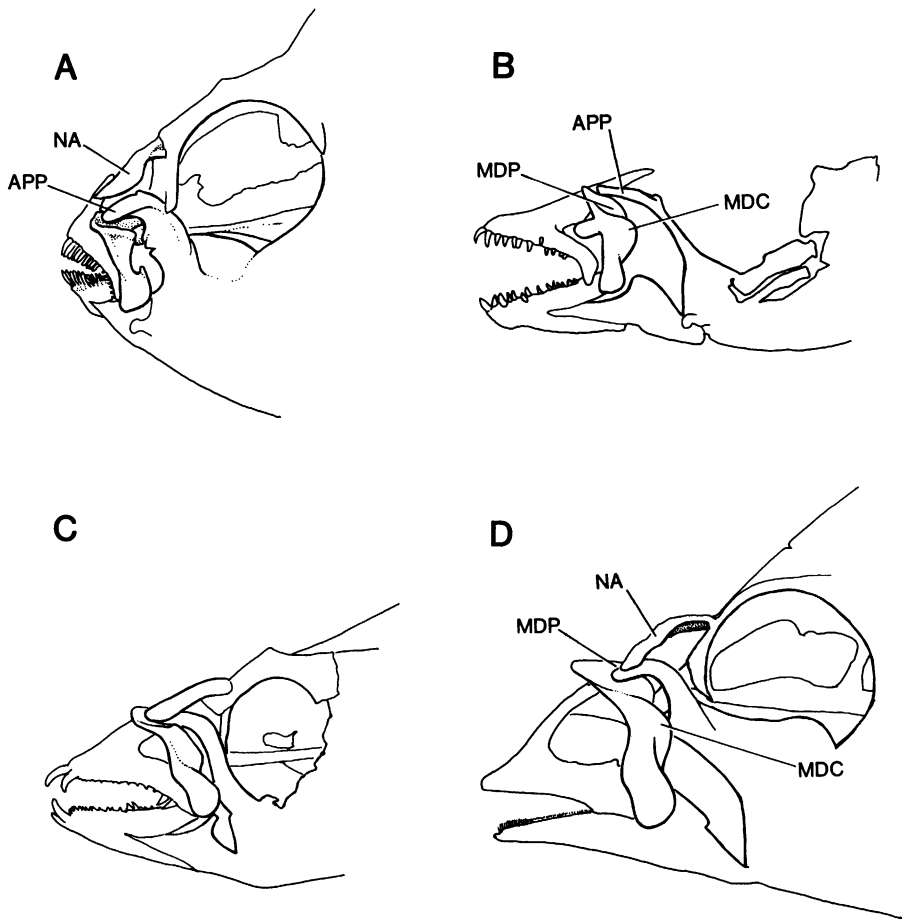


Fig. 13. Buccal jaws of a pomacentrid (A), two labrids (B, C), and a gerreid (D). A, the pomacentrid *Hypsipops rubicundus* (Girard), AMNH 42156; B, *Labrus bimaculatus* L., from Rognes (1973, fig. 80); C, the labrid *Bodianus rufus* (L.), AMNH 30875; D, *Gerres cinereus* (Walbaum), AMNH 21732.

with the articular process in other genera. Among cichlids, premaxillae specialized as discussed above are characteristic of certain taxa with lengthy protrusile mouths (e.g., *Petenia splendida*). But it appears that neither cichlids, pomacentrids, nor embiotocids primitively have the advanced maxillary or premaxillary features of labrids. Upper jaw evidence aligns labrids with gerreids, sparoids, and haemuloids. And each of the last three groups shows some development of a pharyngeal apophysis on the parasphenoid (see below) and an articulatory facet on PB3. Gerreids in addition have a labroidlike basibranchial series (below, and fig. 27). Lastly, certain squamipinnean taxa have a weak pha-

ryngeal apophysis, a labridlike maxilla, but a primitive premaxilla.

PHARYNGOGNATH BRAINCASE: Features of the neurocranium, as well as those of the jaws and palate discussed elsewhere, suggest a relationship among gerreids, Labridae KL, sparoids, and haemuloids.

Derived features of the parasphenoid bone appear to be alternative expressions of some specializations of the dorsal gill arches discussed above. The parasphenoid of labroids shows three features that do not occur in more generalized acanthomorphs such as *Holocentrus* (fig. 16), *Centropomus*, *Morone*, *Epinephelus*, or *Micropterus*. These are:

1. A strong ventral keel from the sides of

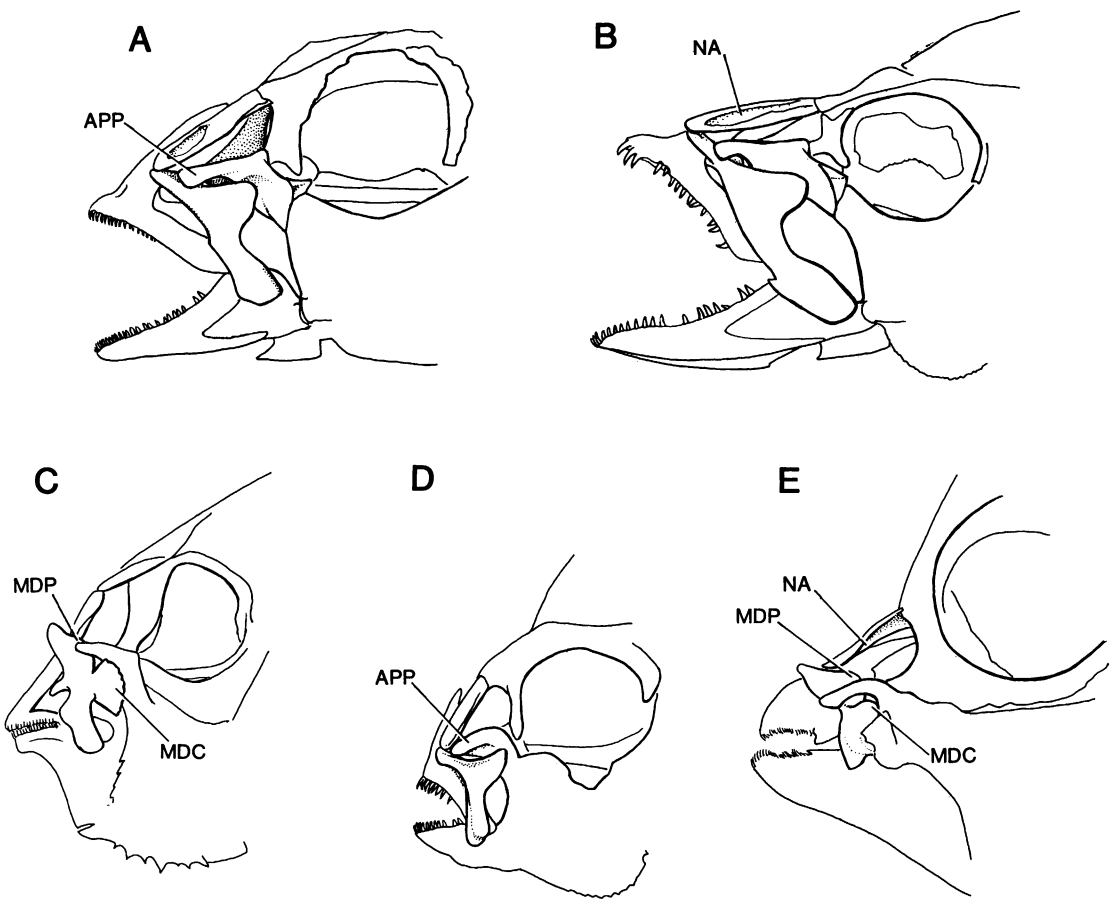


Fig. 14. Buccal jaws of three haemuloids (A, B, D, Haemulidae) and two Squamipinnes (C, Drepanidae, E, Chaetodontidae). A, *Haemulon carbonarium* Poey, AMNH 30825; B, *H. plumieri* (Lacépède), AMNH 21747; C, *Drepane punctata* (L.), AMNH 13922; D, *Anisotremus* sp., AMNH 21569; E, *Chaetodon xanthurus* Bleeker, AMNH 38110.

which an adductor arcus palatini muscle arises that fills the floor of the orbit. The more primitive condition appears to be the confinement of this muscle to the rear of the orbit with a parasphenoidal attachment of rugose bone in the form of a narrow ellipse. The shaft of the parasphenoid anterior to the site of muscle attachment is primitively smooth and convex ventrally. Morris (1982: 143) noted that a parasphenoid keel equal in size to that of many embiotocids occurs in scorpidids and girellids, and that leiognathids also have such a keel.

2. A ventral extension of the median keel in the form of a triangular process posteriorly just in front of the prootic to form an adductor process (AP, figs. 17–26) from which

the posterior fibers of the adductor muscle arise. The adductor process takes various forms (pointed, squared off, or rounded) and is variable in size. It is quite long and squared off in labrids (fig. 17; Rognes, 1973: figs. 11–15), or lower and rounded in pomacentrids; it is least developed in the embiotocids (Morris, 1982: figs. 1–4) and cichlids, where often the adductor process is all that remains of the ventral keel (Stiassny and Jensen, 1987: fig. 6).

3. A pharyngeal apophysis (PHA) more posteriorly on the otico-occipital region of the parasphenoid. PHA consists either of an elevated transverse shelf or of a raised pair of oval knobs oriented anteroposteriorly. The articular surface of PHA has a basioccipital

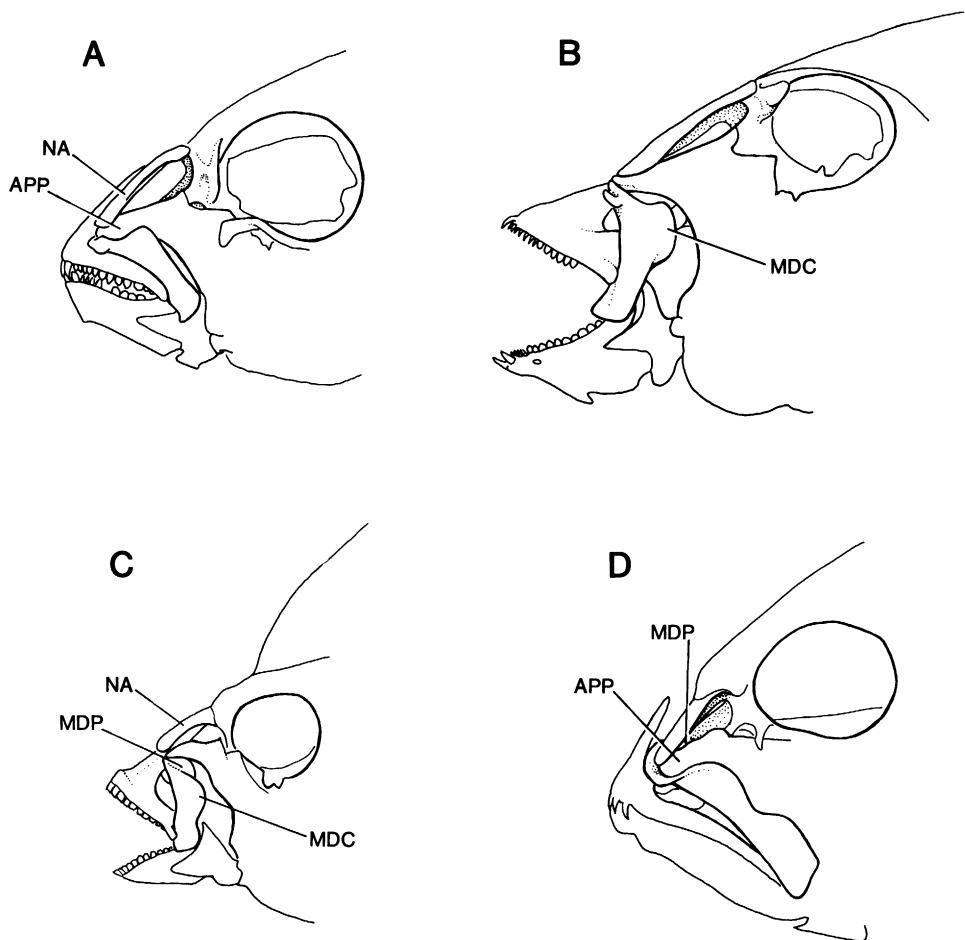
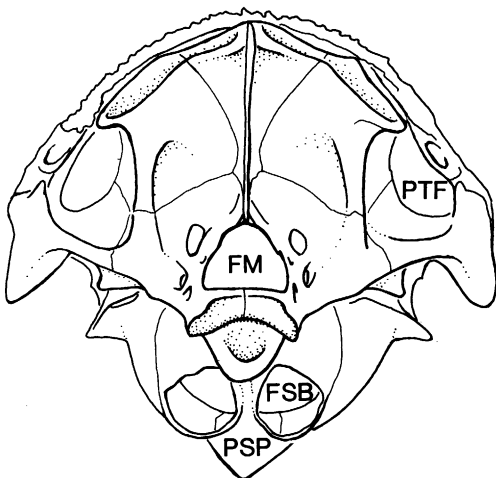


Fig. 15. Buccal jaws of sparoids (A–C, Sparidae; D, Nemipteridae) showing the long nasals sutured to frontals covering a rostral fossa that houses the premaxillary processes. A, *Pagrus pagrus* (L.), AMNH 56321; B, *Calamus calamus* (Cuvier and Valenciennes), AMNH 35480; C, *Lagodon rhomboides* (L.), AMNH 55947; D, *Nemipterus virgatus* (Cuvier and Valenciennes), AMNH 56390.



component in some cichlids (fig. 18; Greenwood, 1978), but is parasphenoidal in pomacentrids, Labridae KL, embiotocids (Stiassny and Jensen, 1987: 282, were mistaken in mentioning a basioccipital contribution to the apophysial surface in embiotocids), and gerreids (figs. 19–21). PHA

Fig. 16. Posterior view of the braincase of *Holocentrus rufus* (Walbaum), AMNH 35496, to illustrate primitive absence of basicranial apophyses associated with dorsal or ventral gill arch specializations. Compare with labrid, sparoid, gerreid, cichlid, lethrinid, and haemuloid neurocrania in figures 17–26.

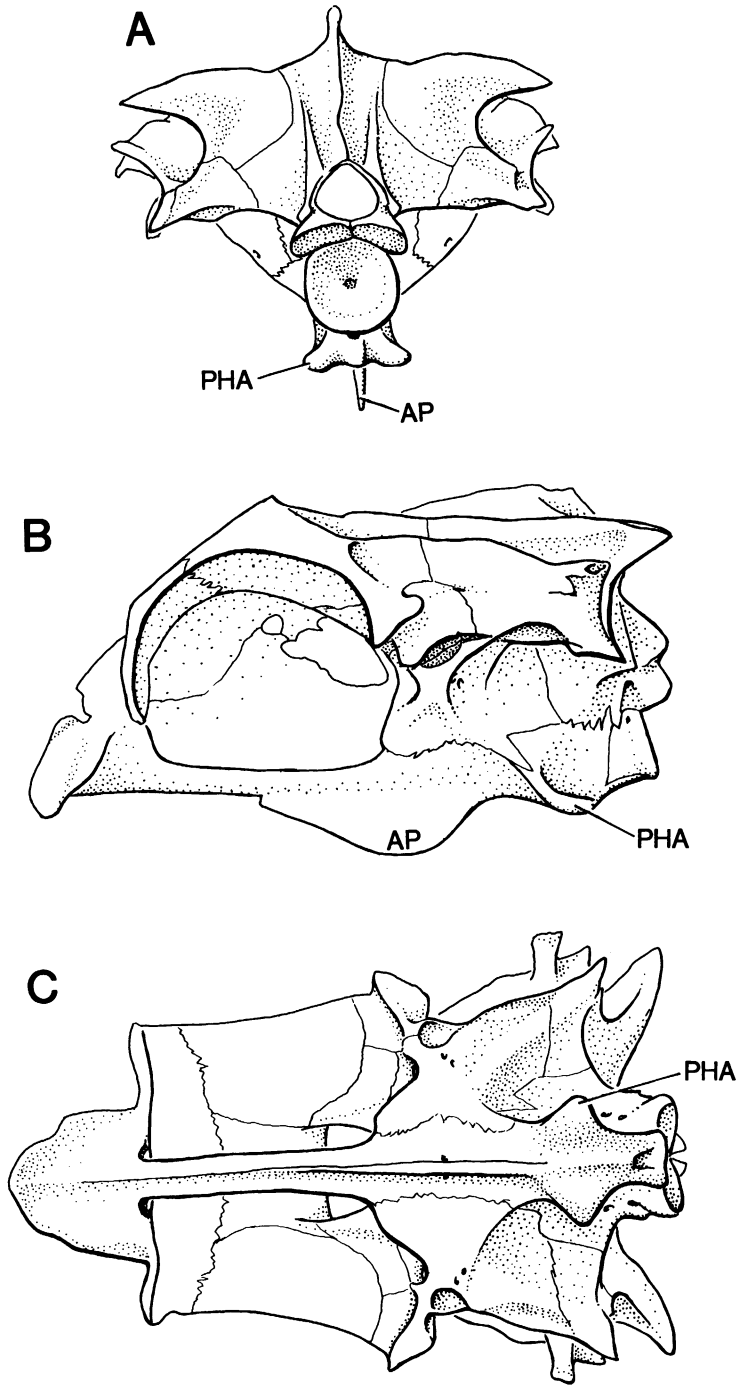


Fig. 17. Pharyngognath basicranial features. The braincase of the labrid *Bodianus rufus* (L.), AMNH 35434, in A, posterior, B, lateral, and C, ventral view.

articulates indirectly (in gerreids) or directly (in labroids) with an articular facet of the third pharyngobranchial. The relations be-

tween PHA and PB3 are discussed at length and figured by Stiassny (1981, 1982; Stiassny and Jensen, 1987).

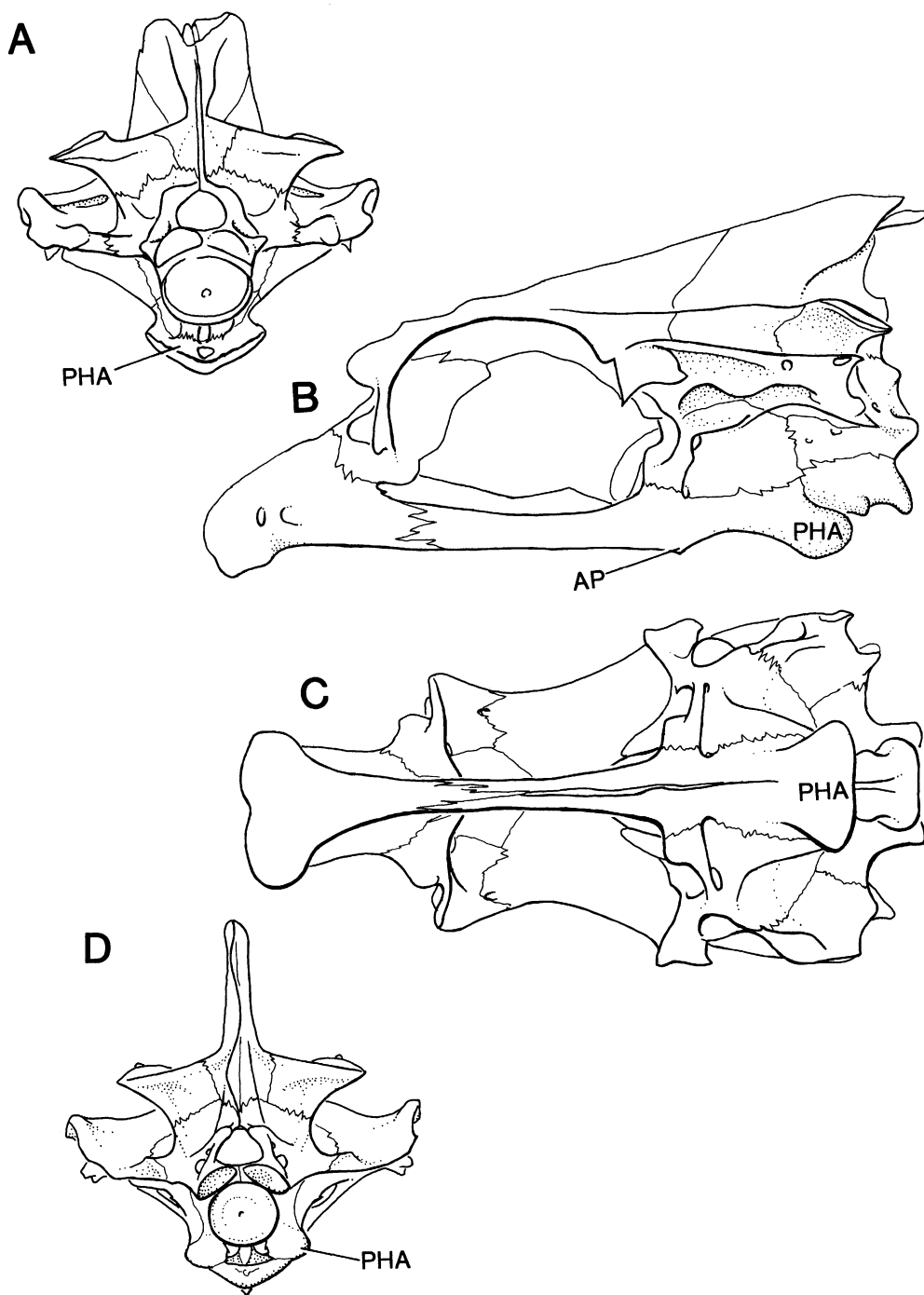


Fig. 18. Pharyngognath basicranial features in cichlids. A-C, Braincase of *Petenia splendida* Günther, AMNH 27833, in A, posterior, B, lateral, and C, ventral view. D, Braincase of *Cichla ocellaris* Bloch and Schneider, AMNH 40023, in posterior view.

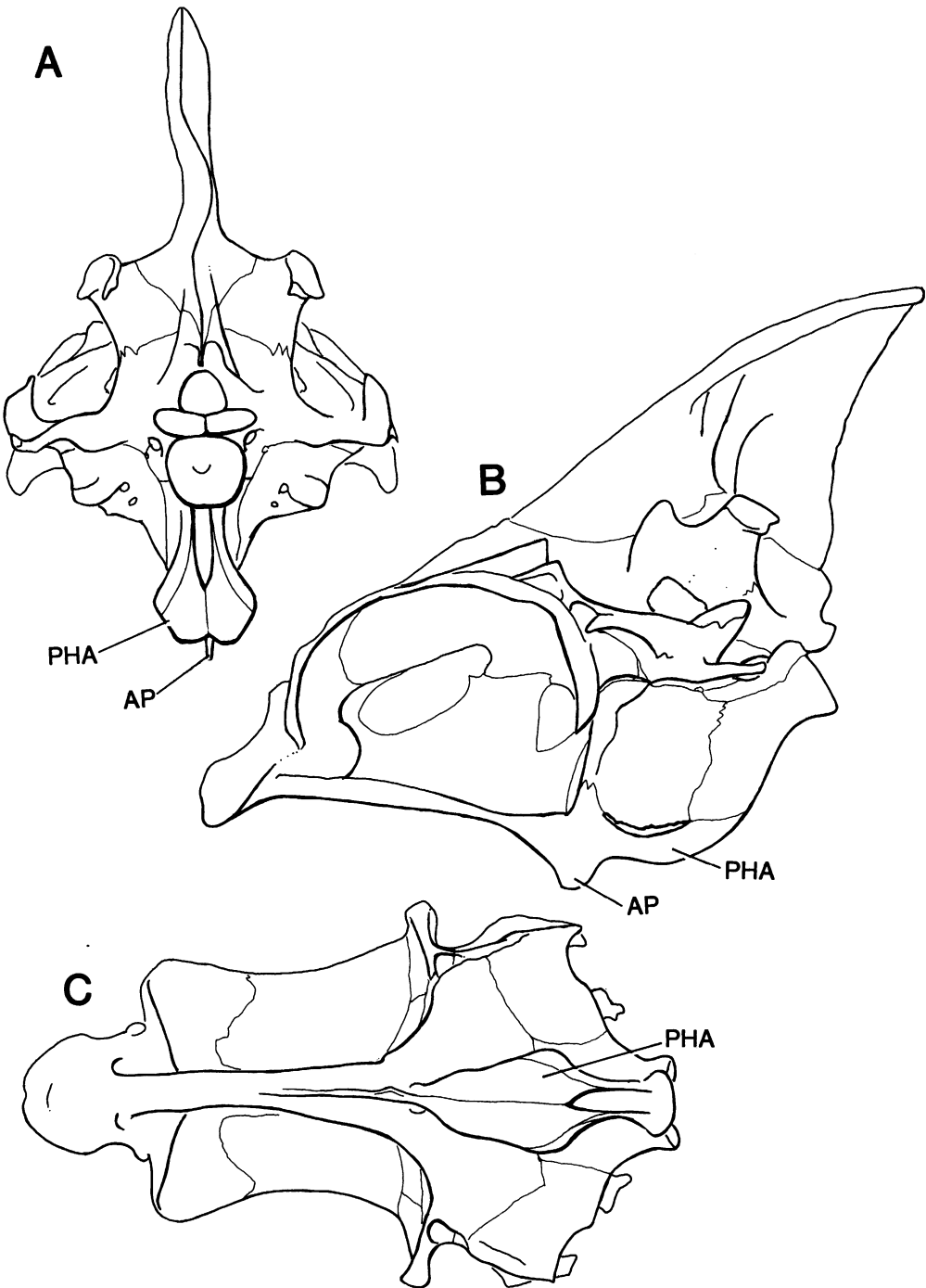


Fig. 19. Pharyngognath basicranial features in the gerreid *Gerres lineatus* (Cuvier and Valenciennes), AMNH 21949. Braincase in A, posterior, B, lateral, and C, ventral view.

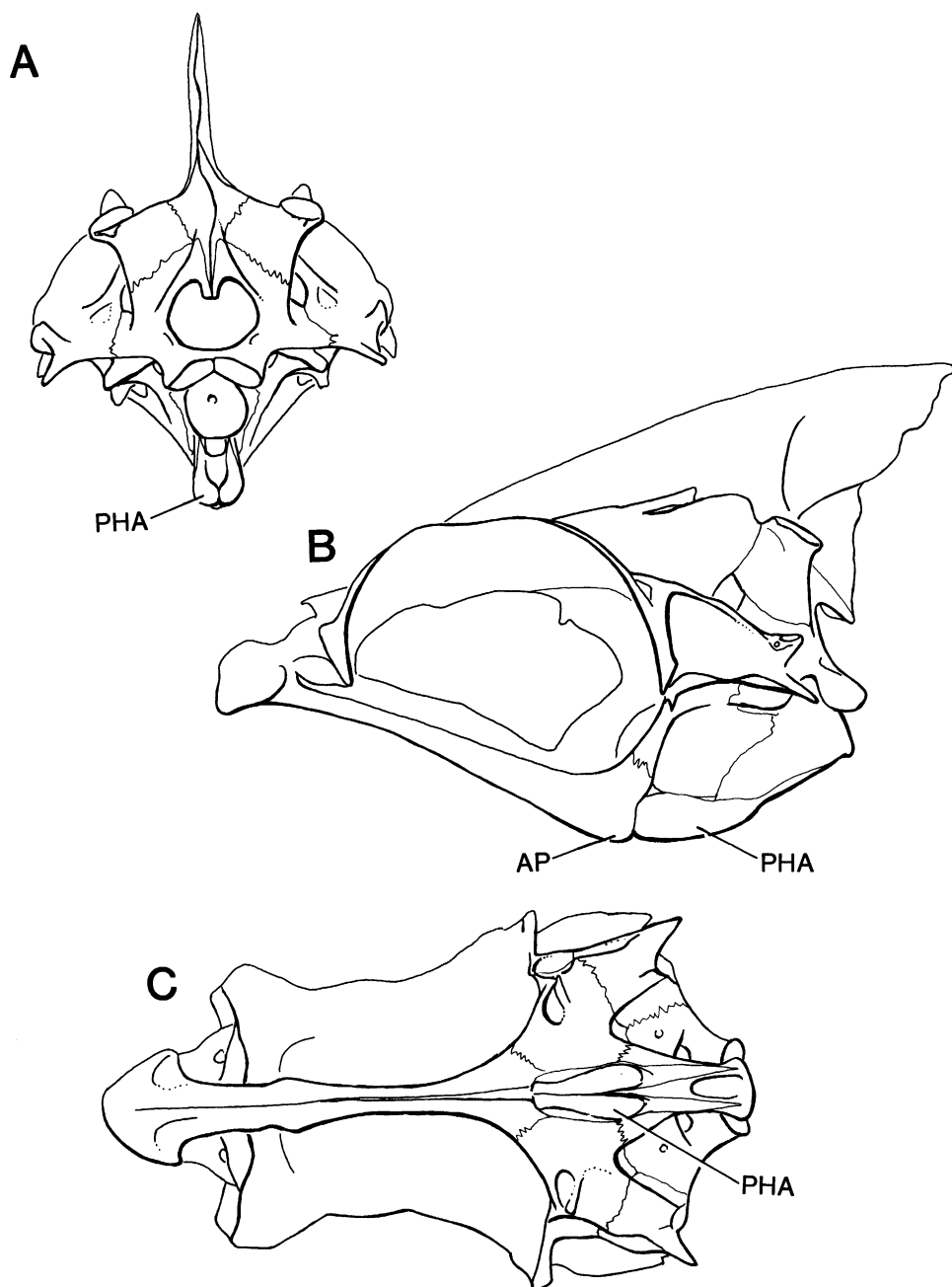


Fig. 20. As figure 19, but *Gerres cinereus* (Walbaum), AMNH 21732.

Basicranial pharyngeal apophyses occur in a variety of teleosts: beloniforms, some centrarchids, gerreids (figs. 19–21), sciaenids, sparids (figs. 23–25), lethrins (fig. 22), and in some of the Squamipinnes (Tyler et al.,

1989: 49). As a character, the pharyngeal apophysis appears ambiguous. Its relation to PB3 in labroids has been described as a diarthrosis (direct bone-to-bone contact), as opposed to an amphiarthrosis (or mixed ar-

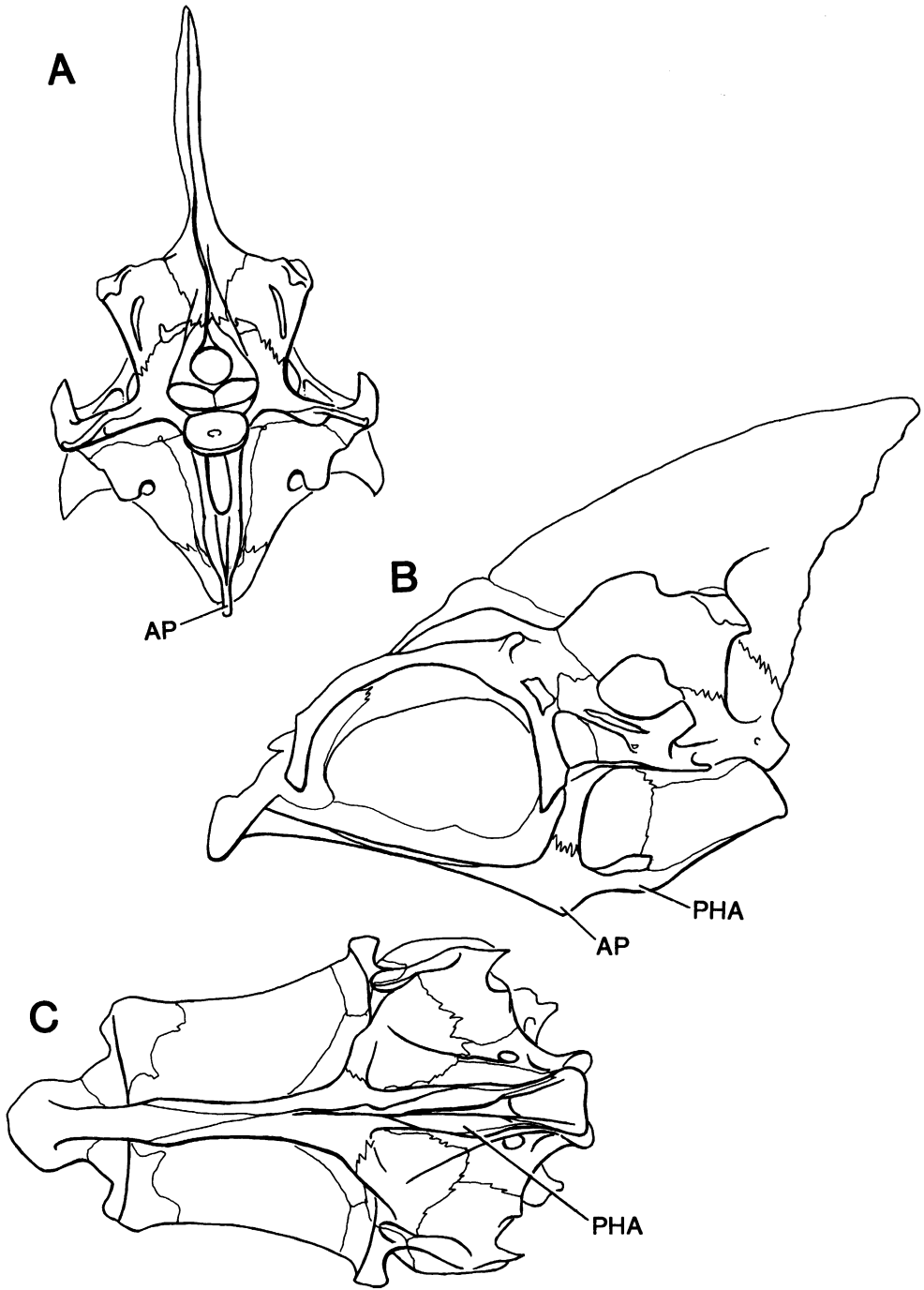


Fig. 21. As figure 19, but the gerreid *Diapterus mexicanus* Steindachner, AMNH 28060.

ticulation in which dorsal gill-arch muscle and connective tissue intervene between PB3 and the bony pharyngeal apophysis), as in

haemuloids, sparoids, and gerreids. The latter three taxa include species with a definite platform (? articular facet; ARPR, figs. 4, 6B)

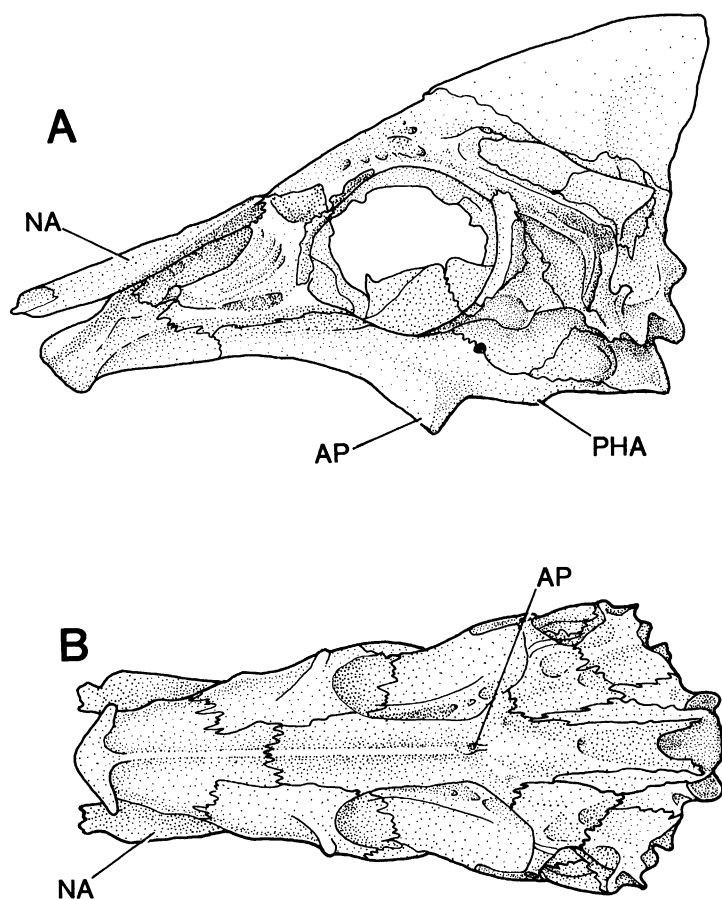


Fig. 22. Braincase of a lethrinid, *Lethrinus* sp., AMNH 30872, in A, lateral, and B, ventral view, to show the pharyngeal apophysis and the long nasal sutured to the frontal to cover the rostral fossa.

dorsally on PB3, and they and the labroids possess very similar pharyngobranchial dentition with decurved acrodin tips and a constricted base (see above, and figs. 5–10).

AN EXPANDED PHARYNGOGNATHI? Characters reviewed above that might be used to align sparoids, haemuloids, and the Pharyngognathi as understood by Günther 1862 [1859–1870] and Gill (1872) [Labroidei of Stiassny and Jensen (1987) plus Gerreidae] include:

1. Two parasphenoidal processes; an anterior one to which the adductor arcus palatini muscle attaches and a posterior apophysis to which attaches an articular process of PB3 of the UPJ (AP, PHA, figs. 17–26).
2. Long nasals firmly united with the frontals

and roofing the fossa for the premaxillary ascending processes (figs. 12–15, 22).

3. Maxilla with a dorsal crest and process forming a groove for the autopalatine (figs. 12–15).

One character of the Labroidei is ventral displacement of the first basibranchial (BB1) as described by G. Nelson (1967) and Stiassny and Jensen (1987). Young embiotocids (e.g., *Cymatogaster aggregatus*, AMNH 1973, standard length 33 mm; and embryos of *Amphistichus argenteus*, Morris and Gaudin, 1982: fig. 8) do not show this feature. BB1 in these small individuals is in line with the basihyal and BB2. Similarly this feature is best seen in cichlids of larger sizes. Such observations suggest that the ventral position of BB1 results from an ontogenetic process

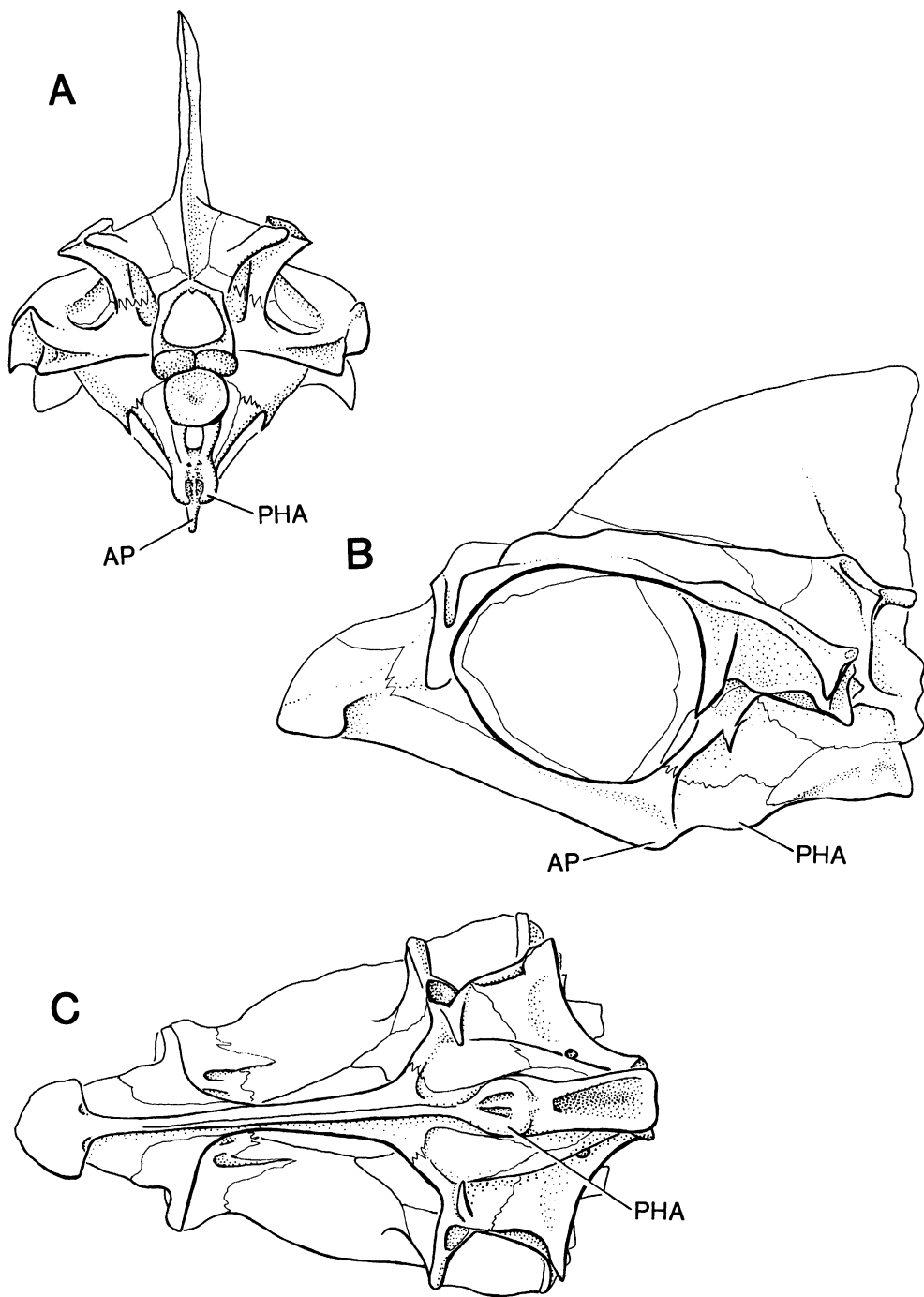


Fig. 23. Pharyngognath basicranial features in the sparoid *Lagodon rhomboides* (L.), AMNH 55947. Braincase in A, posterior, B, lateral, and C, ventral view.

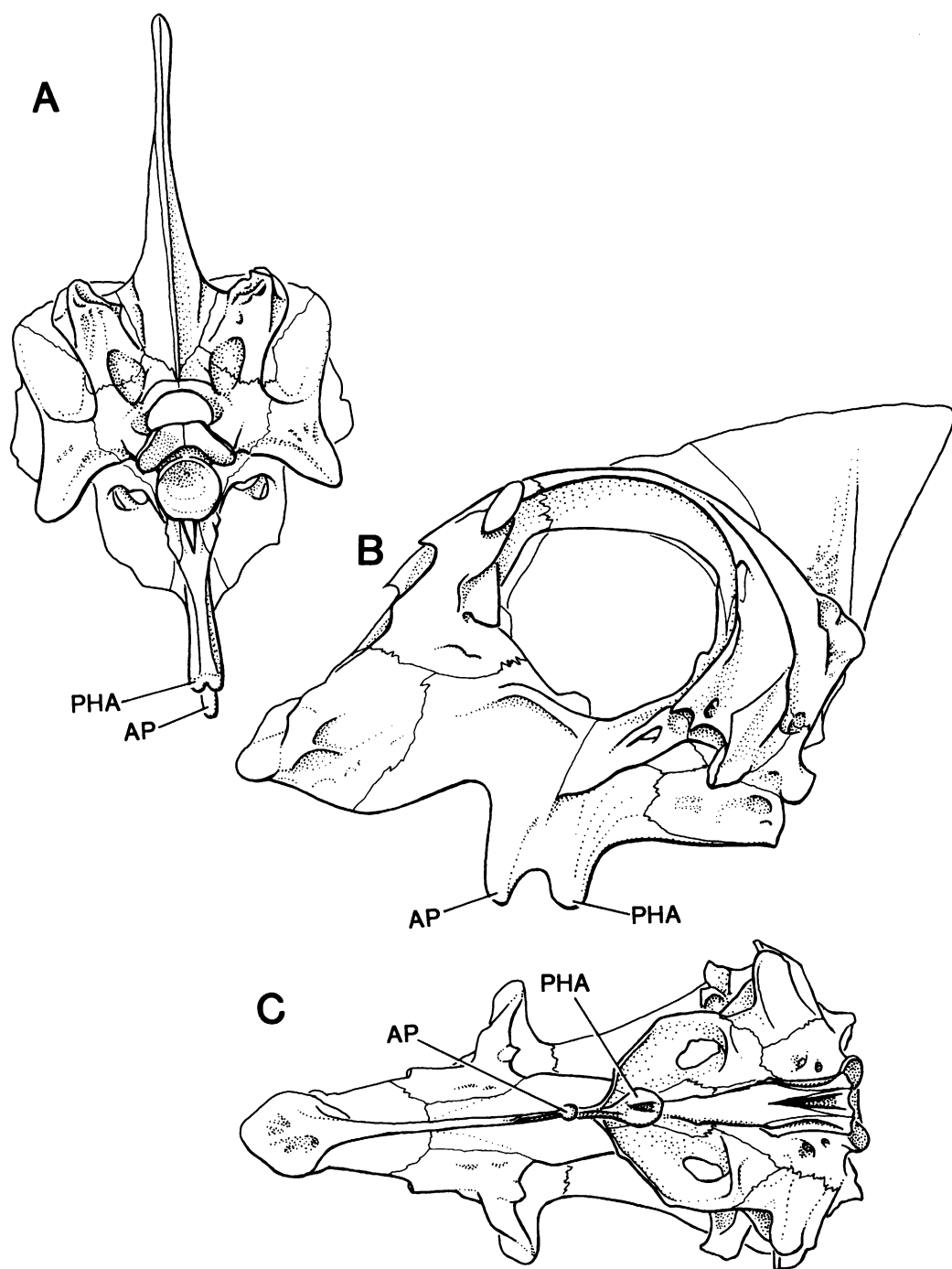


Fig. 24. As figure 23, but the sparoid *Calamus proridens* Jordan and Gilbert, AMNH 21673.

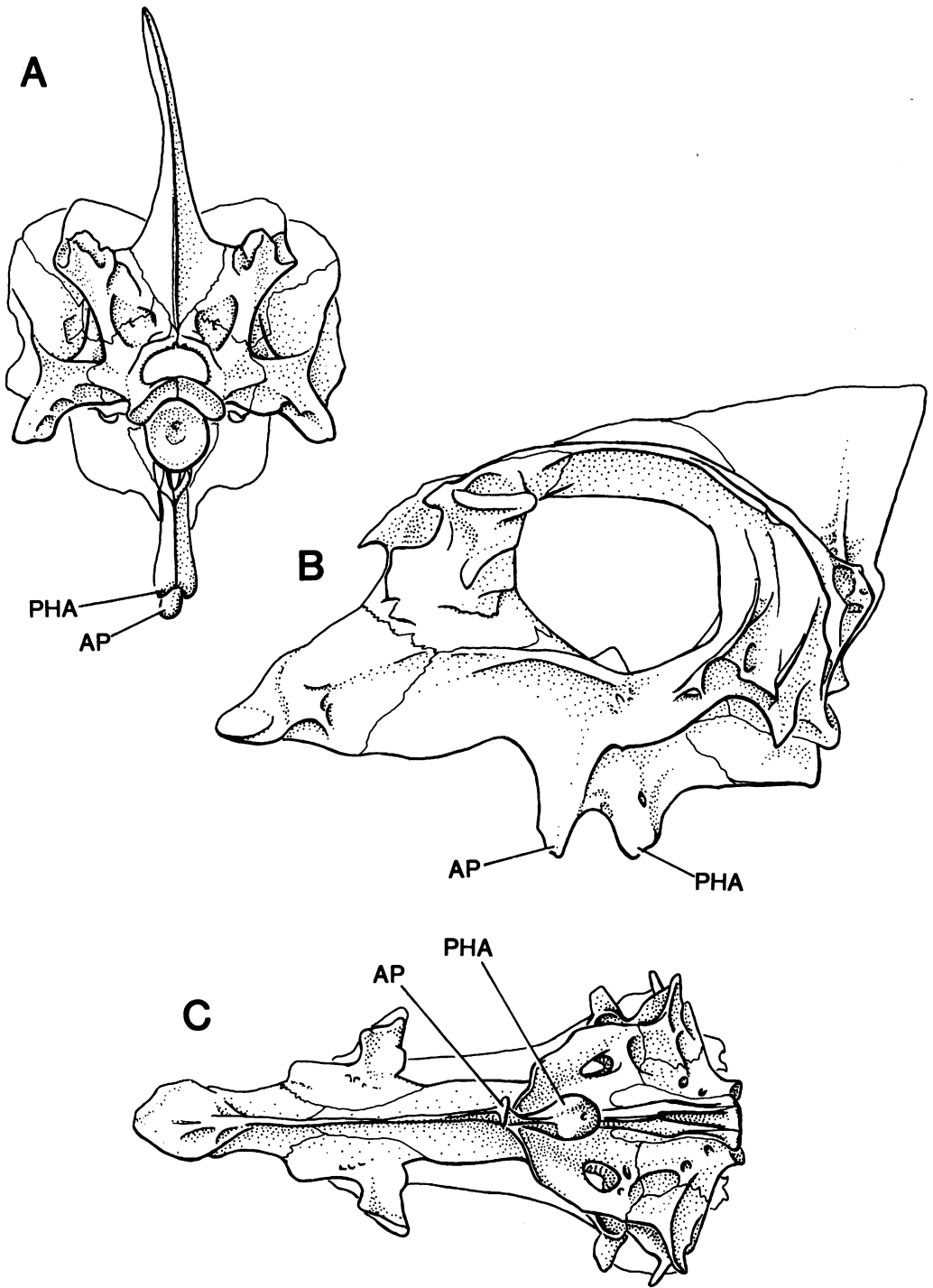


Fig. 25. As figure 23, but the sparoid *Calamus bajonado* (Schneider), AMNH 35442.

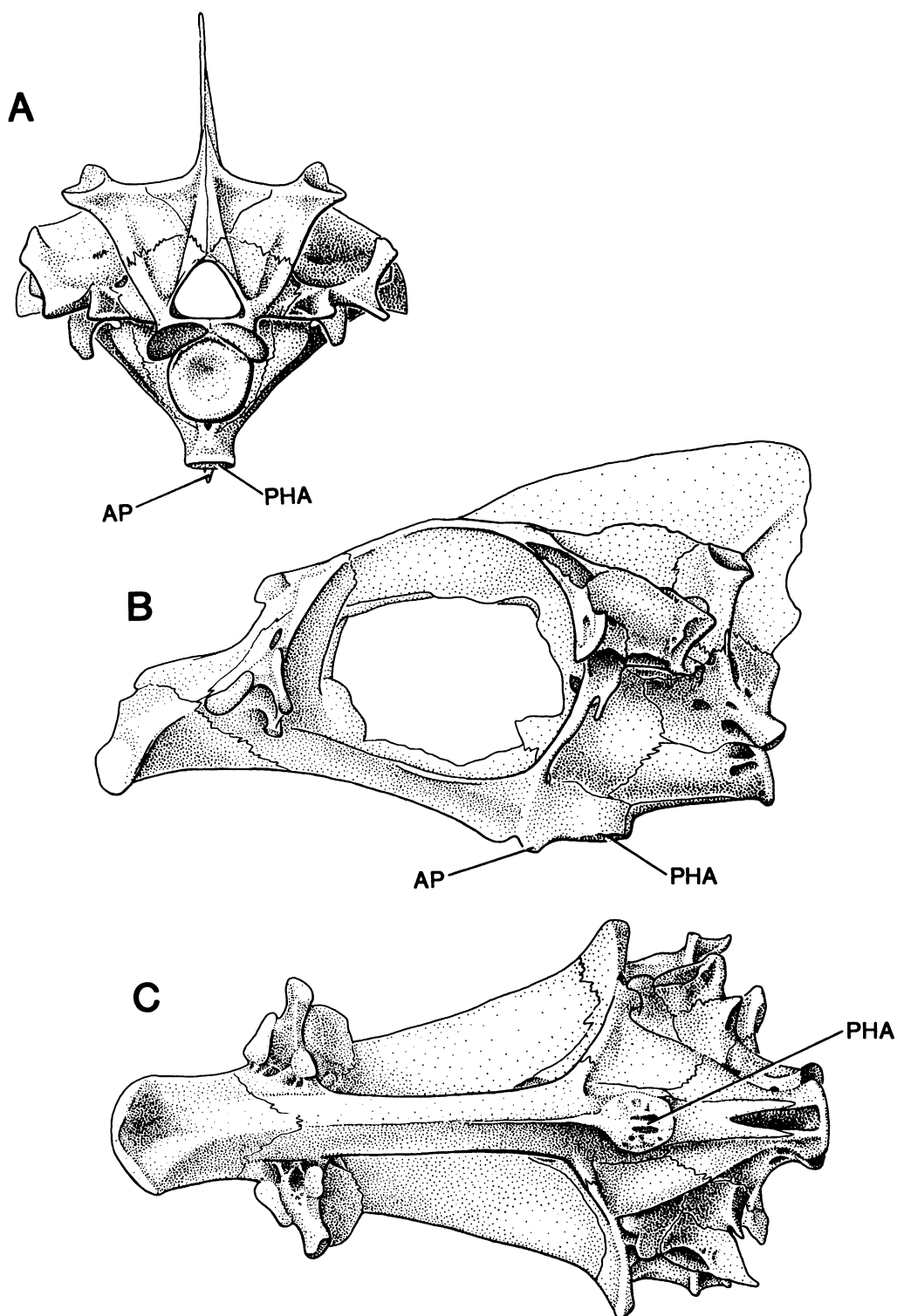


Fig. 26. Pharyngognath basicranial features in the haemuloid *Haemulon carbonarium* Poey, AMNH 30839. Braincase in A, posterior, B, lateral, and C, ventral view.

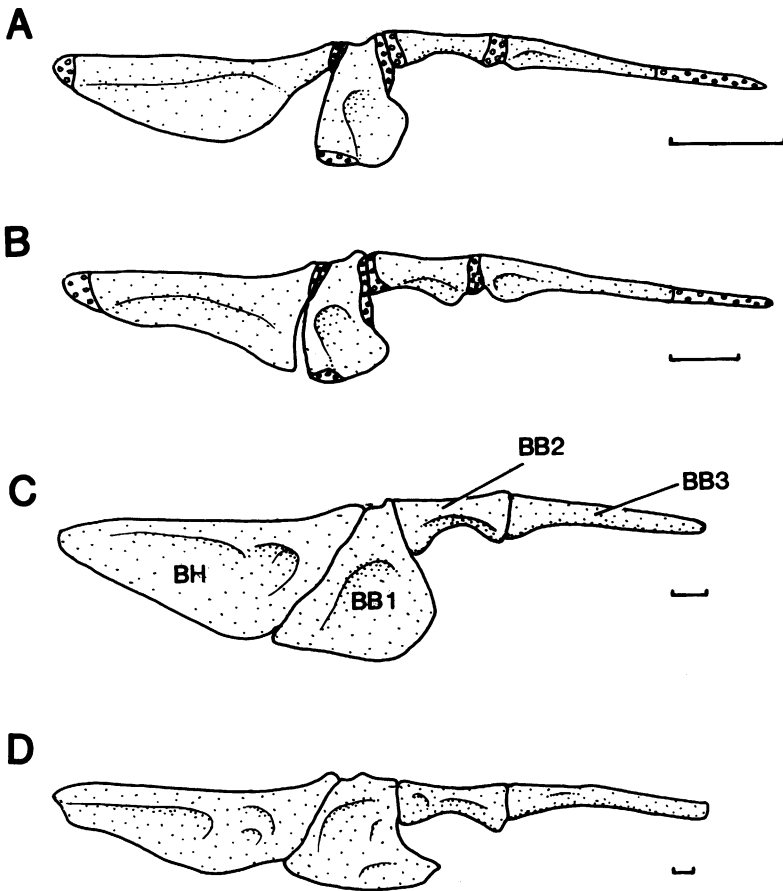


Fig. 27. Basibranchial series of young and adult gerreids in left lateral view. **A**, *Gerres cinereus* (Walbaum), UMMZ 172787, ca. 35 mm standard length (SL); **B**, *G. abbreviatus* Bleeker, BMNH 1974.5.25.2336, ca. 65 mm SL; **C**, *G. cinereus*, BMNH unreg. dry skeleton, ca. 150 mm SL; **D**, *G. cinereus*, AMNH 21949, ca. 200 mm SL. Scale bar at lower right of each = 1 mm.

in which backward growth of the basihyal excludes BB1 from the plane of the basibranchial series by forcing it downward, or that BB1 pulls itself into ventral disalignment by growth of a posteroventral extension below BB2.

The first basibranchial of young gerreids (e.g., *Gerres cinereus*, *G. abbreviatus*, fig. 27A, B) is in line with the basibranchial series, but is very short and deep, with a broad posteroventral process or flange. In adult *Gerres* (fig. 27D) the posteroventral process extends below BB2 much as Nelson (1967: fig. 3B) illustrated for a labrid. In the embiotocids illustrated by Nelson (1967: fig. 2, *Embiotoca jacksoni*) and Morris (1982: fig. 38A, *Hysterocarpus traski*) BB1 is entirely excluded from the basibranchial series by direct artic-

ulation of the basihyal (BH) with BB2. In Stiassny and Jensen's (1987: fig. 10E) illustration of *Embiotoca lateralis* there is no direct articulation between BH and BB2, but BB1 is almost entirely below BH. The pomacentrid illustrated by Nelson (1967: fig. 1, *Chromis ovalis*), is intermediate, with BB1 anteriorly below the proximal end of BH, but articulating posteriorly with BB2 and having a long narrow process that extends back below BB2 as far as the anterior end of BB3. Stiassny and Jensen's (1987: fig. 10C) illustration of *Pomacentrus* shows virtually the same condition. This pomacentrid conformation is almost identical to the relations between BB1, BB2, and BH in some large cichlids such as *Petenia splendida*, AMNH 27845 (cf. Stiassny and Jensen, 1987: fig. 10B,

C). From all of this I conclude that the basibranchial configuration described by Nelson and by Stiassny and Jensen properly defines some group of pharyngognathous "percoids," including pomacentrids, cichlids, embiotocids, gerreids, labrids, and possibly also kyphosids, since Stiassny and Jensen (1987: 288) reported the same configuration in *Girella*, and in *Kyphosus* BB1 is almost completely overgrown by BH (which bears paired toothplates), and so lies beneath the BH-BB axis. Among labroids, embiotocids are linked to Labridae KL by the reduction and specialization of PB2 as a small, edentulous cylinder bent along its middle so that the concave surface faces PB3. I note that PB2 in gerreids (fig. 4) shows the same curvature as in labrids and embiotocids (fig. 8), but is toothed, as it is in cichlids and pomacentrids.

Other "percoid" families show some of the gill-arch features found in all or some labroids, as summarized in the following list:

1. absence of PB2 dentition,
2. first basibranchial ventral to axis of basibranchial series,
3. posterior orientation of PB2 and anterior epibranchials,
4. a functionally median LPJ,
5. teeth constricted proximally and capped by conical, decurved tip of acrodin,
6. PB3 with a dorsal diarthrodial articulation with a parasphenoidal apophysis,
7. No PB4,
8. No IAC,
9. Oral margin of first and/or second epibranchial expanded.

In gerreids (fig. 1) the LPJ consists of two separate elements, but, as in cichlids and haemulids (fig. 3D-I), the right and left parts are so closely united that, functionally, they constitute a median structure. The similarity to the derived LPJ of labroids is heightened by the modification in some taxa of the inner teeth (figs. 1, 3) into a pavement, molariform dentition.

Gerreids also show a slight expansion of the oral margin of the second epibranchial (E2) (fig. 4), but less than that in the pomacentrids examined (fig. 5B, C). The second

epibranchial of the sparoids and haemuloids (fig. 7) studied is not modified in this way. Embiotocids have the oral border of E2 without a keellike expansion, although there is an enlarged uncinat process distally that merges with the oral border (fig. 8B; Stiassny and Jensen, 1987: fig. 14B). In the labrid *Coris* (fig. 11B) and the scarid *Scarus* (fig. 9), the oral border of E2 is expanded respectively in the manner of pomacentrids and cichlids, making embiotocids odd-man-out in this comparison.

Thus a combination of dorsal and ventral gill arch features corroborates a group Labroidei, including cichlids, pomacentrids, embiotocids, and Labridae KL, and within that group features of the dorsal gill arches corroborate a subgroup including embiotocids, pomacentrids, and Labridae KL. Two features of the ventral gill arches suggest a relationship between gerreids and labroids.

Each of the most recent studies of pharyngognath interrelationships begins with a premise that there exists a natural group of families of which the Labridae KL are the most derived. Each has added supporting evidence of the group's naturalness. But the evidence offered pertains entirely to the pharyngobranchial apparatus. Since the time of Müller (1844), one feature has been judged to be crucial; the fused fifth ceratobranchials that form the lower pharyngeal jaw (LPJ). Later studies by Liem and Greenwood (1981), Kaufman and Liem (1982), Stiassny (1981, 1982), Liem (1986), Liem and Sanderson (1986), and especially Stiassny and Jensen (1987) have emphasized additional features: diarthrosis between PB3 and a ventrally projecting, rounded parasphenoid apophysis; a muscular sling, formed from the fourth external levator and obliquus posterior muscles, that suspends the LPJ from the neurocranium; presence of a transversus epibranchialis division 2 of the anterior transversus dorsalis muscle; an undivided sphincter oesophagi muscle; and a first basibranchial lying partially below the longitudinal axis of the basihyal-basibranchial series.

The work of Tarp (1952) and Morris (1982) appears unique in proposing that some pharyngognaths (embiotocids and pomacentrids) are more closely related to some "percoids" (kyphosids, here including scorpidids and gi-

rellids) than they are to other pharyngognaths. In fact, although other authors have refrained from making specific taxonomic proposals, the kyphosids have been mentioned repeatedly in this connection (e.g., Nelson, 1967; Stiassny, 1981; Liem and Greenwood, 1981; Kaufman and Liem, 1982). Also mentioned as possibilities for study are sciaenids, gerreids, and anabantoids. But no other "percoid" family has been considered seriously for inclusion in a group that contains labroids. For Nelson (1967) the kyphosid *Girella* was simply the outgroup for deciding the polarity of labroid characters, as were the anabantoids and other mentioned "percoids" for Liem and Greenwood (1981) in deciding the polarity of cichlid and embiotocid characters, and as were the above-mentioned "percoids" for Stiassny (1981) in making decisions about cichlid, pomacentrid, and embiotocid character polarity.

Hence, in proposing that pomacentrids and embiotocids are sister taxa whose nearest relatives lie with certain nonpharyngognath "percoids," Morris' (1982) and Tarp's (1952) theories stand apart, since they amount to proposals that the Labroidei of Kaufman and Liem are nonmonophyletic.

Ontogenetic data concerning the pharyngeal apophysis of the parasphenoid show that the now well-described labroid condition begins as a V-shaped wedge with the point of the V continuous with an elevated part of the median parasphenoidal ridge from which the posterior or hyomandibular section of the adductor arcus palatini originates. The arms of the V become increasingly thickened by continuing ossification, and eventually are bridged near their tips to form a transverse arthrodial surface heavier at the ends than the middle. This is the pharyngeal apophysis referred to by Liem, Stiassny and others; it extends downward and backward away from the parasphenoid on a bony column or neck that may include bone from the basioccipital (e.g., in certain cichlids). Even in some of the fishes considered previously to be labroids (*sensu lato*), the pharyngeal apophysis retains its original V-shaped structure as a result of failure of the transverse bridging bone to develop fully, as in the pomacentrid *Hypsipops rubicunda*, AMNH 42156. And even in some large cichlids with the transverse bridge, the

underlying V-shaped foundation is still clearly visible (e.g., in *Petenia splendida*, AMNH 28054). The fundamental feature of this apophysis, therefore, appears to be that V-shaped wedge which can be formed entirely from the parasphenoid or from a combination of the parasphenoid and basioccipital.

A V-shaped pharyngeal apophysis that merges anteriorly with a hyomandibular process on a midventral parasphenoidal ridge occurs in gerreids (figs. 19–21), as noted above, as well as in sparoids (figs. 23–25), kyphosids, sciaenids, some centrarchids, and haemuloids. It is associated with hypertrophied LPJs, as noted in Kaufman and Liem (1982), and these authors write of "articulations between the [UPJ] and the basicranium" in gerreids and certain sciaenids, but Stiassny (1981; Stiassny and Jensen, 1987) did not regard these as diarthrodial because of intervening muscle and connective tissues (? a plesiomorphous state of the UPJ-basiocranial character). Kaufman and Liem did not exclude the possibility of a relationship between some of those taxa and labrids, but interpreted all nonlabroid conditions as more primitive. Stiassny (1981) also allowed for the possibility of some linkage among all these taxa.

The problem of the gill arch data—the uncertainty of its significance as evidence of systematic relationship—may be resolved, in part, by (1) treating some of the features as parts of a complex, multistate transformation series, and (2) being aware of the evidence that some pharyngognath features can be induced ontogenetically by diet (i.e., are ecophenotypic). Evidence for ecophenotypy was discussed by Greenwood (1964) for the hypertrophy of the pharyngeal mill of cichlids, whereas Ismail et al. (1982) discussed reasons for believing that the formation of a pharyngeal apophysis on the parasphenoid, or at least, its size, is influenced by "epigenetic factors, due to movements of the UPJ's against the skull floor." In support of their argument, Ismail et al. cited the developmental studies of Bassett (1964, 1971) and Hall (1975).

Returning to the first, or transformational, resolution of the comparative anatomical problem, I envisage the following sequence of character states, from primitive to derived:

1. hypertrophy of the pharyngeal jaws,
2. development of a V-shaped pharyngeal apophysis on the parasphenoid,
3. development of a transverse bony bridge over the arms of the V-shaped apophysis,
4. reduction of connective tissue and muscle over the coalesced toothpatches of the third and fourth pharyngobranchials and the articulation of PB3 with the pharyngeal apophysis on the basicranium,
5. suspension of LPJ from modified fourth external levator and posterior levator muscles,
6. direct bony contact between PB3 and the pharyngeal apophysis,
7. reduction and posterior reorientation of PB2,
8. loss of teeth on PB2,
9. coalescence of the right and left LPJs,
10. development of an articulation between the coalesced LPJs and a notch in the cleithrum.

Item (10) was used by Kaufman and Liem (1982) to define Labridae KL, but Stiassny and Jensen (1987) reported that the pharyngocleithral joint appears to be developed there only in scarids and odacids, whereas there is a very similar joint in certain pomacentrids. Item (9) characterizes embiotocids, pomacentrids, and Labridae KL. Items (7) and (8) characterize embiotocids and Labridae KL. Items (5) and (6) characterize cichlids, pomacentrids, embiotocids, and Labridae KL. Those four groups and gerreids are characterized by (4), and those five and sparoids and most haemuloids (*sensu* Johnson, 1980) by (1–3).

A number of squamipinnate taxa have a well-developed pharyngeal apophysis of a shape, position, and orientation similar to that in the pomacentrid *Hypsipops*, as well as an upper jaw anatomy very like that in many pharyngognaths. I do not regard anabantoids as especially relevant to this general taxonomic problem, because of their distinctive gill arch anatomy.

LABYRINTH FISHES

For functional reasons Liem and Greenwood (1981) included the labyrinth fishes in

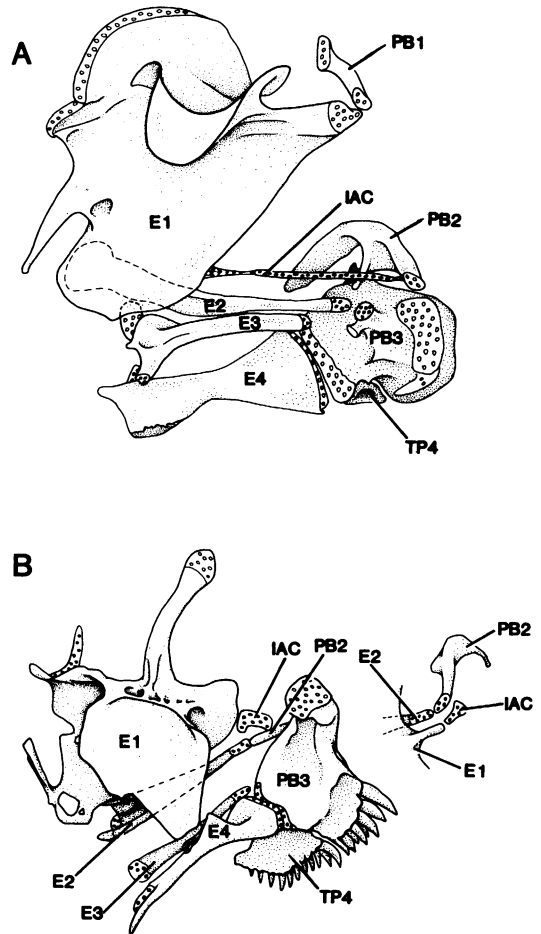


Fig. 28. Left dorsal gill arches in two labyrinth fishes, an anabantid (A) and a belontiid (B). A, *Ctenopoma acutirostrum* Pellegrin, AMNH 42125, dorsal view, showing the highly derived E1 associated with a suprabranchial organ for aerial respiration; B, *Betta splendens* Regan, AMNH 45082, dorsal view illustrating the highly modified E1 with (right) an anterodorsal view showing the relation between PB2 and IAC.

their general discussion of pharyngognathy because of the powerful LPJ and its bite against a tooth-bearing basicranial apophysis; these were described and illustrated in detail by Liem (1963). Liem and Greenwood identified the labyrinth pharyngeal jaws as functionally different from those of labrids and other fishes traditionally combined with them in a Pharyngognathi (cichlids, pomacentrids and embiotocids).

The term Labyrinthici seems to have orig-

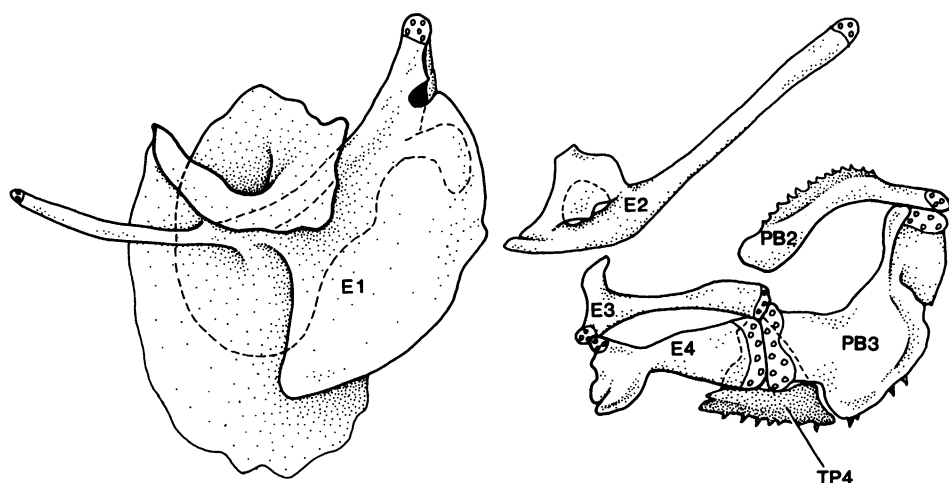


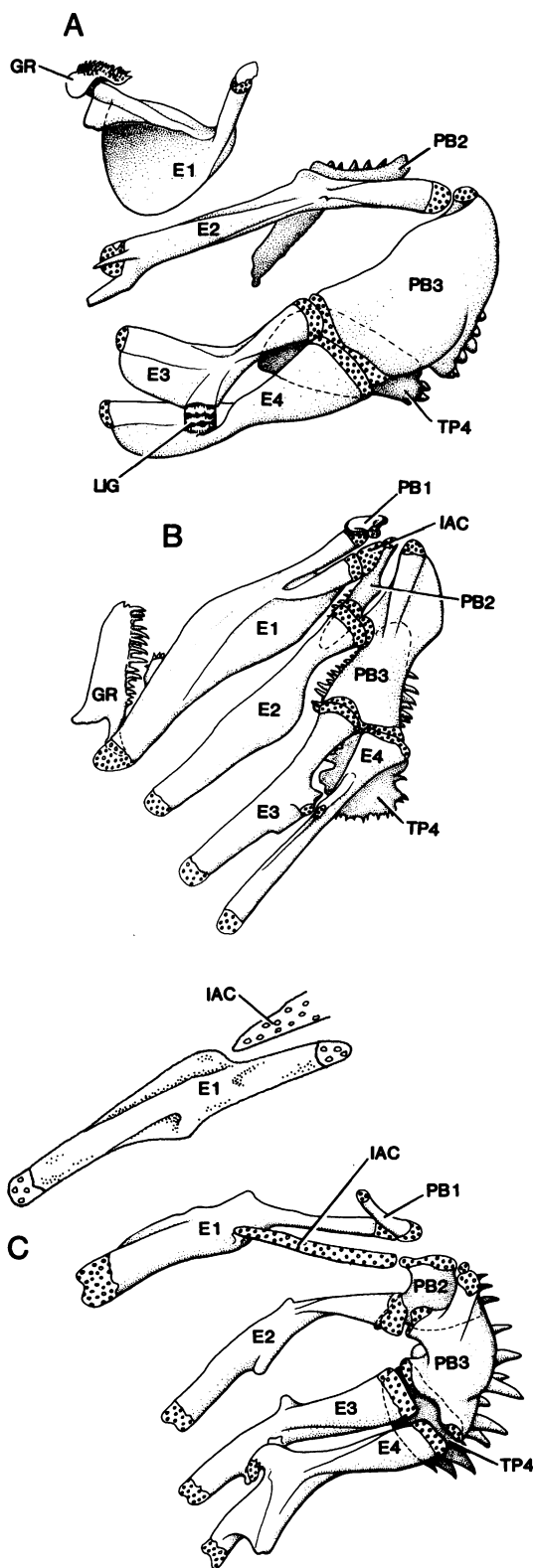
Fig. 29. Left dorsal gill arches of a belontiid, the dwarf gourami *Colisa lalia* (Hamilton Buchanan), AMNH 22110, to show the modified E1 (cf. fig. 28), dorsal view, anterior to left.

inated with Cuvier in vols. 1 (1828) and 7 (1831) of Cuvier and Valenciennes (1828–49) as “acanthoptérygiens à branchies labyrinthiques” or “poissons à pharyngiens labyrinthiformes.” Müller (1845) placed Cuvier’s Labyrinthici (p. 532) or Labyrinthiformes (p. 537) as a family within his order Acanthopteri. Günther (1861) [1859–1879] also treated Labyrinthici as a family, and its contents are equivalent to the Anabantoidei of most current usage (e.g., Liem, 1963; J. Nelson, 1984: Anabantidae, Belontiidae, Helostomatidae, Osphronemidae). Günther placed his Labyrinthici between the nandids and *Luciocephalus*. Gill (1872) used the Labyrinthici as a subdivision of his Acanthopteri, and listed three families (Helostomatidae, Anabantidae, Osphronemidae), with an apparent disclaimer in adopting the group only provisionally as one of five of “very dubious value . . . kept in prominence to attract future examination” (Gill, 1872: xlv). Some subsequent history of ideas on the group, and opinions on relations with Luciocephalidae and Channidae, is in Liem (1963), McAllister (1968), Lauder and Liem (1983), and J. Nelson (1984). Berg (1940) suggested a relationship between Channidae (Ophicephalidae) and Synbranchidae, an idea that was given substance by Lauder and Liem (1983). Gosline (1983) and Travers (1984) proposed a sister-group relationship between the Mastacembelidae and the Synbranchidae, Travers

referring mastacembelids to the Synbranchiformes (an arrangement originated by McAllister, 1968). Gosline (1968, 1971) argued for relationship between the anabantoids (in which he included *Channa* and *Luciocephalus*) and the Badidae, Nandidae, and Pristolepididae. He did not transfer these three “percoid” families to the Anabantoidei, but wrote that “they perhaps should be” (1971: 162); he also hinted (p. 161) that synbranchids might be involved. Barlow et al. (1968) removed *Badis* from the Nandidae as a new family Badidae, and argued (in effect) that it is the sister group of the anabantoids. G. Nelson (1969) found some evidence for relationship between mastacembelids and a nandid, pristolepid, channid, and anabantoid assemblage.

On the question of relationship between badids, nandids, pristolepids, and labyrinth fishes, Liem and Greenwood (1981; also Lauder and Liem, 1983) found further evidence that *Badis* is the sister group of anabantoids, but concluded that their data from functional morphology gave no support to relationship between nandids, *Pristolepis*, and *Channa*, or between any of them and anabantoids. One character relevant to this (fig. 30A, B) is reported below.

Among the eight families that have been associated with the Labyrinthici [Anabantidae, Belontiidae (= Polyacanthidae), Helostomatidae, Osphronemidae, Channidae (=



Ophicephalidae), Luciocephalidae, Synbranchidae, Mastacembelidae], all but the last two are characterized by gill-arch specializations associated with aerial respiration, discussed below. Parasphenoid teeth are present in some (Anabantidae, Belontiidae, Helostomatidae, Osphronemidae, Ophicephalidae); such teeth are not known among synbranchids, luciocephalids [except for Regan's (1909: 768) report], or mastacembelids, but occur in badids, nandids, and pristolepids.

LABYRINTH GILL ARCHES (figs. 28–32): A derived feature that has been taken to characterize labyrinths is a suprabranchial organ associated with a modified first epibranchial (E1). This modified E1 (figs. 28–31) is present in all five anabantoid families (Anabantidae, Belontiidae, Helostomatidae, Osphronemidae, Luciocephalidae) and in channids, but not in synbranchids (fig. 31B) or mastacembelids (fig. 32). The complex E1 and suprabranchial organ are related to adventitious or obligate aerial respiration. The aerial respiration ascribed to mastacembelids, which was one justification for aligning them with synbranchids (McAllister, 1968), is actually inferred from their habit of aestivating, but mastacembelids are not known to have any modification of the dorsal gill arches (Fig. 32) or of anything else (Sufi, 1956) in connection with it. Mastacembelids have neither of the anatomical features (parasphenoid teeth or a modified first epibranchial) characteristic of other labyrinth fishes, and aerial respiration is widespread among teleosts (more than 300 species: Hughes, 1976; J. W. Atz, personal commun.).

Fig. 30. Left dorsal gill arches of a channid (A) and two nandids (B, C), dorsal views. A, *Channa ocellata* (Lacépède), AMNH 10652, B, *Monocirrhus polyacanthus* Heckel, AMNH 22648, C, *Polycentropsis abbreviata* Boulenger, AMNH 43454, with (at top left) a posterior view of E1 showing the absence of an uncinat process associated with IAC, and a platelike ventral expansion. In A and B, note the large, strongly offset comblike gill-raker (GR) associated with the distal end of E1, possibly associated with the development of a suprabranchial organ and a possible synapomorphy between these two taxa. *Monocirrhus* (B) appears to have a primitive (small) IAC, comparable with that in *Kurtus* (fig. 46A), therefore a homoplasy as compared with the long IAC in such nandids as *Polycentropsis* (C).

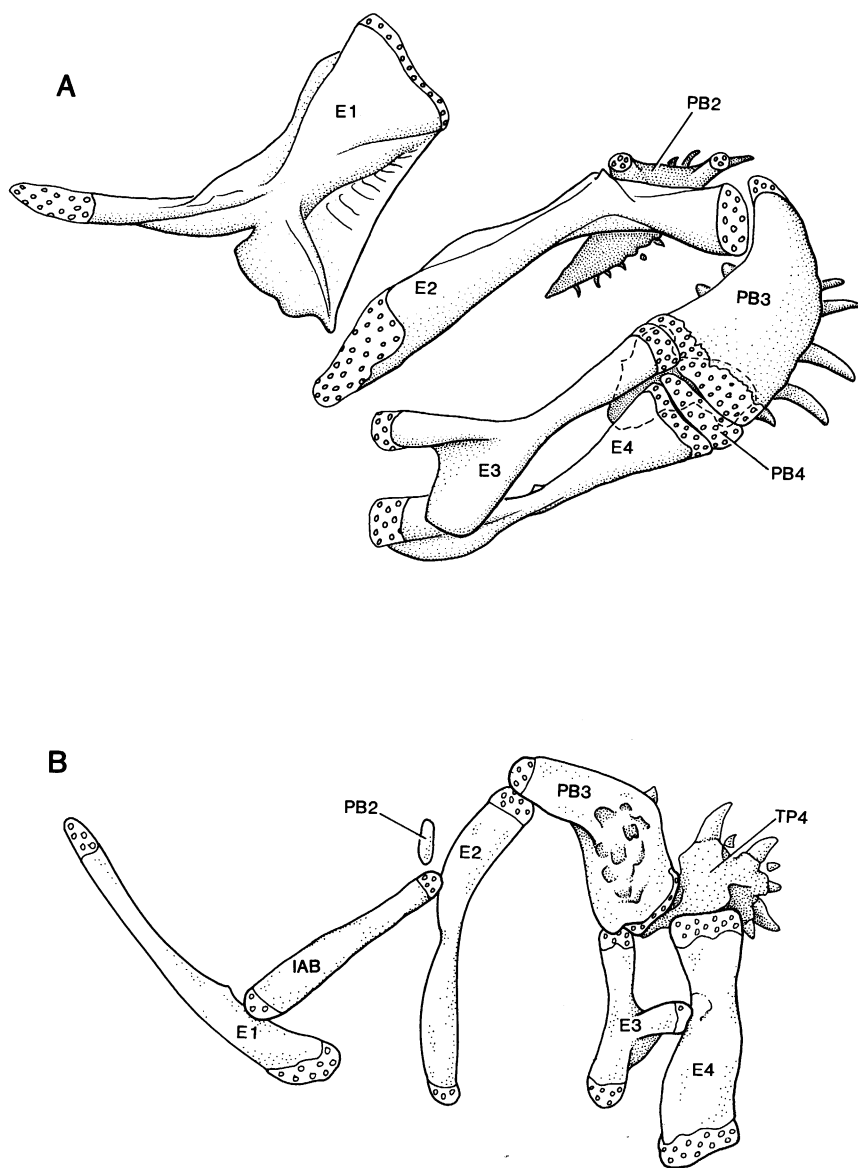


Fig. 31. Comparison of left dorsal gill arches in **A**, the channid *Channa arga* (Cantor), AMNH 10648, and **B**, the primitive synbranchid *Ophisternon aenigmaticum* Rosen and Greenwood, BMNH 1846.2.16-129, dorsal views, anterior up. Note that they share a first epibranchial that is displaced away from the midline.

Gosline's (1968, 1971) and J. Nelson's (1969) alignment of the Nandidae with the labyrinths is supported by the common possession in the Polycentrini and *Channa* of a large, offset, comblike gill raker associated with the first epibranchial (fig. 30A, B; Lauder and Liem, 1983: fig. 59, *Channa*), suggesting that a suprabranchial organ of sorts

might be present in polycentrine nandidids. That proposal is inconsistent with Lauder and Liem's (1983) hypothesis of a sister-group relationship between *Channa* and synbranchids, in which the dorsal gill arches (fig. 30) share little beyond a first epibranchial that is displaced from the midline. Lauder and Liem's hypothesis is also inconsistent with

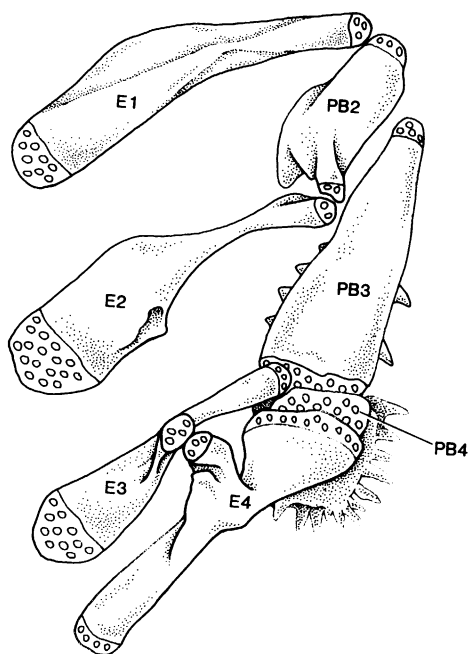


Fig. 32. Left dorsal gill arches of *Rhynchobdella sinensis* Bleeker (= *Mastacembelus sinensis*), AMNH 11078, in dorsal view. Note unmodified E1 and see text for discussion of aerial respiration in mastacembelids. The gill arches yield no anatomic justification for including mastacembelids with the labyrinth fishes.

Gosline's (1983) and Travers' (1984) arguments for a sister-group relationship between synbranchids and mastacembeloids.

COMMENT ON BLENNIOIDS

Lauder and Liem (1983), McAllister (1968), and Gosline (1968) were the last investigators that I am aware of to comment broadly on the general classification of percomorph fishes and of blennioids in particular. Gosline (1968) followed Regan (1929) and recognized a Percoidei (minus the families Gadopsidae, Nototheniidae, Callionymidae, Dracottidae, and most trachinoids). McAllister (1968) recognized the trachinoids as a sub-order distinct from the blennioids. Like Gosline, Lauder and Liem (1983: 172) included some trachinoid families along with the blennioids, implying that what defines the latter applies also to the former. Lauder and Liem cited only Bertin and Arambourg (1958) on the defining characters of blennioids: fishes

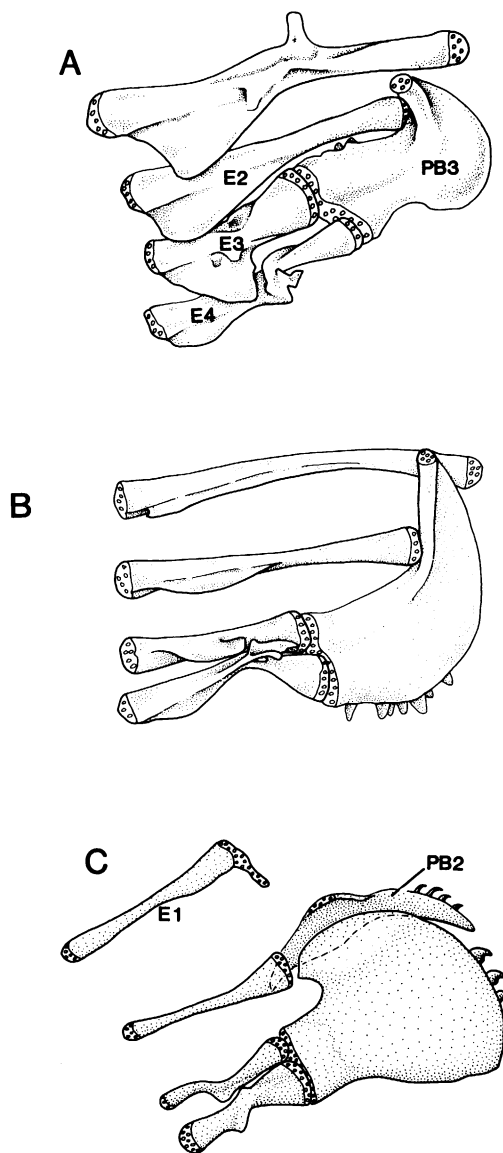


Fig. 33. Left dorsal gill arches of a clinid blennioid (A, B) and a callionymid (C). A, B, *Gibbonsia elegans* (Cooper), USNM 200386, in (A) antero-dorsal and (B) posterodorsal view; the different views obscure the axhead shape of PB3. C, *Synchiropus ? ocellatus* (Pallas), USNM aquarium specimen, dorsal view.

"distinguished by the firm attachment of the fin rays of the pectoral fin to hypertrophied pterygiophores" ("hypertrophied" is merely "well-developed" in Bertin and Arambourg's text).

On the subject of the Blennioidei, I have

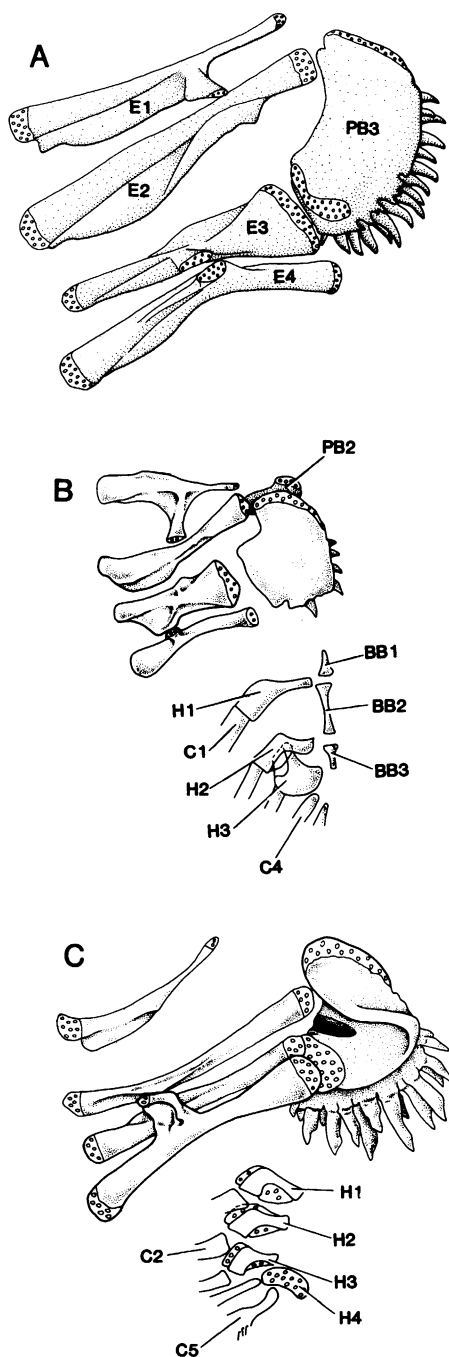


Fig. 34. Left dorsal gill arches of cottoids, dorsal view. **A**, Cottidae, *Myoxocephalus aeneus* (Mitchill), AMNH 20787; **B**, Cottidae, *Oligocottus maculosus* Girard, USNM 188372, with (below) sketch of ventral gill-arch structure; **C**, Cyclopteridae, *Liparis coheni* Able, USNM 213822, with (below) sketch of ventral gill-arch structure—there are no ossified basibranchials.

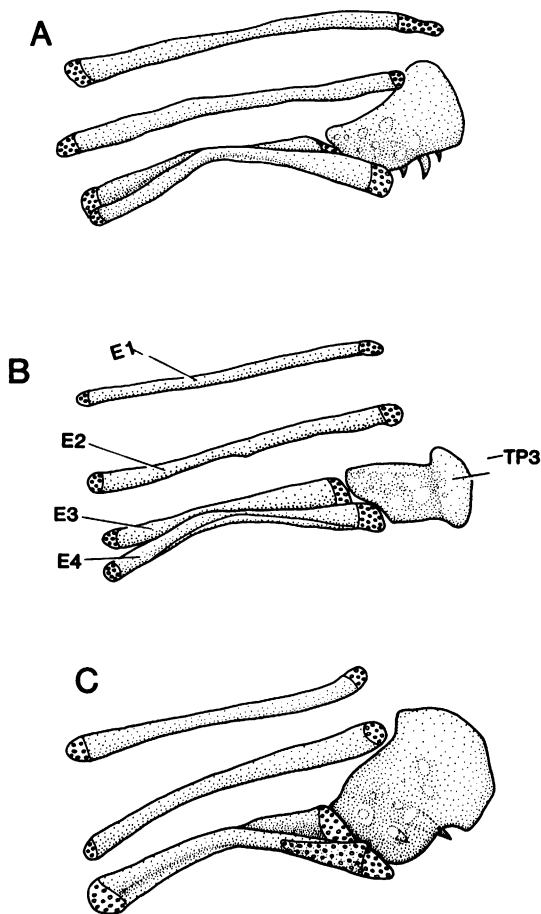


Fig. 35. Left dorsal gill arches of gobiesocids, dorsal view. **A**, *Pherallodus funebris* (Gilbert), AMNH 5557; **B**, *Gobiesox meandricus* (Girard), AMNH 18282; **C**, *Tomocodon fasciatus* (Peters), AMNH 33191. E3 and E4 are directly apposed at their midpoints, and apparently ankylosed. PB3 appears to be represented by the dermal toothplate only, with no endoskeleton.

received much instruction from Victor Springer, who pointed out that blennioids fall into two groups, and gill-arch anatomy is relevant to that distinction. The tropical or “true” blennies lack all but the third pharyngobranchial (PB3), which has the shape of the head of an ax or halberd when viewed from above (figs. 33A, B, 37). This configuration of PB3 occurs in gobiesocids (fig. 35), which also lack PB1, 2 and 4 (as do some cottoids, figs. 34A, C, 47C). It was for these and other reasons that Springer (personal commun.) objected to the alignment of gobiesocids with gadiforms and lophiiforms in

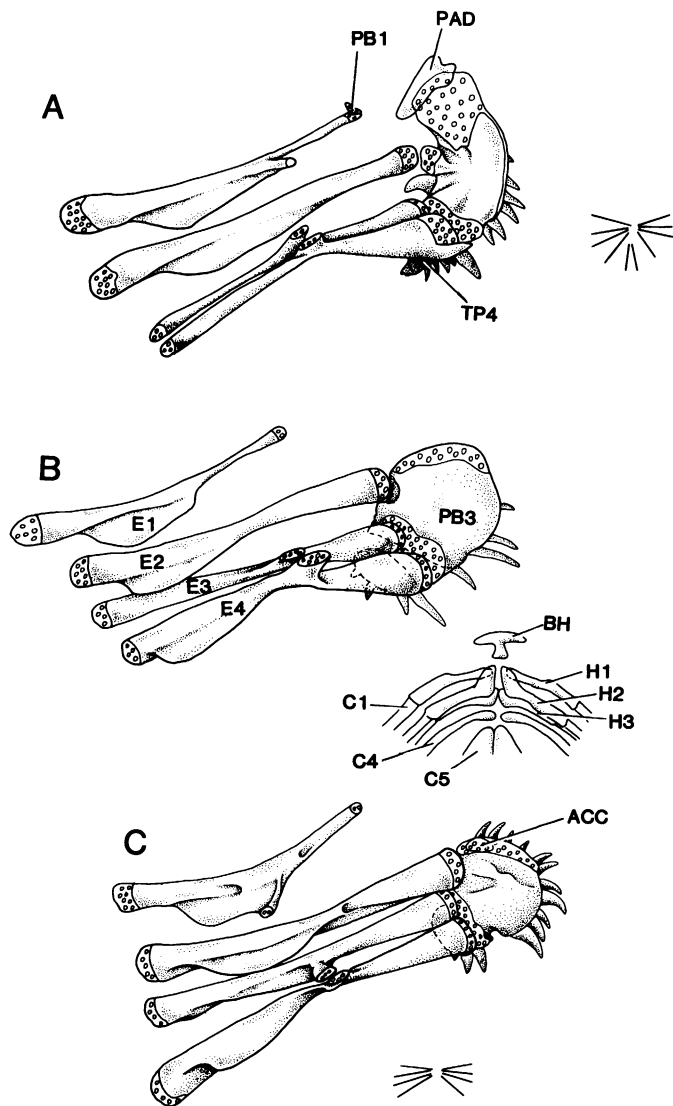


Fig. 36. Left dorsal gill arches of uranoscopids, dorsal view. **A**, *Astroscopus ygraecum* (Cuvier), USNM 185669, with (right) diagram of ventral gill-arch elements converging on an unossified copula; **B**, *Kathetostoma albigutta* (Bean), USNM 185666, with (below right) sketch of ventral gill-arch elements; **C**, *Uranoscopus scaber* L., USNM 198087, with (below) diagram of ventral gill-arch elements, as in **A**.

the Paracanthopterygii (Greenwood et al., 1966; Rosen and Patterson, 1969) instead of with blennioids (Springer's view) or with callionymoids (as Gosline, 1970, had suggested). Callionymoids (dragonets) have a similar halberd-shaped PB3, but have a sizable PB2 tucked under the anterior margin of PB3 (fig. 33C; Nakabo, 1983: figs. 25, 26). Although clingfishes (gobiesocids) might not belong with

paracanthopterygians (Patterson and Rosen, 1989), neither do they belong with dragonets. Clingfishes have the four hypobranchials converging on a short basibranchial copula without ossifications, as do some uranoscopids (fig. 36), but dragonets have a primitive ventral gill arch configuration with well-developed ossified basibranchials (Nakabo, 1983: figs. 25, 26).

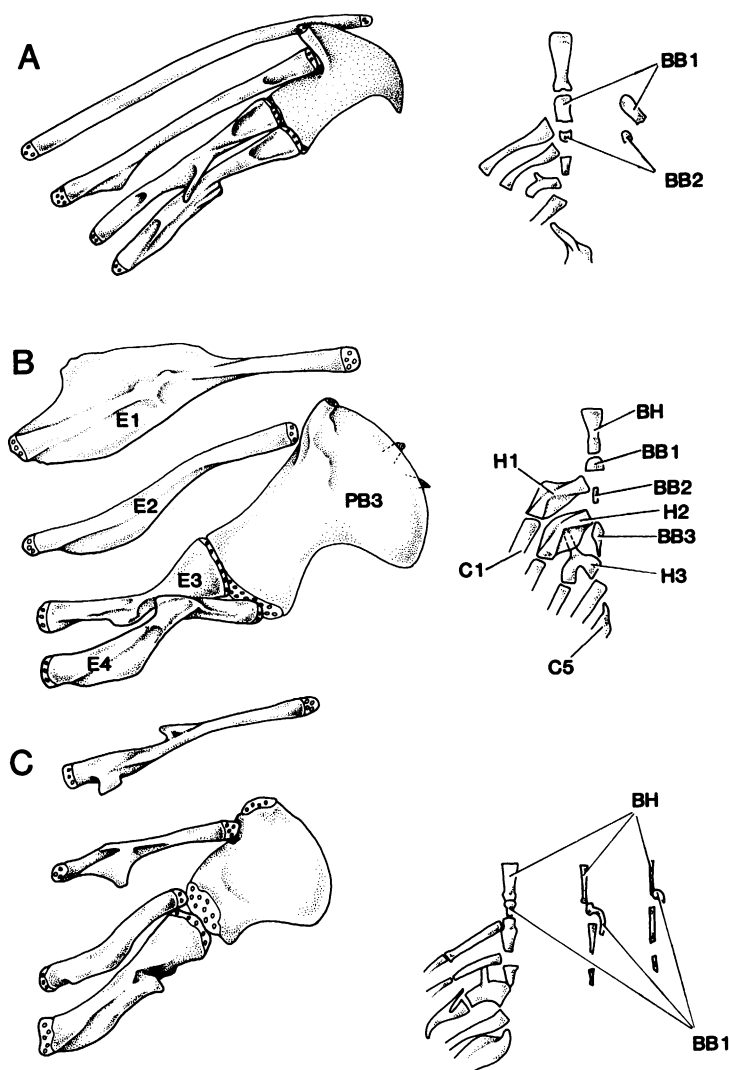


Fig. 37. Left dorsal gill arches of blennioids, dorsal views, with (right) sketches of ventral gill arch elements. **A**, Dactyloscopidae, *Gillelus rubrocinctus* Longley, ANSP uncataloged (BB1-2 are sketched in lateral view at extreme right); **B**, Tripterygiidae, *Gilloblennius tripinnis* (Forster), USNM 214271; **C**, *Blennius trigloides* Cuvier and Valenciennes, USNM 259168-F19 (BH and BB1-3 of this specimen are sketched in lateral view, with a sketch of the same bones in *Blennius normani* Poll, USNM 199533, at extreme right, to show variability in the posteroventral process on BB1, which is short in *B. normani*).

BLENNY GILL ARCHES (figs. 33A,B, 37, 38B, C): Springer also pointed out to me that in blennioids, basibranchial 1 (BB1) has a posteroventral process extending below BB2. But it does not develop to the same extent in all species (fig. 37C). It appears, therefore, that blennioids are characterized by the absence of PB1, 2, and 4, by the shape of PB3, and at least in some taxa, by the presence of an

unusual process on BB1. Springer's views on blennioid classification, in George and Springer (1980: 3), are summarized to restrict true or tropical blennies to the Clinidae (including Ophiclinidae and Peronedysidae), Labrisomidae, Tripterygiidae, Dactyloscopidae, Chaenopsidae, and Blenniidae. The reduced dorsal gill arch anatomy of a single pharyngobranchial (PB3) in the shape of an

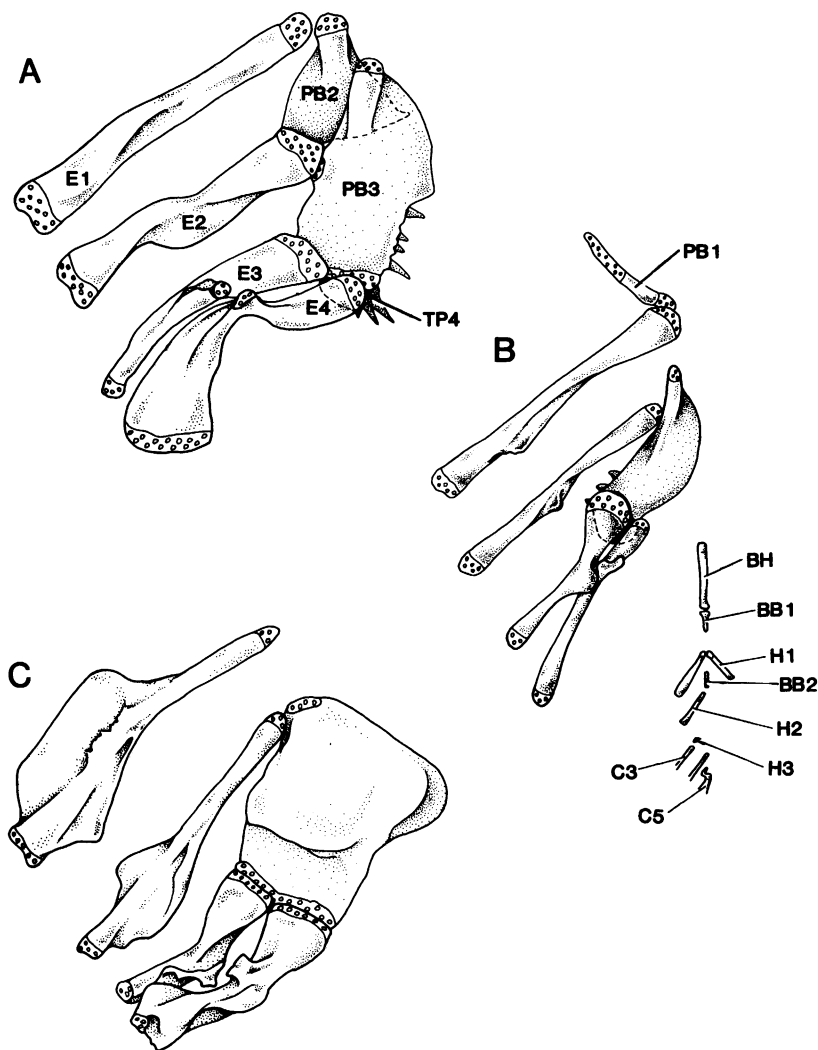


Fig. 38. Left dorsal gill arches of a stichaeid (A) and two blennioids, dorsal views. **A**, Stichaeidae, *Ulvaria subbifurcata* (Storer), USNM 201949; **B**, Chaenopsidae, *Chaenopsis alepidota* (Gilbert), USNM 200391, with (below right) a sketch of the ventral gill-arch elements; **C**, Tripterygiidae, *Lepidoblennius marmoratus* (Bennett), USNM 201625.

ax head is found in all these fishes, except that some chaenopsids (fig. 38B) and labrisomids (Springer, personal commun.) retain PB1. The blennioids of Gosline (1968) included notothenioids, trachinoids, congrogadoids, and zoarceoids as well as (p. 68) a distinct group of tropical blennioids (whose relationship to other fishes "is by no means clear"). The main trouble with this is that the nontropical "blennioids" are rife with primitive features, at least in their dorsal gill arch anatomy.

MONOPHYLETIC GROUPS AND MATERIALS FOR A PERCOMORPH CLASSIFICATION

If there is to be a Perciformes it would have to be defined by having a dorsal gill arch anatomy that includes a long, rodlike interarcual cartilage (IAC) between E1 and PB2. Merely having IAC is not enough, because there are at least six states of IAC in ctenosquamates: (1) the nodule in some myctophids; (2) the short plug in anoplogasterid

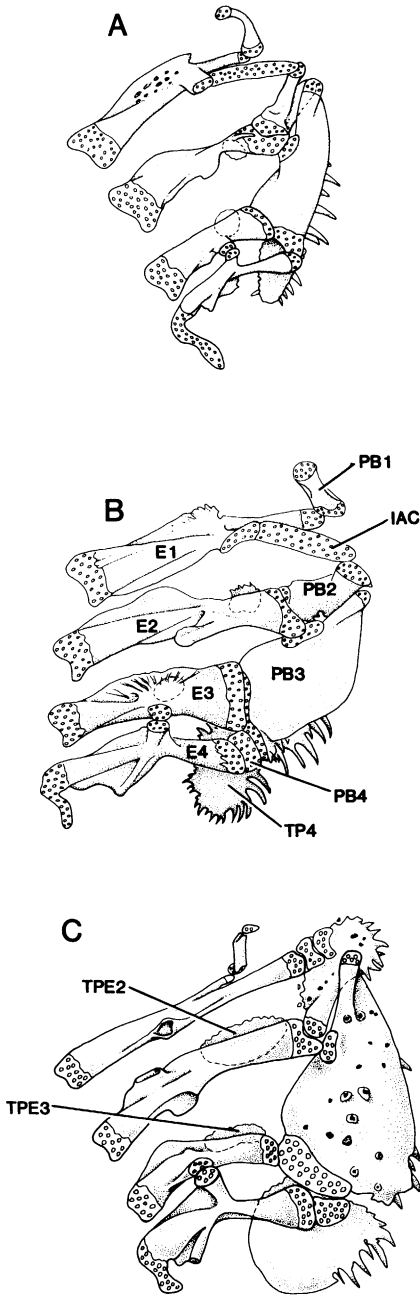


Fig. 39. Left dorsal gill arches of echeneoids (of Johnson, 1984) in dorsal view. **A**, Coryphaenidae, *Coryphaena equisetis* L., AMNH 22117; **B**, Rachycentridae, *Rachycentron canadum* (L.), USNM 260175; **C**, Echeneididae, *Remora remora* (L.), USNM 159685. Johnson (1984) has shown that these three families form a monophyletic group whose sister is the Carangidae; and that within that group, A and B are sister groups. The outlines

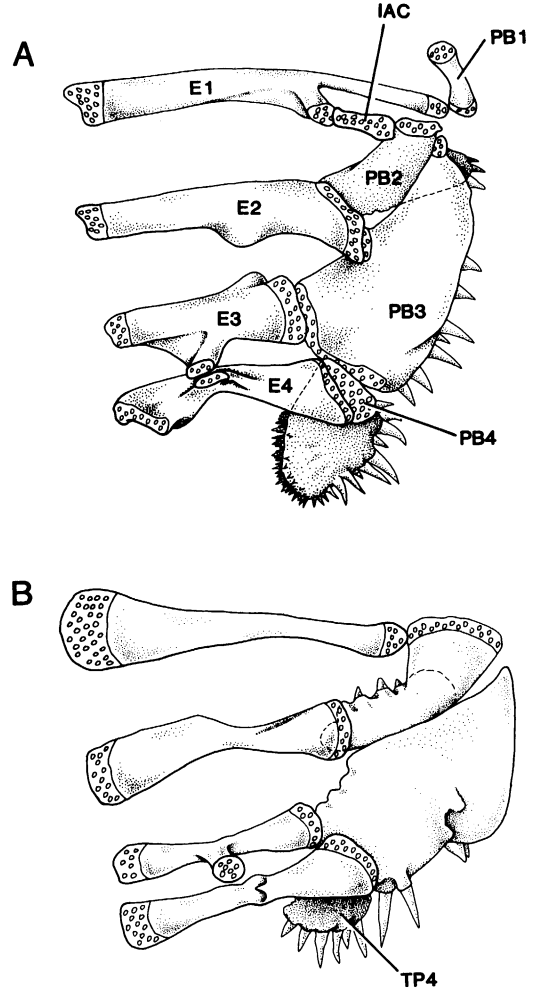


Fig. 40. Left dorsal gill arches of perciforms with unresolved relationships in dorsal view. **A**, Centrarchidae, *Ambloplites rupestris* (Rafinesque), AMNH 39695; **B**, ? Elasmomatidae, *Elassoma zonatum* Jordan, AMNH 21849. The gill arches provide no good reason to regard B as a centrarchid (cf. Johnson, 1984: 465), but according to Chang Chang-Hwa (personal commun., 1988), it appears to be immediately related to centrarchids.

beryciforms and kurtids (fig. 46A); (3) the rodlike form in more normal percoid fishes (e.g., figs. 4, 6); (4) the ossified rod present in synbranchids (fig. 31B) and most carapids

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of toothplates on E2 and E3 are shown by broken lines; these toothplates are not fused to the bones in A, whereas in C TPE2 is free and TPE3 is fused.

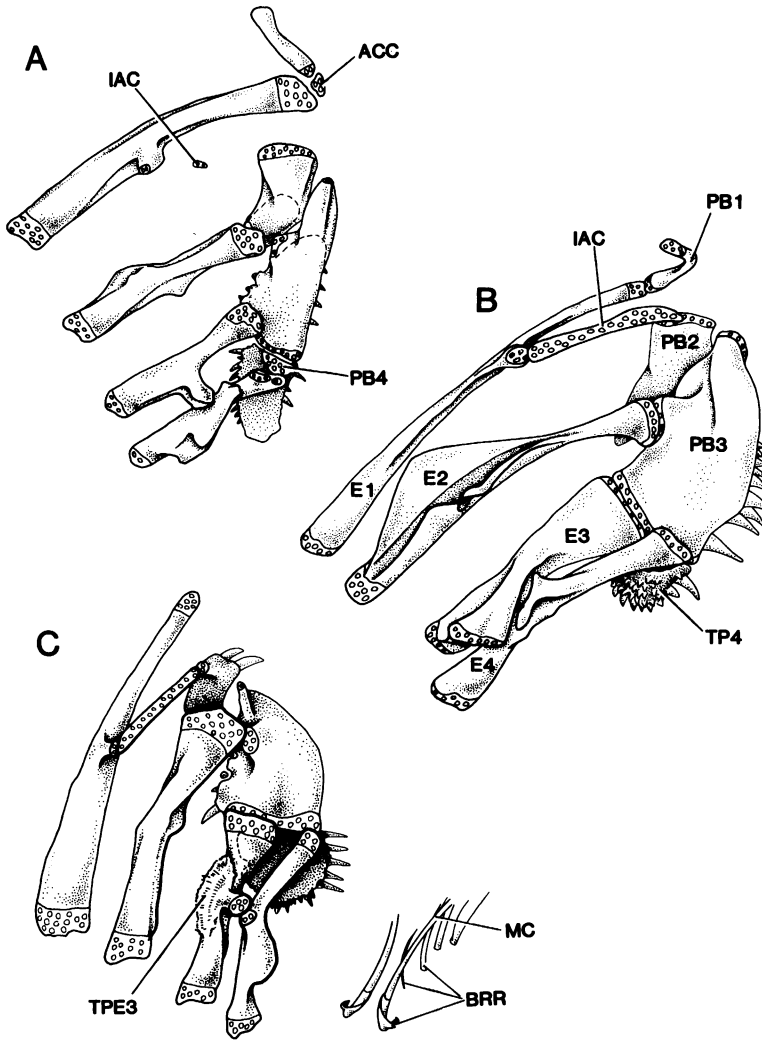


Fig. 41. Left dorsal arches of perciforms with unresolved relationships in dorsal view. A, Cirrhitidae, *Oxycirrhites typus* Bleeker, AMNH 45081; B, Apogonidae, *Apogon townsendi* (Breder), AMNH 23513; C, Mullidae, *Mullus barbatus* L., AMNH 22228 (to right of C is a ventral view, anterior down, of the skeleton of the bases of the mental barbels, with the right branchiostegals).

(Travers, 1981; Patterson and Rosen, 1989: 25); and (5a) a short, stout ligament in the interarcual position, as in *Percopsis* (Patterson and Rosen, 1989: fig. 13) or (5b) a more elongate ligament as in *Raniceps* (Markle, 1989: fig. 2) and *Trichodon* (fig. 48B), which may contain a small IAC close to its attachment to PB2, as in certain gadiforms (Patterson and Rosen, 1989: fig. 12B; Markle, 1989: fig. 3). On the assumption that the

primitive euteleostean condition is direct contact between the cartilaginous tips of the uncinate processes of EB1 and PB2 (Rosen, 1973: figs. 3, 5, 58; Travers, 1981: fig. 14), I presume that the varieties of condition (5) are derived relative to conditions (1) to (3), and that among those three, condition (1) is primitive, (2) is somewhat more derived, (3) is the derived "percoid" condition, and (4) is surely derived from (3). This means that

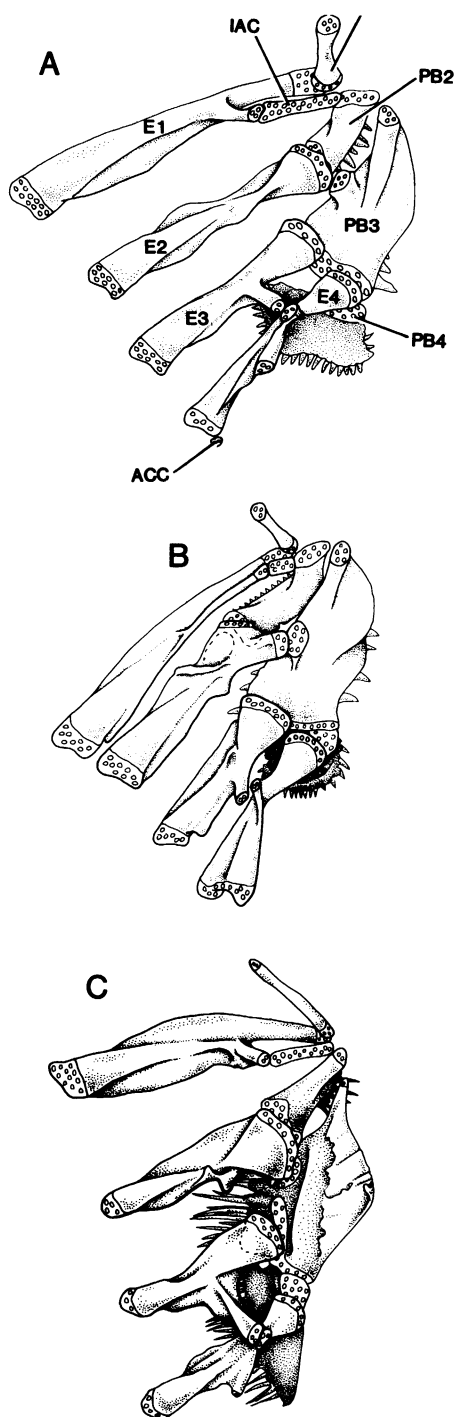


Fig. 42. Left dorsal gill arches of perciforms with unresolved relationships in dorsal view. A, Lobotidae, *Lobotes surinamensis* (Bloch), AMNH

pharyngognaths and labyrinths, atherinomorphs, and paracanthopts as newly defined (Patterson and Rosen, 1989) are linked with perciform acanthopterygians since some pleiomorphic members of all these groups have condition (3) [e.g., labroids (fig. 5) and gerreids (fig. 4), some anabantoids (fig. 28), "atherinoids" (Rosen and Parenti, 1981: figs. 6–9), and ophidioid ophidiiforms (Patterson and Rosen, 1989: fig. 13F, G, H)], unless some of the IACs are homoplastic. The absence of IAC when E1 lacks an uncinat process, or PB2 is small or absent, is certainly likely to be secondary, as in some gadiforms and in bythitoid ophidiiforms among paracanthopts (Patterson and Rosen, 1989; Markle, 1989), some atherinomorphs (Rosen and Parenti, 1981: figs. 14–17), and various acanthopts illustrated here (e.g., figs. 33–38, 44A, B, 47C).

One view of the problem of percomorph relationships seems to boil down to discovering how to link the Pharyngognathi, Squamipinnes, Labyrinthici, Plectognathi, Scombroidei, atherinomorphs, and paracanthopts with a monophyletic Percoidei and with some but not all "beryciforms," and, when assembled in some corroborated hierarchy, all of those with polymixiids and myctophids. Previously I have suggested how the occipital region (Rosen, 1985) and the caudal skeleton (Rosen, 1984) might be used to cluster some taxa to these major groups.

For reasons perfectly illustrated by Regan's (1913) conclusion that about 60 percent of his 95 percomorph families had to be left unresolved in his equivalent of our Percoidei, a nongroup defined by symplesiomorphies ("the absence of the special peculiarities which characterize the other suborders," p. 112), the intrarelationships of percomorphs have justly been considered one of ichthyology's major unsolved problems. Some contributions on this problem (e.g., Gosline, 1968) accepted Regan's solution by treating the Percoidei as a natural group with defining characters. Johnson (1975, 1980, 1984, 1986) and

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22125; B, Toxotidae, *Toxotes jaculatrix* (Pallas), AMNH 1969-79 (TPE2 shown by broken lines); C, Malacanthidae, *Hoplostethus starcki* Randall and Dooley, AMNH 38129.

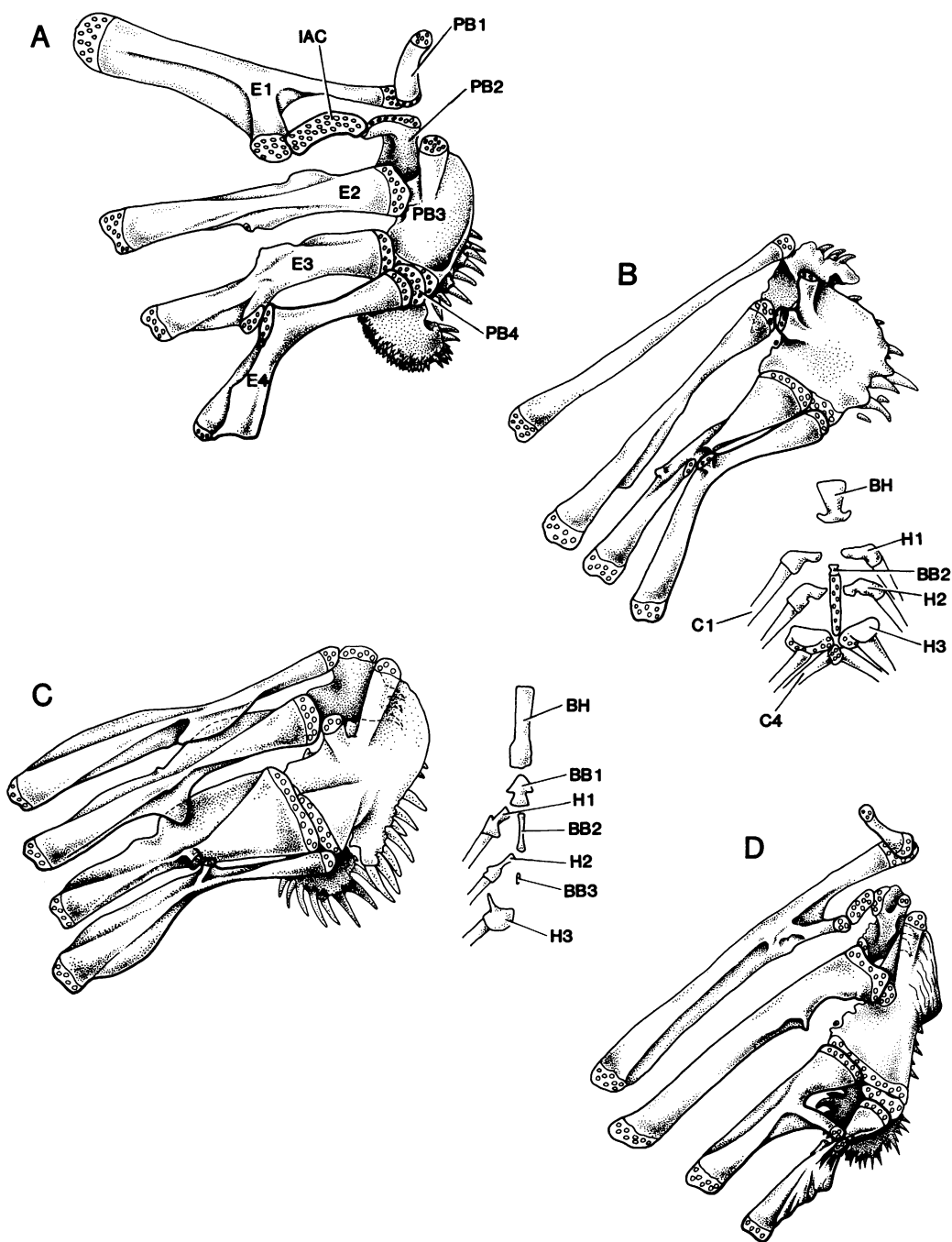


Fig. 43. Left dorsal gill arches of perciforms with unresolved relationships in dorsal view. **A**, Bathyclupeidae, *Bathyclupea hoskynii* Alcock, AMNH 22067; **B**, Leptoscopidae, *Leptoscopus macropygus* (Richardson), USNM 213490, with sketch of ventral gill-arch elements; **C**, Percophidae, *Hemerocoetes monopterygius* (Schneider), USNM 214077, with sketch of ventral gill-arch elements; **D**, Polynemidae, *Polydactylus sexfilis* Cuvier and Valenciennes, USNM 214123.

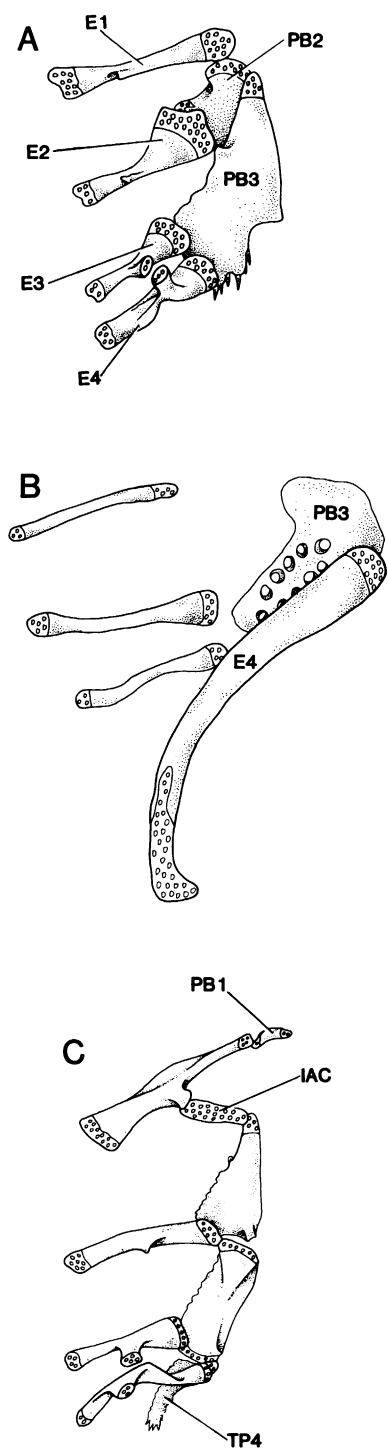


Fig. 44. Left dorsal gill arches of acanthomorphs with unresolved relationships in dorsal view. **A**, Gasterosteidae, *Culaea inconstans* Kirtland, AMNH 40320; **B**, Pegasidae, *Pegasus volitans* L., AMNH 13876 (10 large, clublike teeth on TP3 are shown in transparency); **C**, Ammodytidae, *Ammodytes americanus* DeKay, AMNH 21897.

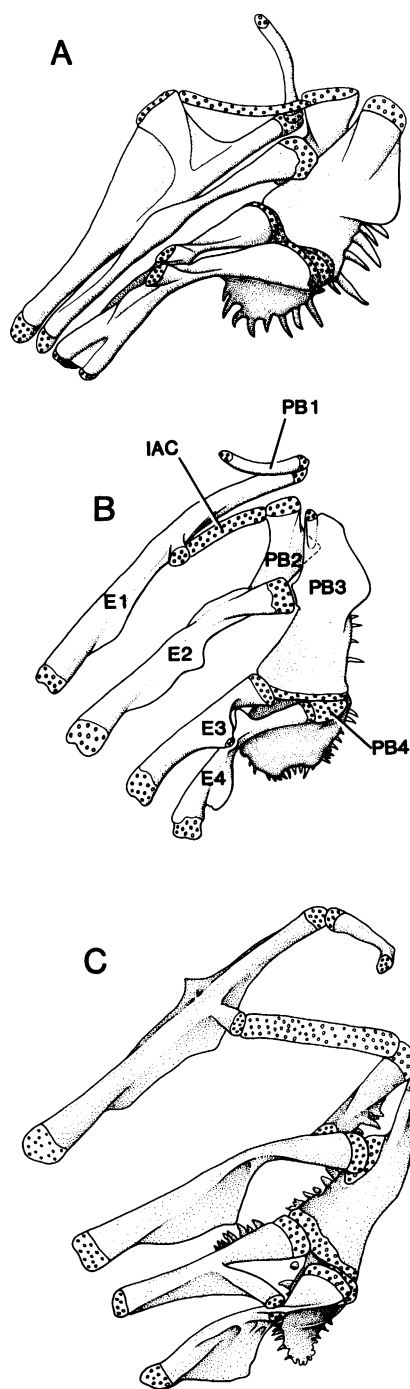


Fig. 45. Left dorsal gill arches of perciforms with unresolved relationships in dorsal view. **A**, Priacanthidae, *Pristigenys alta* (Gill), AMNH 29378; **B**, Grammidae, *Gramma loreto* Poey, AMNH 23811; **C**, Sciaenidae, *Isopisthus parvipinnis* (Cuvier and Valenciennes), AMNH 20764.

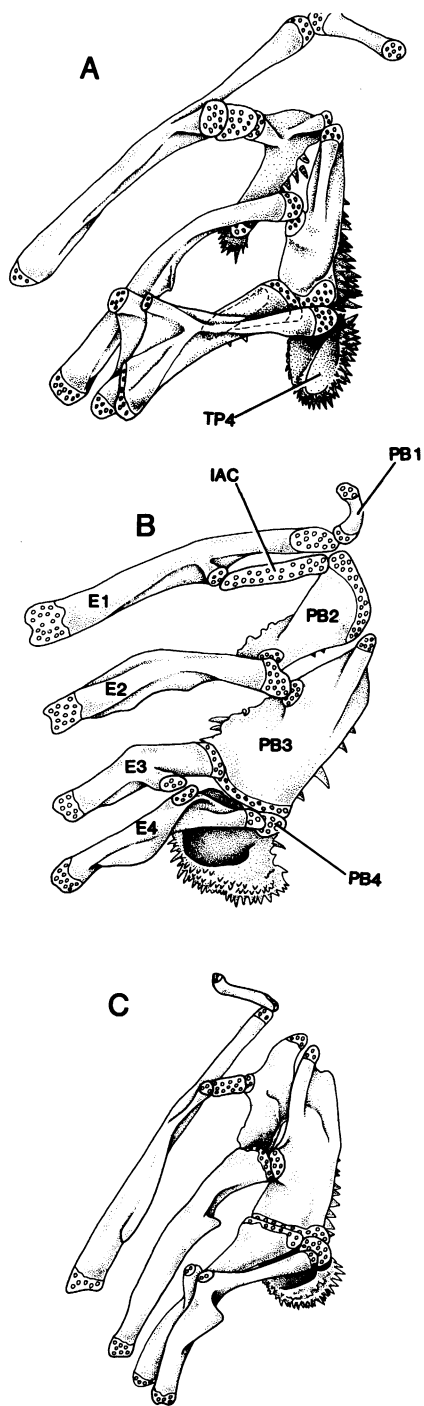


Fig. 46. Left dorsal gill arches of perciforms with unresolved relationships in dorsal view. A, Kurtidae, *Kurtus gulliveri* Castelnau, AMNH 1969-105 (toothplate fused to E3 shown by broken line); B, Percidae, *Perca flavescens* L., AMNH 22340; C, Serranidae, *Rhytichthys bistrispinus* (Mitchill), AMNH 14890.

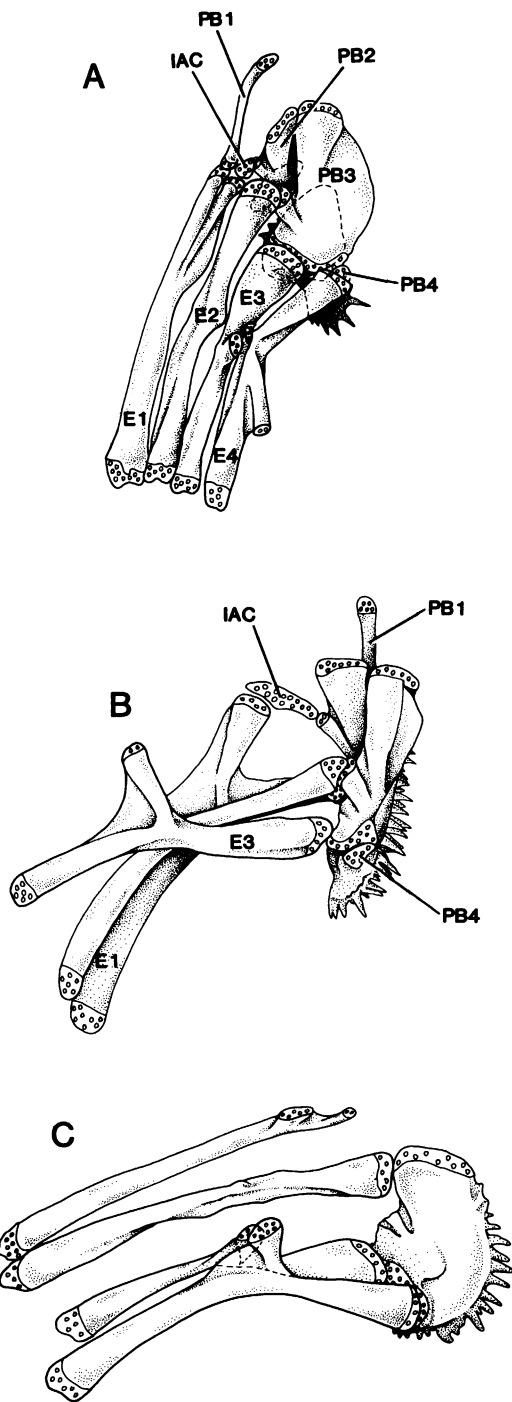


Fig. 47. Left dorsal gill arches of scorpaeniforms. A, B, Scorpaenidae, *Ectreposebastes imus* Garman, AMNH 27991 (B, in posterior view with E4 removed); C, Icelidae, *Icelus spiniger* Gilbert, USNM 208352.

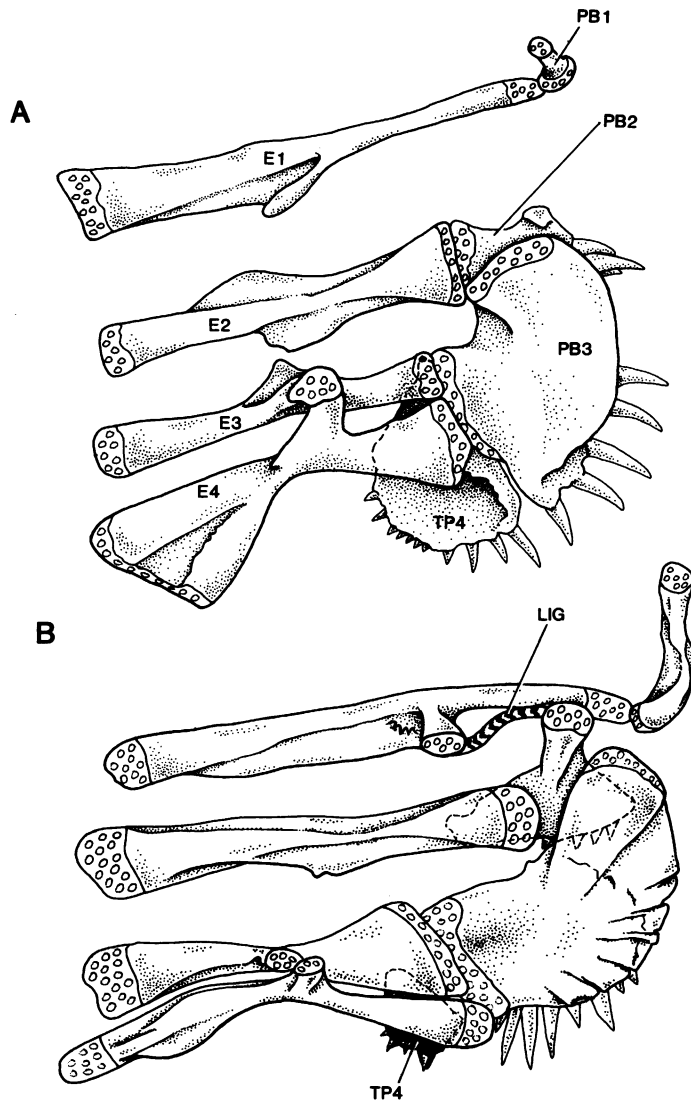


Fig. 48. Left dorsal gill arches of perciforms with unresolved relationships in dorsal view. **A**, Mugiloididae, *Parapercis ommatura* Jordan and Snyder, AMNH 26921; **B**, Trichodontidae, *Trichodon trichodon* (Tilesius), USNM 213532.

Rosen (1984, 1985) attempted a simplification by assembling the families of percormorphs (J. Nelson, 1984, listed 149 families in Perciformes) into cladistically defined natural groups to reduce the scope to the more manageable one of interrelationships among ten groups: the scombroids (Collette et al., 1984; Johnson, 1986), gobioids (Hoese, 1984; Springer, 1983, 1988), Pharyngognathi, Labyrinthici, plectognaths (Rosen, 1984), blennioids (Rosenblatt, 1984; Springer, in progress), Squamipinnes (Mok and Shen, 1983;

Tyler et al., 1989), atherinomorphs (Rosen and Parenti, 1981), scorpaeniforms, and a revised Paracanthopterygii (Patterson and Rosen, 1989). In this scheme there is left a smaller residue of percoid families about each of which questions of taxonomic affinity can be asked in relation to one or more of those 10 groups listed above. The same reasoning applies to the various "beryciform" taxa. Alternatively, some of the 10 core groups and a few of the leftover "percoids" might be linked on the basis of characters of general

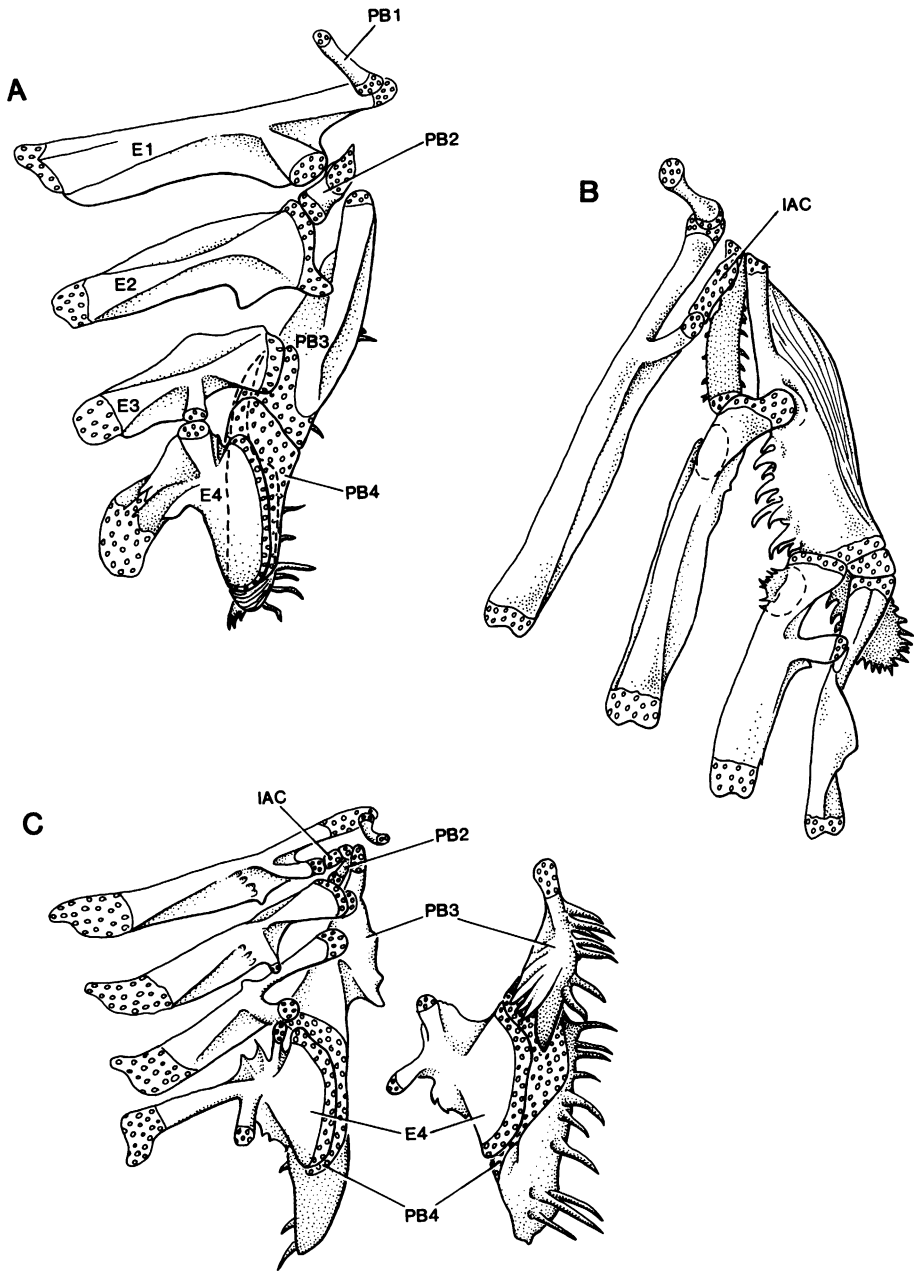


Fig. 49. Left dorsal gill arches of stromateoids and pomatomids, dorsal views. **A**, Nomeidae, *Nomeus gronovii* (Gmelin), AMNH 22249 (broken line beneath head of E3 is outline of a membranous extension of TP4 along lateral face of PB3); **B**, Pomatomidae, *Pomatomus saltatrix* (L.), AMNH 18804 (toothplates on E2, free, and E3, fused to bone, are shown by broken lines); **C**, Stromateidae, *Peprilus triacanthus* (Peck), AMNH 1808, with (right) medial view of PB3, 4, and head of E4.

applicability such as Johnson's (1975) caudal spur, occipital anatomy (Rosen, 1985), caudal skeletal features outlined in Rosen (1984),

and perhaps features of the dorsal gill arches, as sampled in figures 39–50. There will always be a residue of taxa that are difficult to

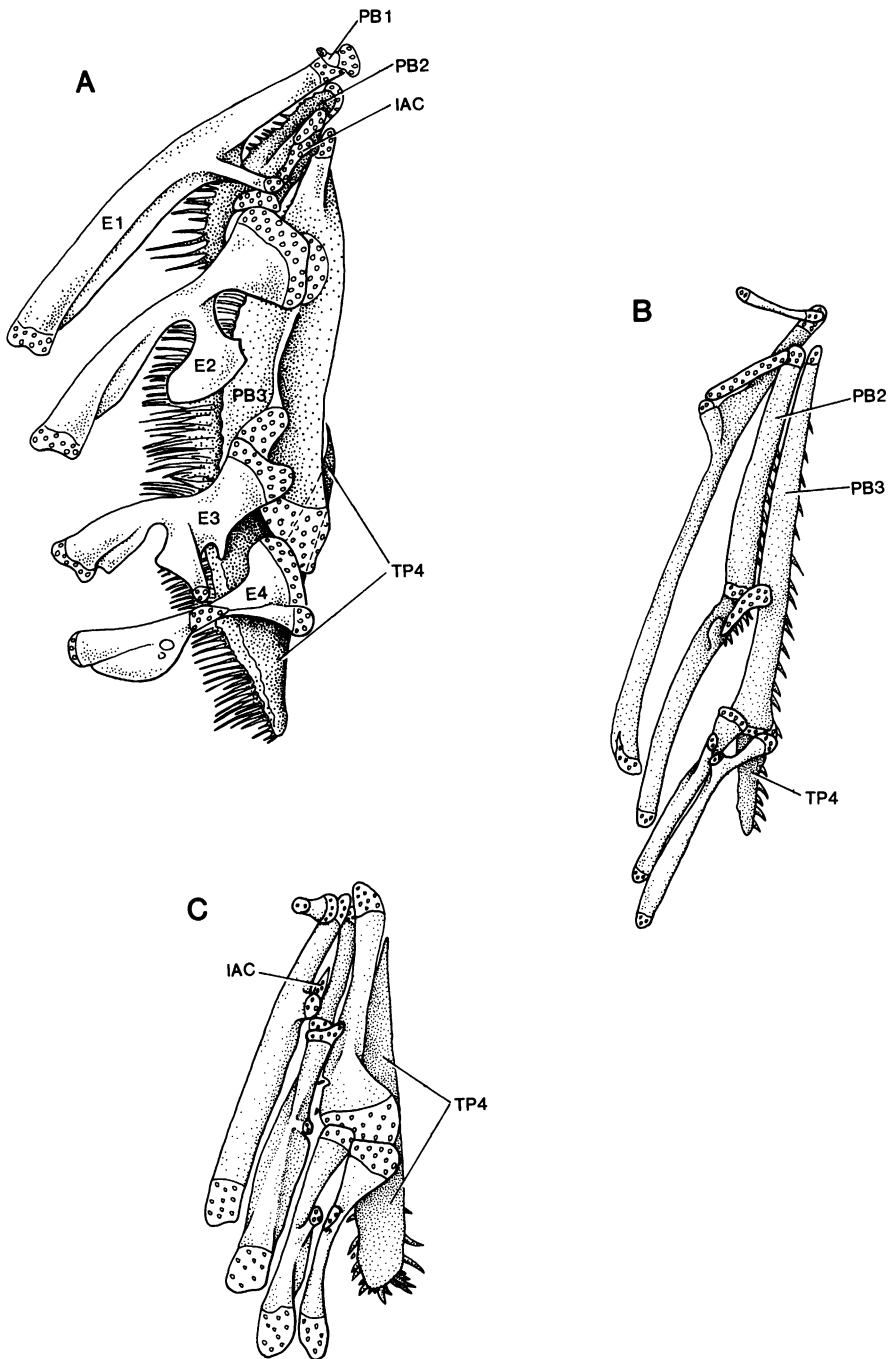


Fig. 50. Left dorsal gill arches of scombroids, dorsal views. A, *Scomber australasicus* Cuvier, AMNH 26894; B, *Trichiurus* sp., AMNH 17566; C, *Xiphias gladius* L., AMNH 15657.

assign, but the problem of percomorph classification appears to be somewhat simpler than it was for Günther (1859–1870), Good-

rich (1909), Regan (1913, 1929), Jordan (1923), Berg (1940), McAllister (1968), Greenwood et al. (1966), and J. Nelson (1976,

1984), although simplification carries no implication of correctness and I am not so naive as to believe that, after reading Gill (1872), I might only be reinventing the wheel. But perhaps we need to invent a new wheel before some of the larger questions of relationship can be dealt with. The narrative is still unconvincing, adorned as it is with significant bald spots.

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