

GILL ARCHES AND THE
PHYLOGENY OF FISHES, WITH
NOTES ON THE CLASSIFICATION
OF VERTEBRATES

GARETH J. NELSON

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INTRODUCTION

THE DERMAL SKELETON associated with the endoskeletal gill arches of fishes is developed in different ways and to markedly varying degrees. To date, however, this part of the dermal skeleton has received little study, with respect either to its basic structure or to its interspecific and intraspecific variability. For teleostome fishes, osteological studies have usually dealt only superficially with the gill arches and in many instances have not included any distinction between their dermal and endoskeletal parts. Frequently, for example, purely dermal elements have been given names more correctly reserved for endoskeletal elements. Contributing to this confusion is the complicating fact that some skeletal elements of the gill arches of a given fish are of a compound nature, including both dermal and endoskeletal components.

Although it breaks down at some levels of analysis (see, e.g., Jarvik, 1959, p. 49), a clear distinction between the dermal skeleton and endoskeleton in the head of fishes seems both possible and necessary for routine anatomical and systematic studies. With respect to the gill arches, this distinction has long been recognized (e.g., in the works of Ridewood, 1904-1905; Gregory, 1933, p. 90; and Rauther, 1940, pp. 444-445) but generally has been overlooked in descriptive accounts and in attempts to bring gill-arch evidence to bear on questions of relationship. Elsewhere (Nelson, 1966, 1967b, 1967c, 1967e, 1968a) the writer, in studies of gill arches of various teleostean groups, introduced a terminology for the dermal elements that morphologically appear to be the most stable, and attempted various interpretations of their functional, phylogenetic, and systematic significance. These studies did not include a detailed consideration of the observational bases of this terminology and of the various interpretations suggested. What follows, therefore, is a more detailed consideration of the dermal gill-arch skeleton with emphasis on that of the Teleostomi. The major phyletic trends involving the dermal gill-arch skeleton are outlined, and some gill-arch characters of apparent systematic significance are considered. An analysis of the

tooth plates of the basibranchial complex has led to a consideration of their supporting endoskeleton, and suggests certain comparisons with elasmobranchs. For this structural complex a new interpretation is offered, one accounting for the variation long known to occur among gnathostome fishes. From the standpoint of gill-arch structure, probable phyletic relationships among the major fish groups are expressed in a provisional higher classification of the vertebrates, including tetrapods.

MATERIAL AND ACKNOWLEDGMENTS

The present paper is in large measure based on personal examination of Recent and fossil fish specimens. The techniques used are the same as those described by the writer in previous papers. Photographs are untouched and in general are of alizarin-stained material. Specimens were made available through the courtesy of the following persons and institutions: Dr. Reeve Bailey, University of Michigan; Dr. William Gosline and Dr. Barry Muir, University of Hawaii; Dr. P. Humphry Greenwood and Dr. Colin Patterson, British Museum (Natural History); Dr. Earl Herald, California Academy of Sciences; Prof. Erik Jarvik, Dr. Tor Ørvig, and Prof. Erik Stensiö, Swedish Museum of Natural History; Prof. Eigel Nielson, Mineralogical Museum, Copenhagen; Dr. Bobb Schaeffer, the American Museum of Natural History; and Mr. Loren Woods, Field Museum of Natural History. The writer is indebted to Mrs. Norma Rothman of the American Museum of Natural History for processing serial sections and preparing figures, and to Mr. U. Samuelson of the Swedish Museum for photographing a specimen of *Acanthodes*. The opportunity for study in European museums was made possible by a National Science Foundation Postdoctoral Fellowship (No. 46007). This study was completed at the Department of Ichthyology of the American Museum of Natural History, the fish collections of which, including one large individual of *Latimeria*, supplied much of the material on which this study is based.

TERMINOLOGY OF GILL-ARCH ELEMENTS

The following terms are applied to the endoskeletal gill-arch elements: basibranchial, hypobranchial, ceratobranchial, epi-branchial, infrapharyngobranchial, and suprapharyngobranchial. The dermal elements most conveniently are called tooth plates, or gillrakers, and named according to which elements support them, with the exception of the plates supported by the fifth ceratobranchials, called lower pharyngeal tooth plates, and those associated with the infrapharyngobranchials, called upper pharyngeal tooth plates. In many cases these tooth plates are fused with their endoskeletal supports, and the compound bones are called, respectively: lower and upper "pharyngeals" or "pharyngeal bones," in some cases also "infrapharyngeals" and "suprapharyngeals," or "hypopharyngeals" and "epipharyngeals."

BASIBRANCHIALS

The term basibranchial never has been consistently and logically applied. Some authors have used it to designate the separate elements of the basibranchial complex of bony and cartilaginous structures; others, only for the ossifications present; others, for theoretical subdivisions, cartilaginous or ossified, that they believed were parts of some compound element, which they believed contained more than one basibranchial; and still other authors, erroneously to describe the dermal tooth plates that overlie the actual endoskeletal basibranchials. It is evident that one term cannot be used in all these senses and still retain much meaning. Accordingly, basibranchial is given here a more restricted definition, namely, the median part of the gill-arch endoskeleton, ossified or not, that primitively lies between successive paired arch-elements, regardless of the nature of the subdivision in the basibranchial series. For the teleostomes, established usage dictates that a basibranchial be given the name or number of the paired arch-elements behind it (for elasmobranchs, see below). For teleostomes, this dictum fairly reasonably can be applied to the definition given above, with the understanding that each basibranchial probably is not a simple derivative of the paired arch-elements. Thus, the posterior element of the

basibranchial series in teleosts, as is often the case, extends posteriorly beyond the paired fifth arch-elements and could be said to include basibranchials 4-6, without the implication that a sixth branchial arch somehow is involved.

Thus defined, the term "basibranchial" would be applicable to a cartilaginous part of a larger element, with or without ossification centers, to a center of ossification, and coincidentally to an independent element (one separated from adjoining elements by articular surfaces). Independent elements are best referred to as "copulae," with a notation of which basibranchials they contain. Thus the basibranchial series in teleosts may be said ordinarily to be formed of three copulae: one (composed of the basihyal) and two others, the anterior (copula 1-3) usually including three ossified basibranchials, and the posterior (copula 4-5, or 4-6) consisting of a single cartilage representing two or three non-independent basibranchials.

BASIBRANCHIAL TOOTH PLATES

The median tooth plates can be designated according to which basibranchial elements support them. The condition of many primitive teleosts (e.g., *Elops*, pl. 79, fig. 3; Nelson, 1968a, fig. 1) includes a basihyal tooth plate (BHP), a basibranchial tooth plate 1-3 (BP 1-3), and basibranchial tooth plate 4 (B4P). In other teleosts (e.g., *Osteoglossum*) a large tooth plate (BPH-3) extends from the tip of the basihyal to the posterior end of the third basibranchial. The paired tooth plates, generally associated with particular arches, are given no special terminology.

HYPOBRANCHIALS, CERATOBANCHIALS, AND EPIBRANCHIALS

There is confusion in the literature concerning the terms epihyal, ceratohyal, and hypohyal, and the homology of the skeletal elements to which these terms are applied. Some authors (e.g., Harder, 1964, p. 27; Harrington, 1955, p. 282; Jordan, 1905, p. 45; McAllister, 1968, pp. 5, 6; Mujib, 1967, p. 1318; Norden, 1961, p. 688; Starks, 1901) have recognized the following paired, endoskeletal hyoid elements in teleostomes: hyomandibula, symplectic, interhyal (stylohyal), epihyal, ceratohyal, and one or two hypohyals. Anatomists, however,

have long almost universally agreed that the elements supporting the branchiostegal rays of teleostomes do not include an epihyal (a serial homologue of the epibranchials) and in general have agreed that the hyomandibula either wholly or in part is the real epihyal (Allis, 1915, p. 620; 1928; Bertmar, 1959, p. 327; Daget, 1964, pp. 293-296; De Beer, 1937, p. 415; Devillers, 1958, p. 612; Edgeworth, 1926; 1935, pp. 85-88; Fox, 1963, p. 804; Gaupp, 1905, p. 904; Goodrich, 1930, p. 405; Gregory, 1933, pp. 80-81; Holmgren, 1943, p. 85; Jarvik, 1954, p. 75; Parker, 1882, p. 165; Rauther, 1940, p. 443; Regan, 1923, p. 450; Schmalhausen, 1950, pp. 440-441). Those authors accepting this homology had to find another name for the ventral arch-element that previously had been called the epihyal. Usually this problem was solved by calling it a "posterior ceratohyal," and calling the old ceratohyal an "anterior ceratohyal," the assumption being that the ceratohyal ossifies in two parts. The problem with this solution is that in teleostomes these two parts possibly are the serial homologues of the ceratobranchials and hypobranchials (see below, and also Daget and d'Aubenton, 1957; Nelson, 1968b). If so, the paired, hyoid-arch elements below the interhyal require renaming, with the "hypohyals" given an entirely new name (the alternative, to rename the ceratobranchials and hypobranchials, as was done by Daget and d'Aubenton, 1957; see also d'Aubenton, 1961, p. 152; Daget, 1964, p. 292, who used the names "*ceratobranchial supérieur*," and "*ceratobranchial inférieur*," respectively, would seem to be an additional and needless complication). In the present paper a neutral terminology is applied. The ventral, paired, hyoid arch-elements here are divided into medial and lateral groups, the medial in teleosts being subdivided into dorsal (which could be called dorsohyal) and ventral (ventrohyal) elements (the so-called hypohyals), the lateral in most teleostomes including anterior (anterohyal) and posterior (posterohyal) elements (the so-called ceratohyals, or ceratohyal and epihyal).

INFRAPHARYNGOBRANCHIALS AND SUPRAPHARYNGOBRANCHIALS

Jollie (1962, pp. 92, 96), for the purpose of brevity, introduced the terms "pharyngo-

suprabranchial" and its shortened version "suprabranchial" to replace the term "suprapharyngobranchial" and reintroduced the original "pharyngobranchial" to replace "infrapharyngobranchial." These suggested terminological changes are not without merit, but at the present time important questions remain to be answered concerning the homology of these elements in the different fish groups (Nelson, 1968b). The present paper, therefore, follows the usual terminology of infrapharyngobranchials and suprapharyngobranchials (dating from van Wijhe, 1882, p. 225).

Confusion about the homology of these elements has been reviewed elsewhere (Nelson, 1968b). It may be added here, however, that the tooth plates underlying the infrapharyngobranchials frequently are confused with and consequently called (infra)pharyngobranchials. Partly for this reason successive infrapharyngobranchials are said by some authors, erroneously, to be secondarily fused. So far as known to the writer, purely endoskeletal, ossified gill-arch elements (or ossification centers) rarely, if ever, become secondarily fused in Recent fishes. Even with the involvement of the dermal skeleton, fusion between compound (dermal and endoskeletal) ossified elements of successive arches probably never occurs, despite many statements to the contrary in the literature.

TERMINOLOGY OF CURRENT LITERATURE

In the present paper an attempt is made to deal with the scattered literature on gill arches in fishes, but little effort is directed toward correcting, or even indicating, the individual inaccuracies in most papers dealing with this subject. It may be mentioned here that, with respect to gill-arch structure, anatomical details in the literature even of recent date seldom can be taken at face value. Tending to be especially unreliable are papers in which the dermal skeleton is not treated as a quasi-independent system, in which fusions are said to occur between ossified, endoskeletal elements, or in which the cartilaginous features of the endoskeleton are neither studied nor described.

Confusion of dermal with endoskeletal elements has caused the most difficulty. The basihyal tooth plate has been called a basihyal (Devillers, 1958, fig. 423); the basi-

branchial and adjacent tooth plates have been termed basibranchials (Günther and Deckert, 1959, figs. 15, 16; Monod, 1963, figs. 39, 40; Le Danois, 1967, pls. 13, 14); the fourth basibranchial tooth plate, a fourth basibranchial (Dineen and Stokely, 1954, fig. 8); the lower pharyngeal tooth plates have been called fifth ceratobranchials (Beebe, 1935a, fig. 6; 1935b, fig. 18; Beebe and Crane, 1936, figs. 31, 40; 1937a, figs. 6, 13; 1937b, fig. 15); in lower teleosts (ostariophysans, osteoglossomorphs, elopomorphs, and clupeomorphs), the often independent upper pharyngeal tooth plates have been called pharyngobranchials (Mayhew, 1924, fig. 10; Joshi and Bal, 1953, fig. 8; Kirchhoff, 1958, fig. 27; and Kampf, 1961, fig. 30); and in higher teleosts the fourth upper pharyngeal plate almost invariably has been called a fourth pharyngobranchial. Rarely does the confusion operate in the reverse direction with toothed compound (endoskeletal and dermal) bones being considered purely dermal (e.g., by Muijb, 1967, pp. 1318, 1320).

A lesser source of confusion has been the possibility of fusion between endoskeletal gill-arch elements of different arches. Thus Goodrich (1930, p. 441, also Cărăusu, 1952, p. 68), implying fusion between successive pharyngobranchials, stated that "the pharyngobranchials of the last three arches similarly form a toothed 'os pharyngeus superior.'" In the same context Günther (1880, p. 59) referred to them as being "more or less confluent," and both Regan (1913, pp. 131-132)

and Norman (1957, p. 217), as being "united" in certain Perciformes (but see Nelson, 1967c, p. 293).

As far as is known to the present writer, ossified pharyngobranchials of successive arches never actually fuse, however intimately associated they might become. Without careful examination, however, it is difficult to distinguish them as separate elements, and they are often portrayed in an indistinct way (Rosen, 1962, fig. 12) or even are explicitly stated to include fused elements throughout groups in which they (in this case the third infrapharyngobranchial and fourth upper pharyngeal tooth plate) actually are invariably separate (cf. table 1; and Liem, 1963, figs. 76-87).

Pharyngobranchials in some cases are reduced and lost as independent elements. In such cases one or more of the remaining pharyngobranchials often are interpreted as compound, including two or more pharyngobranchials (Rosen, 1962, fig. 13). Possibly, in undergoing reduction the fourth pharyngobranchial in some cases fails to separate from the third as a distinct rudiment (see below), but if so, it does not mean that the ossified portion of pharyngobranchial 3 is in any sense compound. In such cases the rudimentary nature of the fourth pharyngobranchial, when it occurs as a separate element in related forms, renders almost meaningless any statement about its fusing with anything else, and in the opinion of the present writer it is best considered simply absent as an independent element.

TABLE 1

SUMMARY OF SOME GILL-ARCH ELEMENTS^a IN SOME TROPICAL FRESH-WATER FISHES

	BHP	H3P	LP	1	2	UP 3	4	5
<i>Nandus, Pristolepis</i>	x	x	x	—	x	x	T	—
<i>Afronandus, Monocirrhus, Polycentropsis, Polycentrus</i>	—	—	x	—	x	x	T	—
<i>Badis, Ophiocephalus</i>	—	x	x	—	x	x	T	—
<i>Luciocephalus</i>	—	—	x	—	x	x	T	—
<i>Anabas, Betta, Ctenopoma, Macropodus, Osphronemus, Trichogaster</i>	—	—	x	—	x	x	T	—

^a BHP, tooth plates supported by basihyal; H3P, tooth plates supported by third hypobranchials; LP, tooth plates supported by fifth ceratobranchials; UP 1-5, tooth plates supported by infrapharyngobranchials; T, tooth plate an independent element; x, tooth plate fused with its endoskeletal support; —, tooth plates absent.

ABBREVIATIONS USED IN TEXT FIGURES AND PLATES

- AF1-4, afferent arteries 1-4
 AD, anterodorsal articular surface
 AV, anteroventral articular surface
 B1-6, basibranchials 1-6
 B1+P, B2+P, B3+P, tooth plate fused with basibranchial 1, 2, or 3
 B4P, tooth plate supported by basibranchial 4
 B6P, tooth plates supported by basibranchial 6
 BH, basihyal
 BH+P, tooth plate fused with basihyal
 BHP, tooth plate supported by basihyal
 BP, basibranchial tooth plates
 BP1-3, tooth plate overlying basibranchials 1-3
 BPH-3, tooth plate overlying basihyal and basibranchials 1-3
 BS, basibranchial series
 C, efferent arterial canal
 C1-5, ceratobranchials 1-5
 C5+P, tooth plate fused with ceratobranchial 5
 CA, cartilage
 CH, ceratohyal
 DP, dorsal process
 DS, dorsal articular surface
 E1-5, epibranchials 1-5
 E1+P, E2+P, E3+P, tooth plate fused with epibranchial 1, 2, or 3
 EA1-4, efferent arteries 1-4
 EH, epihyal
 F1-5, articular facets of paired elements of arches 1-5
 GR, gillrakers
 H1-4, hypobranchials 1-4
 H1+P, H2+P, H3+P, tooth plate fused with hypobranchial 1, 2, or 3
 HCH, paired elements possibly including equivalents of hypohyal and ceratohyal
 HH, hypohyal
 I1-4, infrapharyngobranchials 1-4
 I2+P, I3+P, tooth plate fused with infrapharyngobranchial 2 or 3
 I3+UP4, fourth upper pharyngeal tooth plate fused with infrapharyngobranchial 3
 L, LA, LP, in the hyoid arch, the paired element or elements normally supporting the branchiostegal rays
 L1-2, left pharyngobranchial of arches 1-2
 LDA, lateral dorsal aorta
 LG, ligament
 LJ, margin of lower jaw
 LP, lower pharyngeal tooth plates
 LR, lateral ridge
 M, MD, MV, in the hyoid arch, the most anterior of the ventral paired elements
 MDA, median dorsal aorta
 MR, median ridge
 MRL, medial tooth row of the left infrapharyngobranchial 3
 O1, O4, calcifications corresponding in position to infrapharyngobranchials 1 and 4
 P, dermal plate
 PA, papillae
 PAR, pulmonary artery
 PB, perichondral bone
 PH, "prehyoid" cartilages
 PH1, pharyngobranchial 1
 PHH, pharyngohyal
 PS, posterior articular surface
 Q, quadrate
 R, basibranchial rudiment
 R1-2, right pharyngobranchials of arches 1-2
 S, sublingual bone
 S1-2, suprapharyngobranchials 1-2
 SD, SL, SR, SV, dorsal, left, right, or ventral sublingual
 TP, paired tooth plates
 TP1-4, tooth plates of the paired series of arches 1-4
 TP2A, TP2P, anterior and posterior parts of the paired tooth plate series of arch 2
 TP1+2, tooth plates probably derived by fusion of elements of arches 1-2
 TP1+1, TP2+2, TP3+3, median tooth plates derived by fusion of paired elements of arches 1, 2, or 3
 TPH, tooth plates of the paired series of the hyoid arch
 TPM, tooth plates of the paired series of the mandibular arch
 TR, transverse ridge
 U, urohyal
 UJ, margin of upper jaw
 UP, upper pharyngeal tooth plates
 UP1, 4, 5, upper pharyngeal tooth plates 1, 4, or 5
 VA, ventral aorta
 VS, ventral articular surface

GILL-ARCH STRUCTURE

BY WAY OF INTRODUCTION it should be stated that of interest here are those aspects of the dermal skeleton, observable in the adult, that concern the form and arrangement of the principal tooth-bearing bones associated with the gill arches. Since Hertwig (1874a, 1874b, 1876, 1879) and Gegenbaur (1898, p. 200), it has been common to regard large dermal bones as having arisen during evolution by the fusion of smaller elements. Hertwig accepted the placoid scale of sharks as his basic structural unit, but more recent studies focused on placoid scales have resolved them into complex structures formed of even smaller units (Stensiö, 1961, 1962). At the present time there is little agreement about the primitive structural unit of the vertebrate dermal skeleton, but whether it is approached most closely by the placoid scale, the lepidomorium (Stensiö, 1961, 1962), or the odontode (Ørvig, 1967, 1968) one may safely assume that for most gnathostome fishes the primitive unit was in some way toothlike, that is, at least partly composed of dentine and enamel, or dentinous and enameloid tissues (Ørvig, 1967). It seems clear also that in adult Recent teleostomes such units do not occur in isolation but are combined in various ways to form tooth plates of varying size and shape. A complicating factor is that both assimilative and regressive phases seem to characterize the history of the dermal skeleton, the assimilative referring to the building up of larger structures from smaller ones, the regressive to the reduction of the dermal skeleton, said by some to result in the formation of many smaller structures by the disintegration of larger ones (Ørvig, 1968; see also Miles, 1967; Tarlo, 1967; Westoll, 1967).

As far as the writer has been able to determine, both assimilative and regressive phases have occurred during the history of the dermal gill-arch skeleton. In his opinion it seems justifiable to assume that the large tooth-bearing elements occurring in various locations on the gill arches of different fishes have arisen from smaller elements through assimilative processes. Primitively such tooth plates, whether large or small, doubtless

were free in the skin, and only secondarily became fused with their endoskeletal supports. When free in the skin of Recent fishes, tooth plates are relatively variable in size, shape, and position, even within specimens of a single species. Although so far not well documented, the assumption seems justified that both enlargement of tooth plates by phyletic assimilation, and their fusion with their endoskeletal supports, arose as structural modifications related to specific improvements in the feeding mechanism. In any case, once tooth plates had undergone either or both of these processes, they apparently became relatively stable characters and, as such, are of potential phyletic significance.

Often both assimilative and regressive tendencies are apparent in the gill-arch structure of a given species, for it appears that the dermal skeleton, when it undergoes assimilation in certain areas of the visceral apparatus, concurrently undergoes regression in others. At least, phyletic assimilation leading to large teeth or tooth plates and specialized dental tissues or biting surfaces seems in many cases to have been localized to areas on the jaws (e.g., in acanthodians, arthrodires, sharks, rays, chimaeras, and lungfishes), the basibranchials, and parasphenoid and related palatal bones (rhipidistians, coelacanth, brachiopterygians, and primitive actinopterygians), on the pharyngobranchials and opposing bones (pharyngeals of holosts and teleosts), and in some cases on both the jaws and the pharyngeals (teleosts). If specialized dental structures are highly developed in any of these areas, much or all of the remainder of the surface of the visceral arches tends to have the dermal skeleton reduced or absent.

In some cases, however, the dermal skeleton of the entire visceral apparatus seems to have been modified in a relatively uniform way, e.g., with the proliferation of gillrakers at the expense of tooth plates in forms specialized for microphagous habits (Nelson, 1967e). Finally the dermal skeleton in a few cases is almost or totally lost, with tooth plates and gillrakers tending to be replaced by fleshy

papillae or other types of non-calcified tissues. These problems so far have not been analyzed in any detail, but the present writer would suggest as examples of fishes showing gillraker proliferation the Polyodontidae, Hypophthalmidae, Chanidae, Engraulidae, and Clupeidae, and as examples of fishes showing more or less complete reduction of the dermal skeleton, at least on the gill arches, the Holocephali, Dipnoi, Acipenseridae, Gymnarchidae, Citharinidae, Gymnotidae, Electrophoridae, and Saccopharyngidae.

The differences in location of enlarged or specialized tooth plates doubtless have phyletic and functional significance, but there has been little comparative study of these matters. One may assume that small tooth plates were primitively distributed over the entire buccopharyngeal surface (see below) and functioned in seizing and swallowing large prey. One may further assume that assimilative processes subsequently led to the appearance of enlarged tooth plates in areas of particular functional importance. Possibly these were first the jaws. Later stages might have involved assimilative processes within the buccopharyngeal cavity itself, and one may suppose that assimilation proceeded along an anteroposterior gradient. Indeed, such a gradient seems to be exhibited in those fishes having the primitive dermal skeleton well represented, e.g., *Eusthenopteron* (Jarvik, 1954, figs. 8, 25) and *Elops* (pl. 79, fig. 3; Nelson, 1967f, fig. 1; Nybelin, 1968, fig. 1). Within the buccopharyngeal cavity two main regions are apparent: an anterior region involving the jaws, basibranchials, and opposing bones of the palate; and a posterior region involving the pharyngobranchials and opposing bones. In both *Eusthenopteron* and *Elops*, as well as in many other primitive teleostomes, assimilation in the anterior region seems much more pronounced than in the posterior region. Posteriorly, pronounced assimilation is apparent only in advanced teleosts.

Assimilative processes, such as those involving the appearance of large tooth plates, probably resulted initially in a mechanical system more efficient in seizing and swallowing large prey. Additional advances in this efficiency seem to have been achieved in other ways, e.g., in teleostomes with the de-

velopment of a dermal upper jaw, which in actinopterygians became increasingly protrusile (see Schaeffer and Rosen, 1961; Rosen and Patterson, 1969), probably in conjunction with the development of movable upper pharyngeal bones (Nelson, 1967e, pp. 80-81; 1967f, pp. 284-285).

In actinopterygians, jaw protrusion (with the exception of that of the sturgeons, which is of a special type) developed only in forms in which assimilative processes within the buccopharyngeal cavity apparently had already led to the development of movable pharyngeal bones of some sort. Thus one may imagine that the primitive, dermal upper jaw was freed from any significant participation in seizing prey (this function passing in large measure to the pharyngeals) and gradually was integrated into a structural complex capable of drawing prey into the buccopharyngeal cavity by suction. If so, this shift in function might explain why protrusile jaws often have a reduced dentition, and also Ridewood's (1896, p. 390) puzzling though often-cited remark that "It may be taken as a general rule that the pharyngeal dentition is inversely proportional to the extent of tooth development on the jaws." This remark of course does not take into consideration the facts that the jaws have undergone an extensive radiation of types in higher teleosts, and that in many of these (e.g., scarids) the jaw teeth have achieved a high order of development and specialization which functionally complement those of the pharyngeals.

The appearance of specialized teeth and dental tissues seems to follow the same spatial and temporal patterns, probably first involving the jaws (see Gross, 1967), then the basibranchials, then the pharyngeals, in that order. These teeth and dental tissues seem, as a rule, to be associated with specialized feeding habits involving shearing, chopping, or grinding functions, probably permitting more effective exploitation of varied food sources, and representing various degrees of departure from the primitive, basically predatory, feeding mechanism. In some cases, however, dental specializations of the jaws, whatever their initial adaptive significance, apparently produced highly efficient, predatory types of animals such as sharks (but

doubtfully among arthrodires, cf. Heintz, 1932, fig. 90), and such as *Serrasalmus* among teleosts (Gosline, 1951).

PRIMITIVE GILL-ARCH DENTITION

The primitive arrangement of tooth plates on the gill arches of fishes possibly never will be known with certainty, but the writer has found no reason to reject the assumption of Jarvik (1954, fig. 35; 1960, fig. 26; see also Nybelin, 1968) that primitively the dermal skeleton in the form of small toothed elements was distributed in a nearly uniform manner over the surfaces of the buccopharyngeal cavity. This primitive condition is not known to occur in any teleostome, fossil or Recent, but possibly is represented by the placoid scales scattered over the buccopharyngeal cavity of elasmobranchs (pl. 92, figs. 3, 5; see also Steinhard, 1903; Imms, 1905; Fahrenholz, 1915; and Dean, 1906, pp. 120-121, fig. 94).¹ In teleostomes, if the

¹ During ontogeny, placoid scales do not grow after their formation. Phyletically they seem to have developed from growing scales during the evolution of elasmobranchiomorphs (e.g., Ørving, 1966, pp. 29, 30; Zangerl, 1968). Within the buccopharyngeal cavity, very primitive elasmobranchiomorphs probably had a well-developed dermal skeleton consisting of small elements capable of growth. According to Patterson (personal communication) such elements are known to occur on the gill arches of early elasmobranchs such as *Cladoseleche*, *Ctenacanthus*, and *Goodrichthys*. These growing elements have essentially the same organization as that of the small tooth plates of primitive teleostomes such as *Latimeria* (pl. 83, fig. 2). Buccopharyngeal placoid scales probably arose directly from such small, growing elements, for there is little likelihood that they were formed by disintegration of large elements.

Reduction and ultimate loss of the capacity for growth of the dermal skeleton possibly explain why more complex structures have not been developed within the buccopharyngeal cavity of Recent elasmobranchiomorphs. Thus, placoid scales, seemingly because they do not grow, cannot fuse.

In *Chlamydoselachus*, the buccopharyngeal scales vary in size. Those supported by the most posterior ceratobranchials are particularly large (pl. 92, figs. 3, 5). They form two patches comparable in position with the lower pharyngeal tooth plates of primitive teleostomes. Therefore, there is reason to suspect that the scales are secondarily enlarged and represent an early stage in the development of a pharyngeal dentition. That development has not progressed beyond this stage among elasmobranchiomorphs possibly is due to the specialized, non-growing quality of placoid scales (for a discussion of placoid scales from another perspective, see Ørving, 1951, pp. 377-380).

dermal skeleton is well developed, there are invariably some variously developed gillrakers, or a number of relatively large tooth plates. In some respects, however, the condition in *Latimeria* (pl. 81, fig. 1) probably is not far removed from that primitive for teleostomes. Here the ventral dermal elements are arranged in rows on the gill arches, and, as is usual in teleostomes, an anterior series on the anterior part of the arch and a posterior series on the posterior part are distinguishable. Each series is divisible into distinct upper and lower rows of larger tooth plates, with smaller plates ventrally and more irregularly arranged (pl. 82, fig. 2). Gillrakers as such are absent but doubtless are represented by the ventral row of large tooth plates.² The dermal elements associated with the dorsal parts of the gill arches, in *Latimeria* again in the form of small tooth plates, are more randomly arranged (pl. 83, fig. 2). The absence of well-defined rows probably is related to the virtual absence of the dorsal parts of the gill slits, and the relatively small size of the dorsal endoskeletal elements, both conditions possibly being secondary in *Latimeria*.

It may be added that the dorsal endoskeletal elements are peculiar in being widely separated on each side; in tending to be posteriorly directed, with the posterior elements more prominent and closer to the midline than the anterior; in having the third and fourth epibranchials each with a foramen accommodating an efferent artery; and in having independent pharyngobranchials developed only in arches 1 and 2 (fig. 1). Neither of the foramina seems comparable with anything described in other fishes, namely, the efferent arterial foramen and the canal of some teleosts (Nelson, 1967e). The most posterior efferent artery of *Latimeria* passes posteriorly through the foramen in the fourth epibranchial, not anteriorly as does the fourth

² In Recent fishes there is a complete transition between ordinary tooth plates and well-developed gillrakers, and there can be no doubt that gillrakers are little more than modified plates (despite the odd circumstance that "gillrakers" in larvae sometimes become tooth plates in adults; see Gibbs and Weitzman, 1965, p. 270), and that both types of structures must be considered part of the dermal skeleton of the gill arches (see also Popta, 1901, p. 207; Zander, 1903, p. 236; 1906a, pp. 626-633).

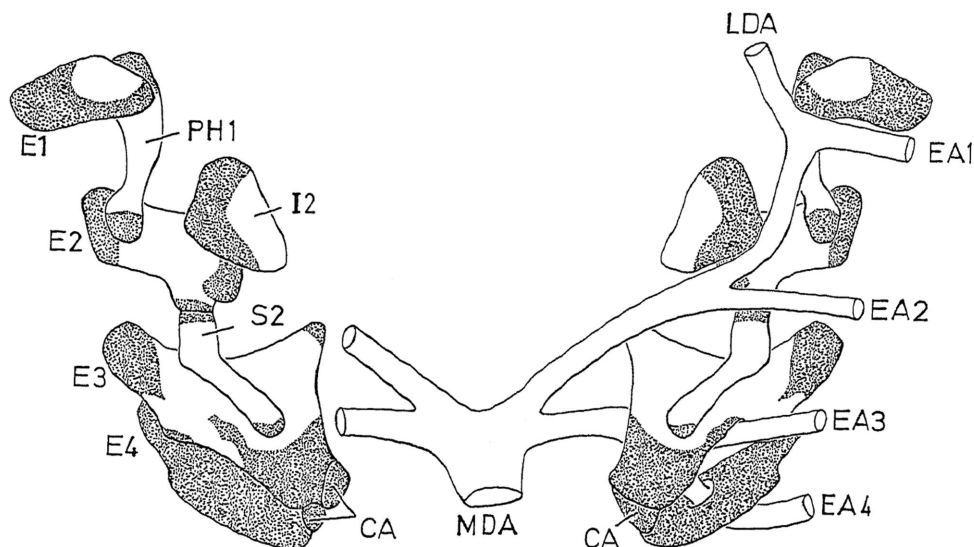


FIG. 1. *Latimeria chalumnae*, gill arches, dorsal parts, dorsal view, with associated efferent branchial arteries.

vessel through the foramen of some clupeids. Despite these differences, the vessels probably are homologous to those of teleosts, for there is no reason to believe that a fourth efferent artery is secondarily reduced in *Latimeria*. It is true that this vessel in *Latimeria* in part lies posterior to the fourth epibranchial, like the "fifth" artery of *Elops* and other teleosts (see Nelson, 1967a), but the significance of this resemblance is obscure.

The pharyngobranchials of *Latimeria* are difficult to compare with those of other fishes. One interpretation, based on the description of Millot and Anthony (1958), has been attempted elsewhere (Nelson, 1968b, fig. 5A). Here may be added the observation that the third epibranchial is continued posteriorly by a large process which, via one or two cartilaginous nodules, articulates with the fourth epibranchial. Whether or not this process includes the equivalent of a pharyngobranchial is difficult to say. The nodules, one on one side, and two on the other, likewise are of nebulous significance.

Neoceratodus (fig. 2) is the only Recent fish with dorsal endoskeletal elements even remotely similar to those of *Latimeria*. In *Neoceratodus*, however, independent pharyngobranchials are absent, and epibranchials 3 and 4 are without foramina. Nonetheless, the third epibranchial is continued posteriorly

by a process similar to, and probably homologous with, that of *Latimeria*.¹

Eusthenopteron like *Polypterus* has the anterior arches apparently better developed than the posterior, with no tendency toward posterior orientation. Among the forms considered above, *Eusthenopteron* has well-developed tooth plates in rows supported by the dorsal parts of the gill arches (Jarvik, 1954, fig. 22). Despite these primitive features, *Eusthenopteron* sheds little light on the apparently more advanced conditions of *Latimeria*, lungfishes, and *Polypterus*.

From the above-mentioned fishes, all of which at one time or another were believed to be closely related, a highly developed pharyngeal dentition is absent, as it is from elasmobranchs and primitive actinopterygians (chondrosts). There is no reason to

¹ Comparisons with other lungfishes and brachiopterygians are fruitless, for in them the dorsal elements are even more reduced. In brachiopterygians, only the first arch is developed to any extent. Its elements have been variously interpreted (e.g., by van Wijhe, 1882, pl. 15, fig. 7; Allis, 1922, pl. 8, fig. 17; Daget, 1950, fig. 35). Daget was correct in showing two elements, each with one center of ossification. They appear to represent an epibranchial and infrapharyngobranchial. Whether the dorsal process of the epibranchial includes the equivalent of a suprapharyngobranchial or not is difficult to say, but it seems certain that an independent suprapharyngobranchial is lacking.

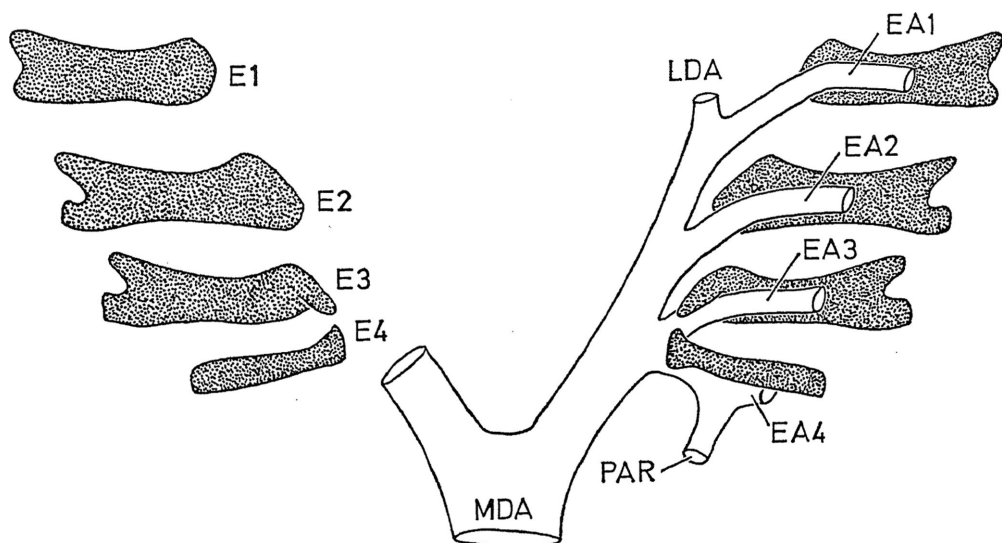


FIG. 2. *Neoceratodus forsteri*, gill arches, dorsal parts, dorsal view, with associated efferent branchial arteries.

believe that the absence of a highly developed pharyngeal dentition from any of these forms is due to secondary loss. In some cases the absence of a dermal gill-arch skeleton doubtless is secondary, but the regressive processes leading to it probably began at a very primitive stage, like that represented by *Eusthenopteron* and *Latimeria*.

UPPER PHARYNGEAL DENTITION

HOLOSTS

In fishes other than teleosts only *Amia* and *Lepisosteus* are known to have a significantly developed upper pharyngeal dentition. In these forms occur one pair of large tooth patches (pl. 82, fig. 1, pl. 92, fig. 4), consisting of small tooth plates supported mainly by the large, cartilaginous, rear part of pharyngobranchial 3, a part possibly representing a reduced fourth pharyngobranchial (see Nelson, 1968b, fig. 5E, F). Not being arranged in conspicuous rows, these tooth plates are not definitely assignable to particular arches, but the third, fourth, and possibly fifth arches might be involved. It is noteworthy that all the tooth plates associated with the gill arches in these and other non-teleostean fishes (with the only known exception of the basibranchial plates in *Calamoichthys*, see below) retain

their presumably primitive independence and are not fused with their endoskeletal supports (pl. 90, fig. 1), especially because dorsal retractor muscles originate on the vertebral column of both *Amia* and *Lepisosteus* (Allis, 1897, p. 671; Edgeworth, 1911, 1928; Holstvoogd, 1965, p. 213). These are the only fishes known to possess dorsal retractor muscles and an upper pharyngeal dentition formed of several tooth plates that are not fused with the endoskeletal pharyngobranchials.

TELEOSTS

In teleosts the upper pharyngeal dentition consists in part of from one to five usually paired tooth plates or groups of tooth plates termed "upper pharyngeal plates 1-5" (UP 1-5), each probably representing the medial part of the anterior series of dermal elements (that series posterior to the gillrakers) associated with a branchial arch (pl. 82, figs. 3-5). In primitive teleosts such as *Elops* (Nelson, 1967f, fig. 1), the dermal elements are in the form of numerous small tooth plates independent of their endoskeletal supports, and in advanced forms the tooth plates, if independent, are consolidated into larger elements. Typically some plates are fused with the second and third infrapharyngobranchials. Tooth plates are fused also with some

epibranchials: the first epibranchial in some engraulids and at least one mastacembelid, the second epibranchial in some ophidiids and batrachoidids (and apparently at least one macrourid, according to Zander, 1906b, fig. 12), and the third epibranchial typically in myctophiform, paracanthopterygian, and acanthopterygian fishes (according to Patterson, 1964, p. 355, tooth plates are fused even with the fourth [third?] epibranchial of a Cretaceous holocentrid). In deep-sea fishes there tend to be even more extensive fusions between dermal elements (including gill-rakers) and their endoskeletal supports (personal observations).

In myctophiforms, paracanthopterygians, acanthopterygians, and some other teleosts the element bearing the most posterior tooth patch of the upper pharyngeal complex commonly is called the fourth pharyngobranchial. As far as the present writer has been able to determine, however, this element is purely dermal in origin, corresponding to the fourth upper pharyngeal plate, or to the fused fourth and fifth plates of "lower teleosts" (see below). It accordingly was termed the fourth upper pharyngeal plate (Nelson, 1967c, table 1, UP4).

Cross sections through the fourth tooth plate of both *Elops* and *Aulopus* show that the plate, as are the pharyngeal tooth plates of *Amia* (pl. 90, fig. 1), is outside of and separate from the perichondrium of its endoskeletal support, the fourth infrapharyngobranchial. Because there is little doubt of the homology between the fourth tooth plate of these fishes and that of more advanced teleosts, there accordingly is no basis for believing that this toothed element includes a primitively ossified fourth infrapharyngobranchial, however primitive or advanced the fish in which it occurs might be.

Another problem concerns the interpretation of the most posterior plate of some osteoglossomorph, elopomorph, clupeomorph, characiform, siluriform, salmoniform, and myctophiform fishes. In the characin *Hydrocyon* this element was recognized and designated a "fifth pharyngobranchial" for the first time by Kampf (1961, fig. 30), with the implication that it represents an element of, or is associated with, the dorsal part of the fifth arch, which in all Recent teleostomes is

reduced, presumably secondarily. In *Elops*, clupeid, and osteoglossomorph fishes the element was recognized to be a tooth plate, and designated "upper pharyngeal tooth plate five" (Nelson, 1967b, 1967f). Weitzman (1967a, p. 530) subsequently suggested that this plate more probably was derived with the fourth upper pharyngeal plate, from the dermal element series of the fourth arch.¹

The fourth upper pharyngeal plate appears

¹ In fact, evidence concerning the origin of this plate from either the fourth or fifth arches is conflicting. On the basis of its distribution among the "lower teleosts" (see above) and its absence from all "higher teleosts" allied with acanthopterygians (with the exception of the Aulopodidae and related forms) it would seem to be a primitive character at least among teleosts. In *Elops* its position is mostly posterior to, and it is mostly unsupported by, the fourth infrapharyngobranchial. Both of these observations are consistent with a derivation from the fifth branchial arch rather than from the fourth. The absence of a fifth infrapharyngobranchial as a supporting element by itself is no more remarkable than the secondary absence of endoskeletal supports from other fishes: (1) from some eels (Nelson, 1966) and probably also *Polypterus* (fig. 3C) the absence of fifth ceratobranchials supporting the lower pharyngeal tooth plates (in *Polypterus* it is likely but not certain that the lower pharyngeal plates, as are those of many eels, secondarily are supported by the fourth ceratobranchials); (2) from *Amia* and *Lepisosteus* (Nelson, 1968b, fig. 5E, F), the absence of an independent fourth infrapharyngobranchial supporting the upper pharyngeal tooth plates; (3) from most acanthopterygians (e.g., *Chromis* and *Embiotoca*, Nelson, 1967c, figs. 1, 2) the absence of a fourth infrapharyngobranchial supporting the fourth upper pharyngeal tooth plate. But the fifth tooth plate cannot be assigned with certainty to the dermal-element series of the fifth arch, firstly because the elements composing it probably have been assimilated in different lineages (e.g., in both *Hiodon* and *Elops* the plate is composed of several elements, whereas more advanced forms [e.g., *Osteoglossum* and *Albula*] of both lineages have consolidated, single plates [Nelson, 1967f, fig. 1; 1968a, table 1; and personal observation]); secondly, because these consolidations probably have taken place in the absence of a supporting endoskeletal element of the fifth arch (the dorsal part of the fifth arch is not known to be well developed in any teleostome); and thirdly, because on present evidence it cannot be demonstrated that the unconsolidated tooth plates originally were part of a series posterior to the upper part of a fifth gill slit, for this is reduced at least in Recent teleosts (this reduction apparently occurs during early ontogenetic stages, in relation to a secondary association between fourth and fifth epibranchials [Bertmar, 1959, p. 249]). At this stage the dermal elements seem not yet to have developed). Thus, however the fifth tooth plate was derived, it is reasonably certain that it is a dermal element occurring only in primitive teleosts.

secondarily to have been lost in a few higher teleostean lineages, as has already been pointed out as probable for the lineage leading to the labroid fishes (Nelson, 1967c; cf. Monod, 1951; Quignard, 1962). Among beryciforms, evidence for this type of secondary reduction seems to be shown in *Hoplostethus*, in which the third infrapharyngobranchial is continued posteriorly by a toothed process the position of which is occupied usually by the fourth tooth plate (fig. 4B). In the apparently more specialized *Photoplepharon*, however, all traces of an additional tooth plate have disappeared (fig. 4A).

It must be admitted that such traces of a fourth tooth plate as appear in *Hoplostethus* as compared, for example, with the independent plate of *Polymixia* (Nelson, 1967f, fig. 2) and in *Bodianus* as compared with *Embiotoca* (Nelson, 1967c, figs. 2C, 3C) so

far constitute the only known evidence of a secondary reduction of this tooth plate by means of fusion. That the fifth tooth plate of lower teleosts was, at least in some cases, reduced by a similar process is suggested by the condition observed in one specimen of *Aulopus nannae*, which had the fifth plate independent on one side, but apparently fused with the fourth on the other.

The loss of the fourth and fifth tooth plates is a character of possible systematic significance, but so far not sufficiently understood. An independent fifth tooth plate is known only among primitive teleosts (at least the Hiodontidae, Osteoglossidae, Elopidae, Megalopidae, Albulidae, Halosauridae, Clupeidae, Engraulidae, Chirocentridae, some Osmeridae, Argentinidae, Retropinnidae, Aulopodidae, Harpodontidae, Chlorophthalmidae, Bathypteroidae, and probably

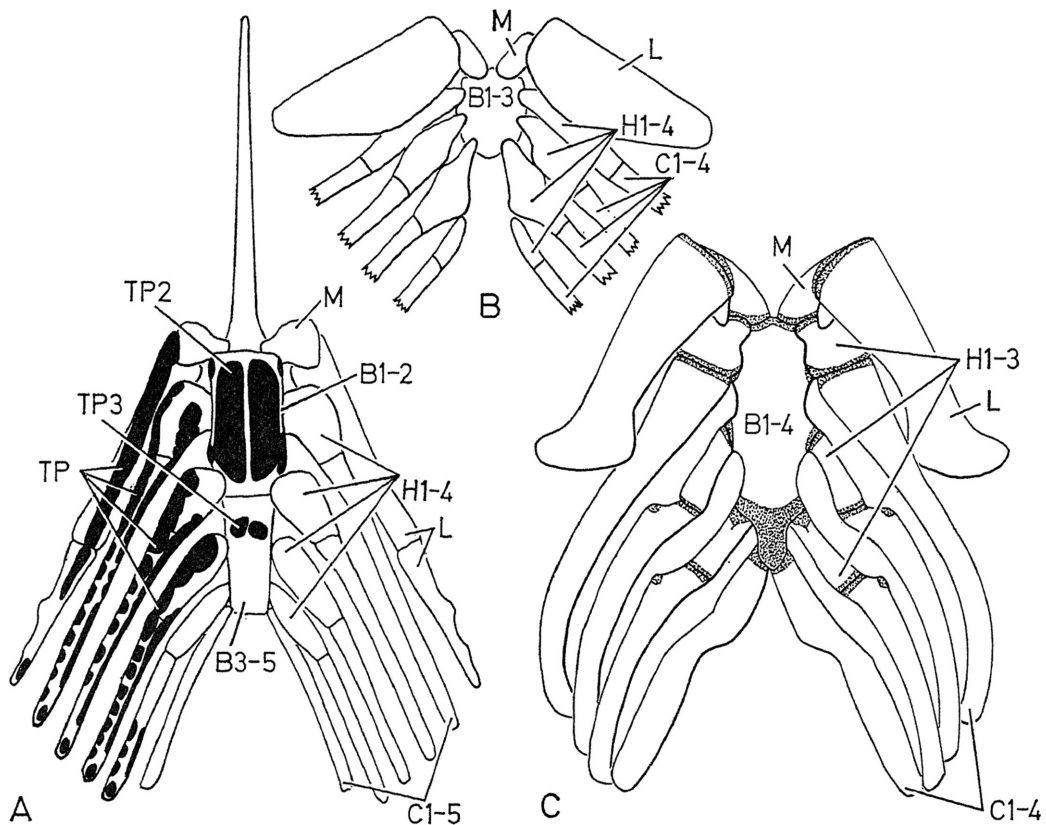


FIG. 3. Gill arches, ventral parts. A. *Eusthenopteron foordi*, dorsal view (modified from Jarvik, 1954, fig. 8B). B. *Glyptolepis* sp., ventral view (modified from Jarvik, 1963, fig. 16A). C. *Polypterus bichir*, ventral view (modified from Allis, 1922, pl. 8, fig. 16).

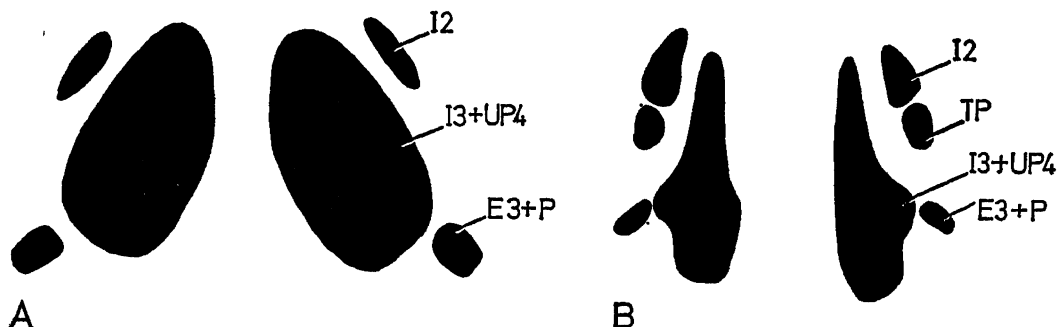


FIG. 4. Upper pharyngeal tooth patches. A. *Photoblepharon palpebratus*. B. *Hoplostethus mediterraneus*.

others). The fourth tooth plate is present in more teleosts than usually is supposed. Among beryciforms, however, the fourth tooth plate is absent as an independent element in trachichthyids (*Gephyroberyx*, *Hoplostethus*, *Paratrachichthys*, *Trachichthys*); anomalopids (*Photoblepharon*); stephanoberycids (*Stephanoberyx*, *Malacosaurus*); and monocentrids (*Monocentris*, *Cleidopus*; see Starks, 1904, pp. 606, 619) in which its absence probably characterizes a trachichthyoid lineage (see Patterson, 1967a, p. 104). However, the tooth plate is present in *Hoplopteryx* (Patterson, 1964, fig. 52; according to Patterson, p. 341, *Hoplopteryx* is a primitive trachichthyid), diretids (*Diretmus*), anoplasterids (*Caulolepis*), and melamphaeids (*Melamphaes*; see also Ebeling and Weed, 1963, fig. 3), as well as in all berycids and holocentrids (see Starks, 1904, pp. 609, 612; Patterson, 1964, p. 354). Whether the absence of this plate from trachichthyoids has anything to do with its absence also from zeids (*Cyttus*, *Neocyttus*, *Pseudocyttus*, and *Zeus*; see Starks, 1898a, pl. 34, fig. 4), or for that matter from gasterosteids (*Gasterosteus*) and syngnathoids (Jungerson, 1910, pl. 6, figs. 7–9) is difficult to say; it is present, however, in caproids (*Capros* and *Antigonia*, see Starks, 1902, p. 569) and aulostomoids (*Aulostomus* and *Fistularia*; see Jungerson, 1908, fig. 18; 1910, pl. 2, figs. 1, 3).¹

¹ It may be added also that the plate apparently has been independently reduced in other teleostean lineages: (1) the Scorpaeniformes (at least the Triglidae [the tooth plate being absent from *Peristigidae*], Synancejidae [*Synanceja*], Cottidae [*Cottus*, see also Johnson, 1918, p. 470, pl. 3], but not the Scorpaenidae [the tooth plate being present in *Scorpaena*, see also Starks,

On the basis of these facts, the fourth and fifth plates seem independently to have been lost many times. However, the possibilities remain that within a given lineage or sub-lineage the loss of either of the plates occurred only once, and that the absence of either or both of them characterizes a monophyletic subgroup. Whether in all cases the tooth plates were lost in the same ways, namely, through fusion of the fifth with the fourth plate, and the fourth with the toothed third infrapharyngobranchial, is not known, but

1898b, pl. 24, fig. 15]); (2) the Perciformes (a, the Labridae, Odacidae, and Scaridae [see e.g., Nelson, 1967c], but not the Cichlidae, Pomacentridae, Embiotocidae or other percoids; b, the Clinidae [*Clinus*], Tripterygiidae [*Tripterygion*, see Gosline, 1963a, p. 94], Blennidae [*Cirripectus*], Callionymidae [*Callionymus*], but not the Anarhichadidae [*Anarhichas*]; c, the Balistidae [*Balistes*], Monacanthidae [*Aluiteria*], but not the Acanthuridae [*Acanthurus*]; the tooth plate is present in most or possibly all members of other perciform suborders); (3) the Atheriniformes (a, the Exocoetidae and some Belonidae, but not the Scomberesocidae; b, some cyprinodontoids [*Cyprinodon* but not *Anableps* or the atherinoids *Menidia* and *Melanotaenia*; see Regan, 1911, pl. 9; Collette, 1966, figs. 2, 3; Starks, 1899, p. 4; Rosen, 1964, fig. 13, where, however, the fourth tooth plate is not shown as an independent element]); (4) the Paracanthopterygii (Batrachoididae [*Porichthys*, *Thylassophryne*], Gobiesocidae [*Gobiesox*, see Starks, 1905, p. 297], Antennariidae [*Histioides*], but not the Muraenolepididae, Gadidae, Merlucciidae, Carapidae, Ophidiidae, Zoarcidae, Macrouridae, Amblyopsidae, Percopidae, and Aphredoderidae [see also, Emery, 1880, pl. 2, fig. 13; Zander, 1906b, figs. 3–8, 10; but see fig. 5; Rosen, 1962, figs. 13, 14; Nielsen, 1966, figs. 4, 9; Rosen and Patterson, 1969]); (5) the Anguilliformes, in which the fourth tooth plate apparently has been independently lost at least seven times (Nelson, 1966, table 1); (6) the Osteoglossomorpha (the Notopteridae but not the Hiodontidae; the Pantodontidae but not the Osteoglossidae [see Nelson, 1968a, table 1]).

seems likely. In some groups, however, the fourth tooth plate, before its disappearance as an independent element, has become very small, suggesting that its eventual loss might have been due to continued reduction rather than fusion (e.g., atherinomorphs). But it should be mentioned in this connection that there possibly is no fundamental difference between these two "types" of loss (see Ørvig, 1962, p. 59).

The loss of these tooth plates doubtless has functional significance, perhaps a different significance in each of the lineages in which it occurred; and these are problems deserving further study. At present it can be suggested only that the repeated reduction of these plates is an aspect of a general trend toward consolidation of the extensive, upper pharyngeal dentition of primitive teleosts such as *Elops*. The result of this consolidation always seems to be approximately the same: a single pair of toothed areas (formed mainly if not entirely by the third infrapharyngobranchials fused with one or more pairs of tooth plates) equipped with "retractor" muscles usually originating on the vertebral column.

Another type of reduction in the upper

pharyngeal dentition is shown among the Ostariophysi. Some characids, such as *Hoplias* (pl. 82, fig. 3), show the pattern more or less normal for primitive teleosts, including separate and toothed upper pharyngeal tooth plates 4 and 5. Others, apparently more advanced, retain a toothed fifth plate, but have the fourth toothless and partly wrapped around (but outside the perichondrium of) the cartilaginous fourth infrapharyngobranchial (fig. 5A). It possibly was a condition such as that of *Leporinus* from which was derived the distinctive pattern of nearly all catfishes. In *Diplomystes* there are three infrapharyngobranchials (fig. 5B, I1-3), in *Schilbe* and some others, two (fig. 5C, I1, I3), and in others only one (I3). Of these conditions, that of *Diplomystes* is the most primitive and allows the more advanced condition of most catfishes to be interpreted with a high degree of certainty, despite the varied interpretations in the literature (cited below). But the nature of the upper pharyngeal tooth plates and that of their endoskeletal supports remain obscure. In all catfishes a maximum of a single pair of upper pharyngeal plates is known (J. Lundberg, personal communication), but whether this

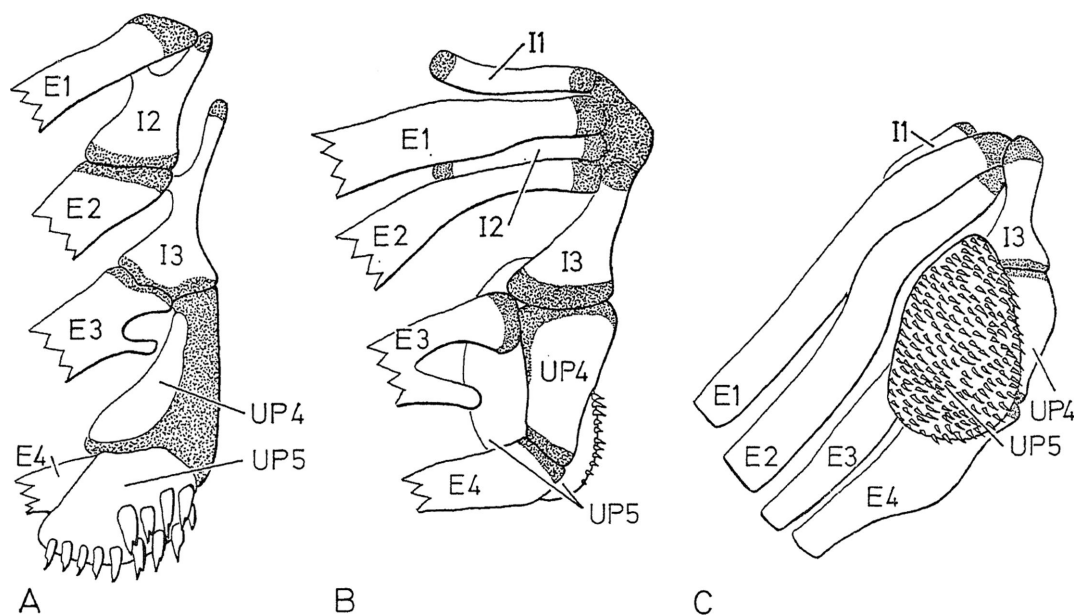


FIG. 5. Upper pharyngeal tooth plates and associated bones. A. *Leporinus* sp., ventral view of right side. B. *Diplomystes papillosus*, dorsal view of left side. C. *Schilbe* sp., ventral view of right side.

is the fifth tooth plate, the fourth, or the fourth and fifth fused, is not known. Without this information it is difficult if not impossible to determine the nature of the endoskeletal support. This element, mostly cartilaginous, has perichondral bone over its dorsal surface (pl. 89, fig. 1). Whether this bone layer is only a much-modified tooth plate, as suggested in figure 5B-C, or has arisen secondarily in the area of the insertion of the "retractor" muscles, is not known. That this bone layer represents a primitively ossified fourth infrapharyngobranchial is not likely, for such an element is not known with certainty to occur in any fishes.

Notable is the fact that the toothed upper pharyngeals of catfishes are equipped with "retractor" muscles (Takahasi, 1925, figs. 14, 15; Ledeboer and Wunder, 1934; Holstvoogd, 1965, p. 215), making them functionally comparable with the upper pharyngeals of other fishes. It would seem, however, that in catfishes neither the toothed upper pharyngeals nor their retractor muscles are homologous with those of acanthopterygian and those of related fishes.¹

If this interpretation is correct, the pharyngeal apparatus of catfishes is of a highly specialized type unique in fishes. Its closest parallel possibly is that of some characins in which, however, the condition is more primitive, there being no "retractor" muscles

¹ In catfishes the upper pharyngeals are the fourth or fifth upper pharyngeal tooth plates, and the retractors seem to be modified levators, as was maintained also by Holstvoogd (1965, p. 215, fig. 10B); in acanthopterygian and related fishes the upper pharyngeals are the toothed third infrapharyngobranchials, and the retractors have developed from the esophageal musculature (Nelson, 1967f; but see Favaro, 1902).

Neither the upper pharyngeals of catfishes nor those of acanthopterygians seem to be homologous with those of *Amia* and *Lepisosteus* which have only patches of unconsolidated tooth plates probably not referable to the dermal-element series of a single arch. Whether in these holosts the retractor muscles represent a distinct type is not known, for in the literature there is disagreement about their homology and their embryological development (Allis, 1897, p. 752; Wiedersheim, 1904, p. 21; Edgeworth, 1911, p. 267; 1928, pp. 79-80; 1935, p. 167; Holstvoogd, 1960, p. 50). Nevertheless, on the basis of present information it would seem that of upper pharyngeal structures there are at least three types of which the superficial similarities (a single pair of prominent tooth patches, plates or toothed infrapharyngobranchials with attached retractor muscles)

attaching directly to the fifth tooth plates. It would seem unlikely that catfishes evolved from certain advanced characins, and such resemblances, if real, are likely to be due to parallel evolution. The catfishes are all highly advanced in these regards, and it is impossible to determine from how primitive a level the catfish pharyngeal apparatus was derived. The pharyngeal apparatus of cyprioids in certain respects (e.g., the complete reduction of upper pharyngeal tooth plates) is more advanced than that of catfishes, but itself probably was not derived from such a highly specialized type in which any of the upper pharyngeal plates were highly functional. It seems possible, however, that, as far as these gill-arch characters are concerned, catfishes could be more closely related to either of the two other main groups of Ostariophysi.

BASIBRANCHIAL DENTITION

PRIMITIVE TELEOSTS

The dermal elements associated with the ventral parts of the endoskeletal gill arches are more complex than those associated with the dorsal parts. Present in many cases are paired elements usually clearly referable to the anterior of the paired series of one or more of the arches. In addition, median elements in many cases occur over the basibranchials. In most, if not all, cases the median elements seem likely to have arisen through the fusion of paired elements. In some cases there seems to be fairly good evidence indicating such an origin, but in others such evidence is lacking. Elsewhere it has been suggested that the condition in *Elops* is close to that primitive for teleosts. In *Elops* a small tooth plate occurs over the basihyal, and behind this an elongate tooth

arose convergently. Whether the upper pharyngeals and muscles of *Pantodon* (Le Danois, 1967, pl. 22, fig. a; Nelson, 1968a, p. 80) *Myroconger* (Nelson, 1967g, p. 562), muraenids (Nelson, 1966, p. 402; 1967d, p. 358), and stomiatoids (Tchernavin, 1953, p. 32; Günther and Deckert, 1953, p. 29; 1955, p. 306; 1959, p. 24) include one or more additional basic types on present evidence seems unlikely, and the similarities between those and the upper pharyngeal complex of myctophiform, paracanthopterygian, and acanthopterygian fishes may tentatively be regarded as results of parallel evolution until they are shown to be otherwise.

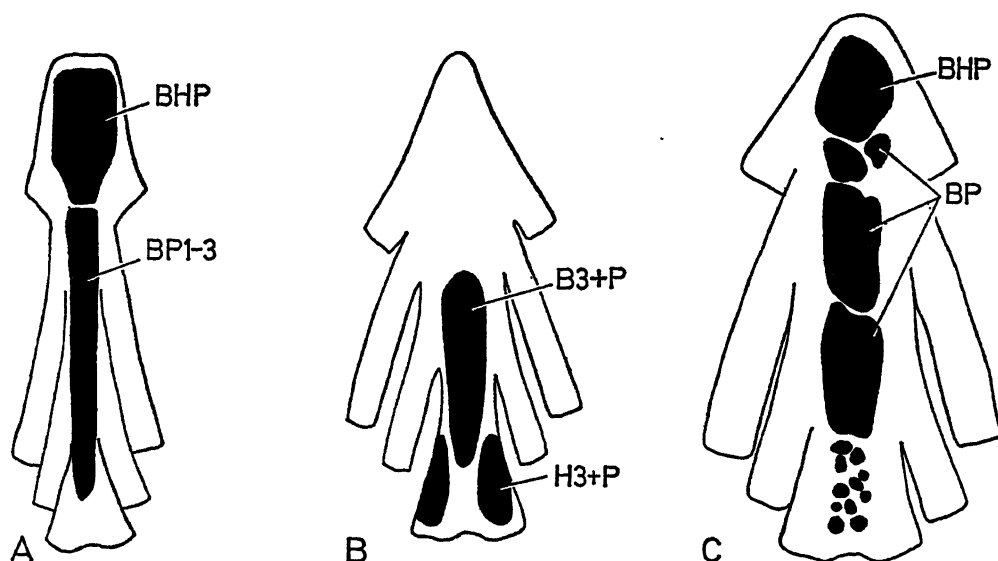


FIG. 6. Basibranchial tooth patches. A. *Elops lacerta*. B. *Glyptothidium longipes*. C. *Polymixia nobilis*.

plate over basibranchials 1-3 (fig. 6A; pl. 79, fig. 3). A similar condition occurs, with little variation, in what seem to be primitive representatives of most lower teleostean groups that are usually recognized: Osteoglossiformes (*Hiodon*; pl. 80, fig. 1), Ostariophysii (*Ichthyoborus*), Elopiformes (*Megalops*, *Elops*), Salmoniformes (*Retropinna*, *Osmerus*), Clupeiformes (*Chirocentrus*), and others. In more advanced members of these groups, these elements often occur in an advanced and toothless condition: e.g., the basihyal plate of some characiforms (*Hoplias*, fig. 7B), elopiforms (*Albula*, fig. 7A), clupeiforms (engraulids), and clupeids (see Nelson, 1967b, figs. 3, 5), and the basibranchial plate of some salmonids (Norden, 1961, pl. 6, figs. A, B).

Within these lower teleostean groups the basibranchial tooth plates have undergone also secondary modifications, resulting in some cases in specialized tooth plates, and in others reduction and loss of teeth. Some of the modifications have been taken up elsewhere (Nelson, 1968a). Rarely do these plates develop a heavy crushing dentition, and only two cases are known in Recent forms, one being *Albula* (fig. 7A; pl. 84, fig. 4), the other *Pristolepis* (fig. 7D; pl. 84, fig. 5). In each case a different tooth plate is

involved: in *Albula* the basibranchial plate bears the teeth and the basihyal plate is toothless; in *Pristolepis*, the basihyal plate is fused with the basihyal, and this compound structure secondarily is extended posteriorly over the basibranchial series. A more primitive condition, from which that of *Pristolepis* likely was derived, is that of *Nandus* (fig. 7C).

Among fossil actinopterygians a basibranchial plate with a crushing dentition is known in *Bobasatrania* (Nielsen, 1952, figs. 1, 2), *Plethodus* and its allies (Dixon, 1850, pl. 32*, fig. 4, pl. 33, fig. 2; Woodward, 1899, pl. 8, figs. 1-7; 1907, pl. 22, figs. 1-9; Loomis, 1900, pl. 21, fig. 4, pl. 22, figs. 1, 4; Hay, 1903, figs. 21, 25) and *Phyllodus* and its allies (Agassiz, 1833-1843, pl. 69A, figs. 1-9; Casier, 1966, figs. 49, 50, pl. 33, figs. 1-10; 1967, pl. 8, figs. 12-13; Cocchi, 1866, pl. 1, figs. 1-8, pl. 2, figs. 1-15, pl. 3, figs. 1-8, pl. 4, figs. 1, 2, pl. 6, fig. 3; Darteville and Casier, 1949, pl. 19, figs. 1-7; Fowler, 1911, fig. 108; Gildersleeve, 1933, figs. 1-19; Leriche, 1900, fig. 1, pl. 1, figs. 1-5; 1902, fig. 5; 1909, pl. 6, figs. 1, 2; 1923, pl. 8, fig. 22; Myers, 1936, fig. 1; Owen, 1840-1845, pl. 47, figs. 1, 2; Priem, 1901, fig. 4, pl. 11, figs. 15-18; 1908, fig. 58; Weiler, 1929, pl. 3, figs. 6-8; White, 1931, figs. 159-162; Wood-

ward, 1901, fig. 19).

In *Bobasatrania* whether the single plate is a basihyal plate or basibranchial plate, or perhaps one representing both, is difficult to say.

Plethodonts, because of their crushing basibranchial dentition, often have been considered relatives of osteoglossids or albulids (for recent discussions, see Bardack, 1965; Patterson, 1967b). Among plethodonts there are forms with either a broad or a narrow crushing surface on the parasphenoid and basibranchial plates. At least the forms with a broad crushing surface apparently have both basihyal and basibranchial plates (Hay, 1903, figs. 21, 25; these specimens have been re-examined in the present study), a character primitive for all major teleostean groups. *Albula*, it may be added, is more advanced in basibranchial structure, having lost the dentition of the basihyal plate. In contrast, *Pterothrissus* has a toothed basihyal plate and lacks a crushing dentition, conditions that are primitive relative to those of *Albula*. Other resemblances between some plethodonts and albulids (e.g., in the general shape of the parasphenoid) possibly are due to the retention of primitive characters. Finally, Recent osteoglossomorphs do not include forms with a specialized, crushing basibranchial dentition (Nelson, 1968a), a feature that apparently is confined to *Albula* among Recent fishes.

Phyllodontids have been considered relatives of pycnodontids (Agassiz, 1833-1843,

pt. 2, p. 243) and labroids (see other references cited above). Phyllodontid tooth plates appear not to be comparable with those of pycnodontids, the crushing teeth of which are supported by the vomer and lower jaw (see Dunkle and Hibbard, 1946, fig. 1; Lehman, 1966, p. 170). Most authors have considered phyllodontid plates to have been pharyngeal in position, comparable with the "pharyngeals" of labroids, with the convex *Phyllodus* plate usually being considered as fused left and right upper pharyngeals (third infrapharyngobranchials). Because of the close similarity between phyllodontid plates and the basibranchial plate and parasphenoid of *Albula* there is little doubt of their homology (see Estes, MS). It may be added that fused upper pharyngeals in fishes are known only in some exocoetoids: at least in *Ar-rhampus*, *Euleptiorhampus*, *Nomorhampus*, and *Chriodorus* (pl. 84, fig. 7; Collette, personal communication); whereas others retain the bones in the more primitive unfused condition: at least in *Cypselurus*, *Exocoetus*, (pl. 84, fig. 6), and *Zenarchopterus* (pl. 84, fig. 8), and apparently also in *Dermogenys* (Rosen, 1964, fig. 12A). In these forms the upper pharyngeals are intimately associated, and in some cases are separated by a suture, but are not fused as usually seems to be believed (see Regan, 1911, p. 333, fig. A; Collette, 1966). If not fused, each of the pharyngeals has a distinctive anteroposterior row of teeth along its medial edge, the suture being situated between the medial tooth rows

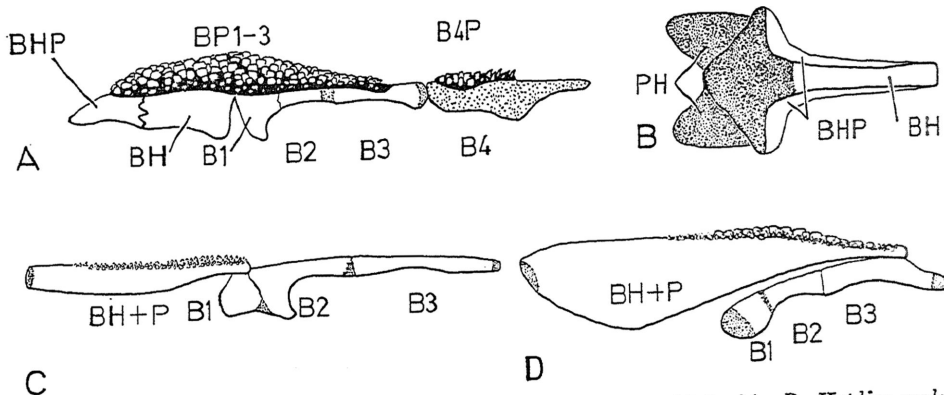


FIG. 7. A. *Albula vulpes*, basibranchial series, lateral view of left side. B. *Hoplias malabaricus*, basihyal complex, ventral view. C. *Nandus nebulosus*, as in A. D. *Pristolepis facialis*, as in A.

of the two bones. If fused, the pharyngeals have a different tooth pattern, without this distinctive bilateral arrangement of antero-posterior rows (cf. pl. 84, figs. 6-8; Regan, 1911, pl. 9, figs. A, B). Because this fusion is unknown in any other fishes, it doubtless developed during the evolution of exocoetids; among these it possibly distinguishes a monophyletic subgroup. In any case, there is little resemblance between these fused upper pharyngeals and phyllodontid plates. Accordingly, there is no basis for any belief in their homology.

There apparently is only one basibranchial tooth plate in *Phyllodus*, and among Recent forms it is comparable only with that of *Albula*. Presumably also in *Phyllodus* the basihyal plate was reduced, as is that of *Albula*. Hence, on present evidence there is little alternative except to place the Phyllodontidae in the Elopomorpha in the vicinity of the Albulidae, pending discovery of articulated material referable to *Phyllodus* or to one of its allies (Estes, MS).

Pristolepis and its relatives for some time have been considered oddities among spiny-rayed fishes because of the presence of parasphenoid teeth, a character otherwise known only in osteoglossomorph, elopomorph, and clupeomorph (*Diplomystus*; see Patterson, 1967c) fishes among the lower teleosts. As are the basihyal teeth opposing them, the parasphenoid teeth of *Pristolepis* probably are secondarily increased in area, but those in other forms (*Nandus*, *Badis*, *Ophiocephalus*, anabantoids) are restricted to a small, posterior patch. It is a curious fact that, except for anabantoids, these parasphenoid teeth oppose not the basihyal, basibranchials, or lower pharyngeals but a pair of tooth plates fused with the third hypobranchials (Day, 1914, p. 44, pl. 16; Srinivasachar, 1955, pl. 28, fig. 5). These plates are probably homologous with others of the paired, anterior series of dermal elements associated but not fused with the endoskeleton of the third arch. If the parasphenoid teeth are primitive, they likely would have been retained with the loss of basibranchial dentition only because these paired plates had developed through assimilation and fused with their endoskeletal supports. In coming to oppose the parasphenoid dentition they functionally

could have replaced the basibranchial teeth.

Among lower teleosts prominent tooth plates fused with the second hypobranchials are developed in close association with the basibranchial dentition (as in pristigasterids; Nelson, 1967b, fig. 8). In other cases the main basibranchial tooth plate seems to have spread over but remained unfused with the second hypobranchials (as in some engraulids; Chapman, 1944a, fig. 7). Whether or not the toothed hypobranchials of nandids and their allies originally developed in relation to this primitive basibranchial dentition is impossible to determine on present evidence, but must be considered a possibility in view of the retention in some equally advanced forms of an apparently primitive, although reduced, basibranchial dentition, namely, that of some myctophiforms, paracanthopterygians, and acanthopterygians. In these, the basibranchial teeth posteriorly tend to be confined to a small patch fused with the third basibranchial. The significance of this apparent shift to a posterior position is not known, but the toothed hypobranchials of nandids possibly represent a further manifestation of this tendency. In any event, being shifted to the third hypobranchials, the teeth could be brought into play with the lower pharyngeals, once the basibranchial series became divided into anterior (C1-3) and posterior (C4-5) copulae (see below). If so, it is easy to imagine how the peculiar condition of anabantoids could have arisen, by a backward shift of the bite of the parasphenoid teeth, with the result that they came to oppose the lower pharyngeals. If such was the evolutionary role of the third hypobranchial tooth plates, they, in opposing the parasphenoid teeth, would be an important character suggesting that nandids, pristolepids, ophiocephalids, and even anabantoids, from which hypobranchial teeth are absent, are closely related to one another and constitute a primitive but diversified group of spiny-finned fishes with a worldwide distribution in tropical fresh water (see also Gosline, 1968, p. 12).

It is an interesting although perhaps coincidental fact that paired tooth plates fused with the third hypobranchials occur also in probably all Mastacembeliformes (see Maheshwari, 1967, fig. 6), although they do not

oppose parasphenoid teeth, which are absent. Among Recent teleosts the third hypobranchials seldom have plates fused with them (as also in some trachichthyids, atherinids, and apparently in some ophidiids). For this reason it seems possible that this character may be phyletically significant, indicating a relationship between nandids, their allies, and mastacembeliforms (see also Job, 1941). It may be added that both third hypobranchial and parasphenoid teeth seem secondarily to have been lost in those nandids with an extreme degree of jaw protrusion (as in *Polycentropsis*, and in South American forms); that in mastacembelids, the toothed third hypobranchials tend to be opposed by tooth plates supported by the epibranchials of the first arch (these in some cases become fused with the first epibranchials, e.g., in British Museum specimens labeled "*M. cunningtoni*"); and that unfortunately neither toothed hypobranchials nor parasphenoid teeth appear to occur in *Luciocephalus* (personal observations; see also Liem, 1967, p. 108; Regan, 1910, p. 768, however, said he observed a few small parasphenoid teeth in *Luciocephalus*). Each of these forms, however, may have lost such vestiges of the "basibranchial-parasphenoid bite" of primitive teleosts in relation to specializations of the feeding apparatus, particularly of the jaws.

The primitive teleostean pattern of basibranchial tooth plates can be traced into the myctophiform (pl. 85, fig. 3) and paracan-

thopterygian (pl. 87, fig. 1) assemblages. Some forms such as *Aulopus* seem to show the complete pattern, but paracanthopterygians show reductions of various sorts usually beginning with the loss of the basihyal tooth plate (apparently absent from all paracanthopterygians except *Polymixia*; e.g., fig. 6B; Emery, 1880, pl. 4, fig. 47; Zander, 1906b, figs. 9, 11, pl. 10, fig. 6; Gosline, 1954, fig. 3; Nybelin, 1957, figs. 25-32, 50; Cohen, 1964, fig. 4; Nielsen, 1966, fig. 8a; Rosen and Patterson, 1969) and the gradual loss of teeth on the basibranchial plate such that only a small patch is left posteriorly. What seems to be secondary subdivisions of the basibranchial plate sometimes occur, particularly when parts of the plate fuse with different basibranchials, as basibranchials 1-3 of some engraulids and basibranchial 3 of esocids (pl. 85, fig. 2). Rarely does the tooth plate become subdivided without its parts becoming fused with the basibranchials as in *Etrumeus* (Nelson, 1967b, fig. 1).

ADVANCED TELEOSTS

Among acanthopterygians a basihyal tooth plate is retained, but apparently invariably is fused with its endoskeletal support. However, the basibranchial plate seems secondarily reduced in most or all acanthopterygians. But in a number of forms median plates occur, having arisen in most or all cases apparently by the fusion of paired elements.

One such example is the beryciform

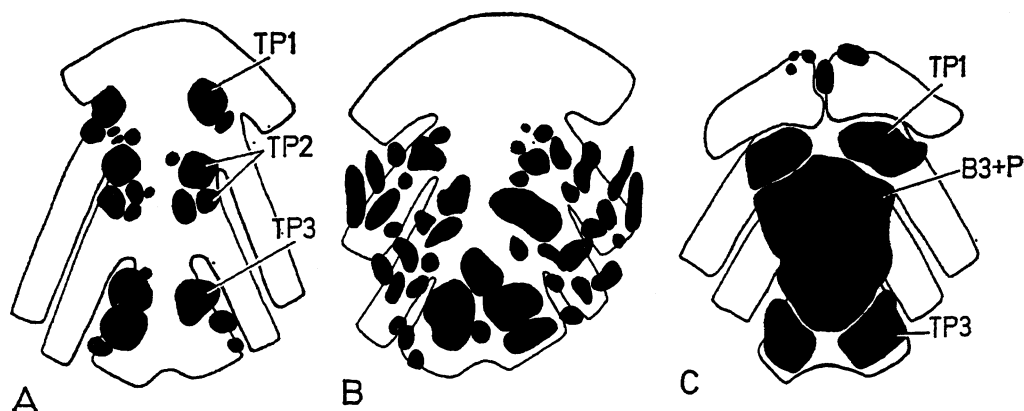


FIG. 8. Basibranchial tooth patches. A. *Trachichthys australis*. B. *Monocentris japonicus*. C. *Cleidopus gloriamaris*.

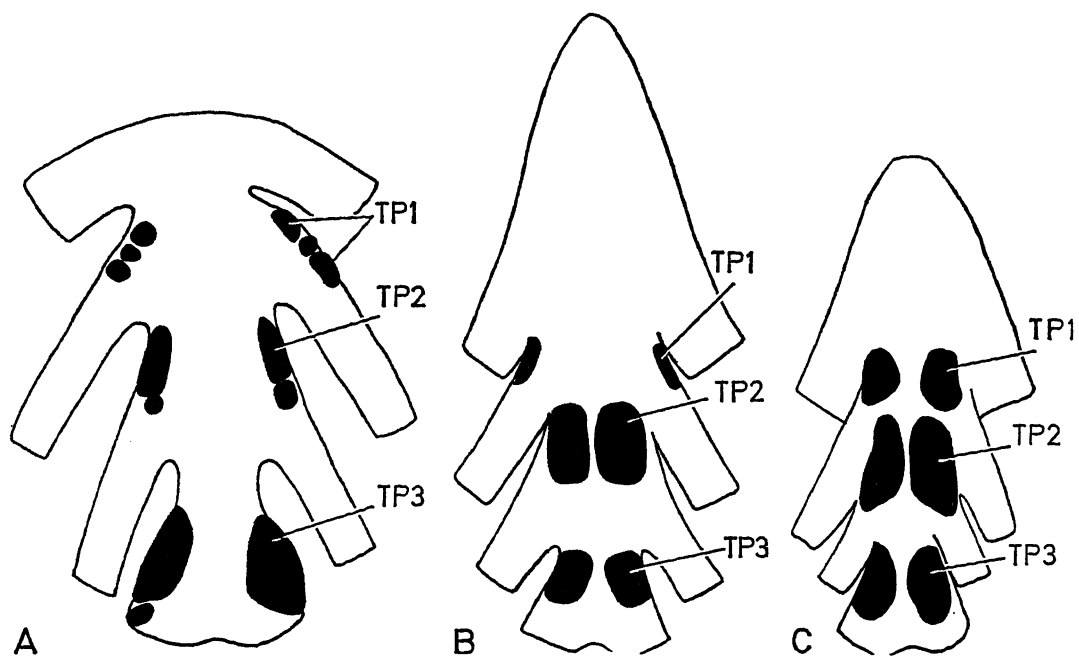


FIG. 9. Basibranchial tooth patches. A. *Hoplostethus mediterraneus*. B. *Holocentrus longipinnis*. C. *Myripristis adustus*.

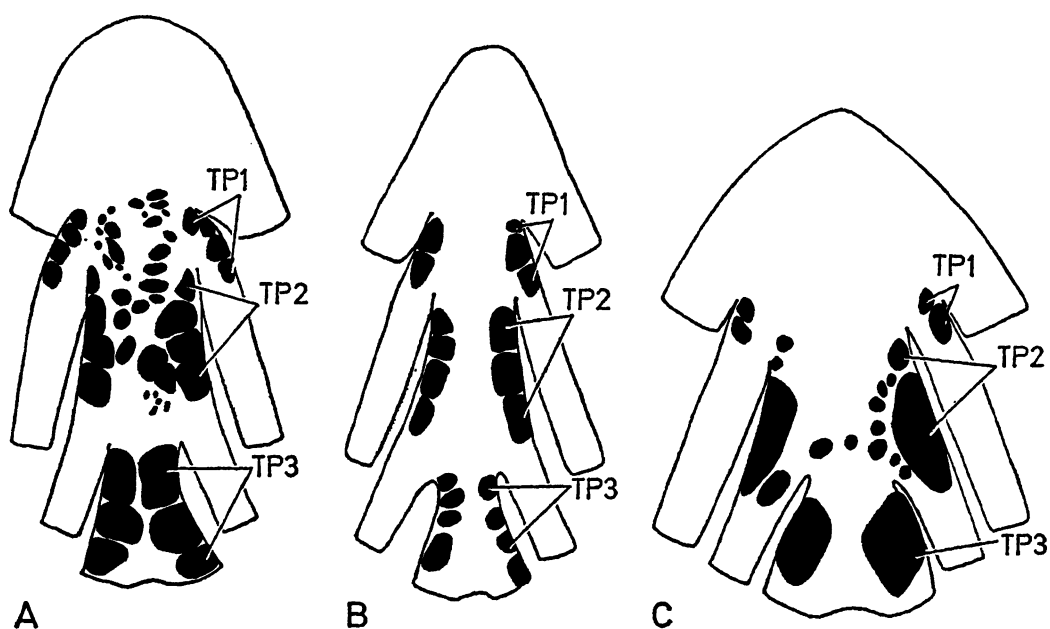


FIG. 10. Basibranchial tooth patches. A. *Centroberyx affinis*. B. *Beryx splendens*. C. *Ostichthys japonicus*.

Cleidopus, which has the tooth plates fused with basibranchial 3 (fig. 8C). No other beryciform is known to have such a median plate, although several have prominent paired plates (figs. 8–10), and some, such as *Myripristis* (fig. 9C), have them closely approximated in the midline. In comparison with *Myripristis* other holocentrids more closely resemble *Holocentrus* (fig. 9B), having the most anterior paired tooth plates widely separated. Berycids (fig. 10B) have all the plates more or less separated and, compared with those of holocentrids, unconsolidated. It is not difficult to imagine that those of *Myripristis* developed through some such series beginning with the condition in berycids. It would not be surprising to find a similar trend in the more generalized relatives of *Cleidopus*, but such seems not to be the case. *Trachichthys* (fig. 8A) is little more advanced than *Beryx*, but in more advanced forms, such as *Monocentris* (fig. 8B), there seems to be only a random arrangement of irregular plates, with no two examined specimens having the same pattern. It seems most likely that the median plate of *Cleidopus* arose by consolidation of tooth plates like those of *Monocentris*. It perhaps is noteworthy that the tooth plates of *Cleidopus*, *Monocentris*, and *Trachichthys* have a curious

appearance, being rounded rather than flat, and giving the branchial apparatus a characteristic knobby appearance, recognizable even at a glance.

Among the acanthopterygians median tooth plates occur also in the long-bodied remoras *Phtheichthys* and *Echeneis* (pl. 86, fig. 3). The short-bodied remoras lack median plates but have paired plates developed to varying degrees (pl. 86, fig. 2), as also does the apparently related *Rachycentron* (pl. 86, fig. 1). A noteworthy resemblance between *Rachycentron* and the short-bodied remoras is the arrangement of the enlarged plates in a paired longitudinal series converging posteriorly at a wide angle. If, as seems likely, the condition in *Rachycentron* is primitive, that in *Echeneis* must be advanced. Exactly how the median plates arose is difficult to say: overlying basibranchials 2–3 of *Rachycentron* are two patches of small plates, which if they were to fuse would duplicate the median plates of *Echeneis*; another possibility is that the median plates arose through fusion of large and distinctly paired plates (as is suggested in pl. 86, fig. 3).

Another example similar to that of echenids is shown in carangids. In many of these forms, tooth plates are randomly arranged over the basibranchial series. However, in

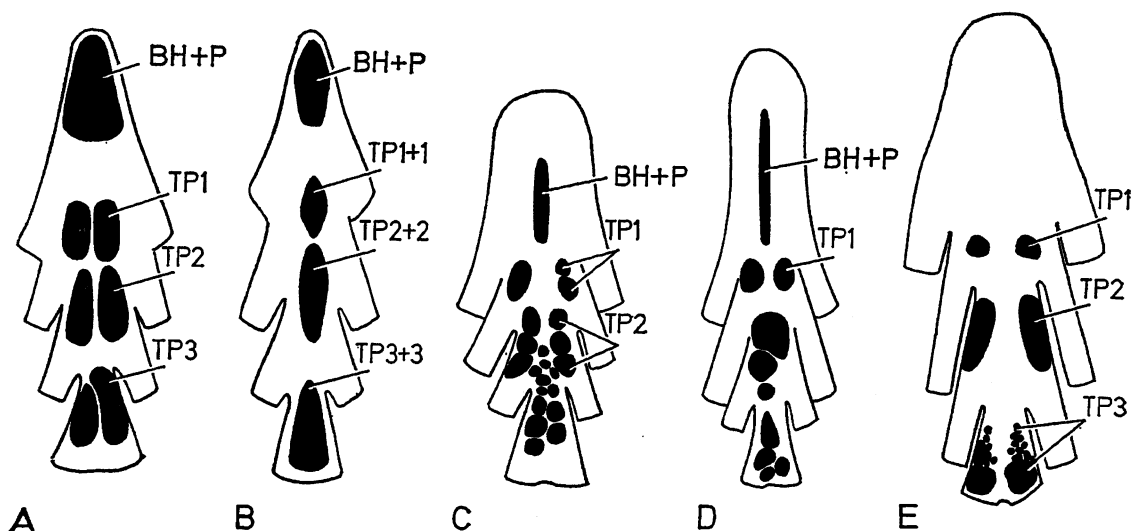


FIG. 11. Basibranchial tooth patches. A. *Chorinemus occidentalis*. B. *Parona signata*. C. *Trachurops crumenophthalmus*. D. *Trachurus trachurus*. E. *Sarda sarda*.

Trachurus and *Trachurops* (fig. 11C, D), the arrangement is somewhat more regular.

In *Chorinemus* (fig. 11A) there are three pairs of tooth plates. It is hard to imagine how the three median plates of *Parona* (fig. 11B) could have arisen, except through fusion of such paired elements.

Among most of the examined scombrids no regular arrangement of the tooth plates was discovered (but for *Sarda*, see fig. 11E) although many forms had numerous plates irregularly arranged. The basihyal in all examined forms was toothless (but for *Makaira*, see La Monte, 1958, fig. 9).

Somewhat more interesting examples of tooth-plate consolidation are shown in members of the family Pomatomidae. For a primitive condition that possibly gave rise to the more advanced condition in pomatomids, there is little to choose from, except that shown in many lower percoids having three pairs of well-developed plates overlying hypobranchials 1-3 as in *Lates* (fig. 12A; see

also pl. 87, fig. 2). In *Scombrops* the apparently usual condition consists of three pairs, with the most anterior extending forward over the basihyal. In one specimen, however, the anterior plate was found to be bilaterally asymmetrical, composed of one plate on one side and two on the other (fig. 12B). These facts suggest that the anterior plate in *Pomatomus* (fig. 12C) arose by the bilateral fusion of two anterior pairs as seen in *Lates* and *Scombrops*. In *Pomatomus*, the posterior plates usually are separate, but among some 110 specimens, there were three showing various degrees of fusion between the posterior tooth plates (fig. 13).

Finally may be mentioned the only known Recent acanthopterygians possibly retaining a vestige of the median basibranchial plate of lower teleosts. Many members of the family Centrarchidae have a small patch of teeth on basibranchial 3, indicating that a tooth plate is fused with it. Toothed basibranchials are known also in some atherinids (see below).

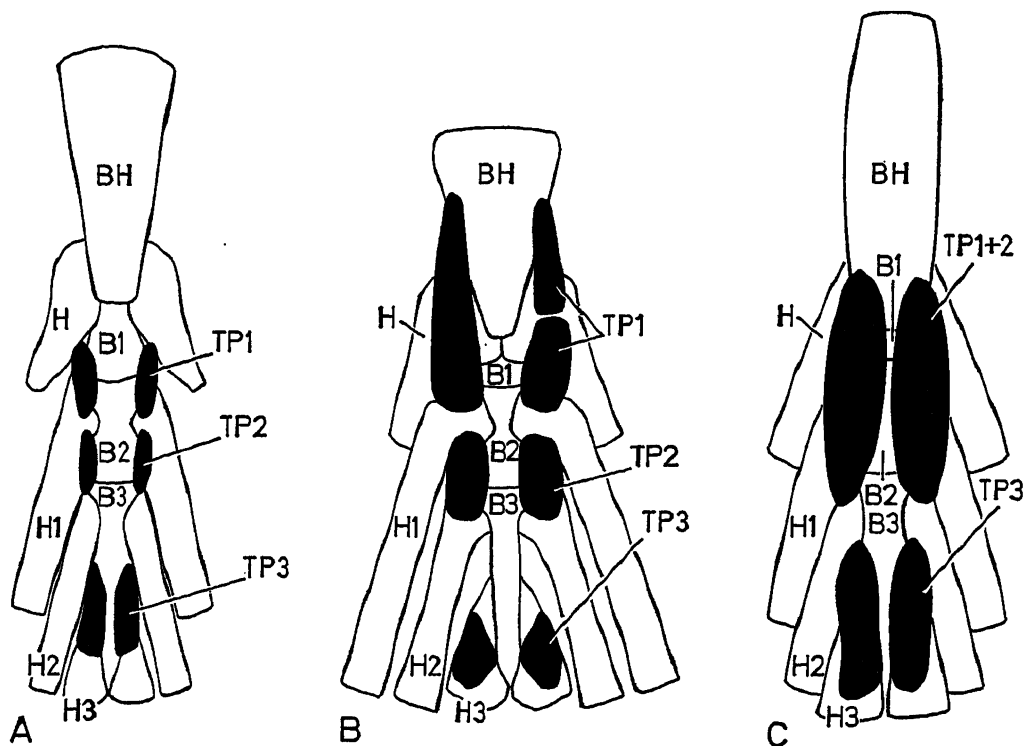


FIG. 12. Basibranchial tooth patches and associated bones. A. *Lates* sp. B. *Scombrops cheilodipteroides*. C. *Pomatomus saltatrix*.

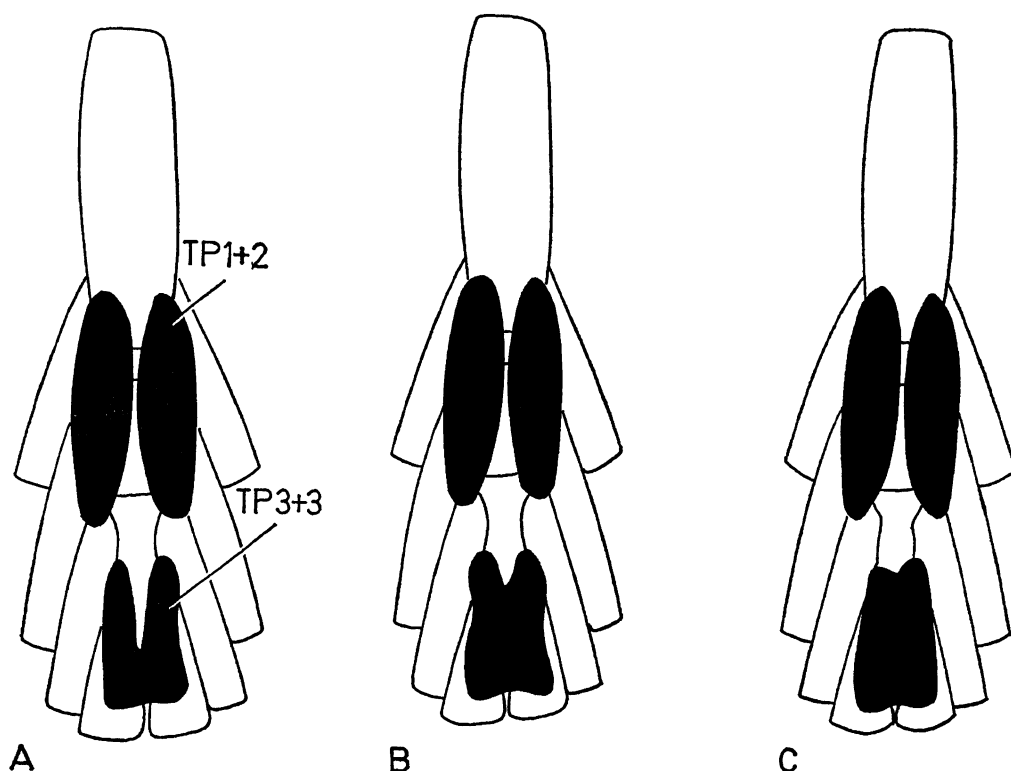


FIG. 13. *Pomatomus saltatrix*, basibranchial tooth patches of three specimens.

The peculiarities noted above in the examples chosen among acanthopterygian fishes, aside from any value they may have as indicators of relationship (as, e.g., between *Phtheichthys* and *Echeneis*, *Chorinemus* and *Parona*, *Scombrops* and *Pomatomus*, *Cleidopus* and *Monocentris*), demonstrate with what ease the dermal skeleton can undergo modifications in the form of its individual elements. They also demonstrate, in a manner convincing to the present writer, that dermal elements during evolution often are modified through processes of fusion. Not only do paired elements fuse in the midline, but elements of different arches do so on either side as well (bilateral fusion is shown also in the ontogeny of the lower pharyngeals of *Conger*; Nelson, 1966, p. 399). These observations have some bearing on current controversies over the likelihood of fusion of dermal bones elsewhere on the head of fishes (Parrington, 1967; Jarvik, 1967b).

Although not well documented, in primi-

tive acanthopterygians a basibranchial dentition probably occurred essentially like that widespread in lower teleosts. In no Recent acanthopterygian (with the exception of some atherinids) is the second basibranchial known to be toothed, as in lower teleosts is usual when there is fusion between any of the basibranchial plates and their supports (e.g., in clupeoids). However, a toothed second basibranchial is present in at least some myctophiforms (e.g., *Aulopus*, *Synodus*), paracanthopterygians (*Polymixia*), and (according to Patterson, 1964) a fossil acanthopterygian (*Aulolepis*), as shown either by teeth on the second basibranchial or, if the teeth are lost, by the dorsal laminae extending fore and aft from the second basibranchial apparently representing a reduced tooth plate (personal observation; see also Patterson, 1964, figs. 21, 31). Further modifications of the basibranchial dentition apparently resulted in its shifting posteriorly, so that in its more advanced condition all that is left

of it is a tooth patch of varying size on basibranchial 3.¹

It is difficult to say whether or not the basibranchial plate when being further reduced invariably sank below the pharyngeal surface, lost its teeth, and, if fused with one or more basibranchials, consequently became largely unrecognizable, as apparently has tended to happen in salmonoids and argentinoids (see, e.g., Böker, 1913, pl. 27; Chapman, 1943, fig. 6; 1944b, fig. 6; Norden, 1961, pl. 6, figs. A-B), stomioids (Weitzman, 1967b, p. 24), clupeids, characoids, aulopodoids, and others (personal observations). Occasionally it seems to have become free of the underlying basibranchials and fragmented into several small pieces, as apparently has happened in at least some specimens of *Polymixia* (fig. 6C). On the whole it seems that fragmentation is the less common method of reduction, although another interesting example of this kind of reduction was observed in a specimen of *Centroberyx affinis*, in which the mesopterygoid teeth, in the form of small plates, were free in the skin overlying the mesopterygoid.

It is possible that "fragmentation" really involves successive generations of dermal elements (Jarvik, 1959; Ørvig, 1967, 1968). In some other teleosts an additional generation seems to have developed in some areas: in *Hoplias* there is a reduced, toothless basihyal plate (fig. 7B) closely associated with the basihyal, both elements well below the surface of the tongue, on which occur a paired, secondary series of basihyal tooth plates (pl. 85, fig. 1). In other cases it appears

that a secondary proliferation of small dermal elements may extend over the entire gill-arch surface. Such tendencies appear in beryciforms, such as *Monocentris* (fig. 8B), perciforms of the families Carangidae and Scombridae, and perhaps most notably in the trichiurid *Eupleurogrammus*, in which small, closely set tooth plates cover the entire surface of the gill arches as well as some of the paired ventral parts of the hyoid arch. The condition in *Eupleurogrammus* seems exceptional, for none of the other examined trichiurids (*Aphanopus*, *Lepidopus*, *Benthodesmus*, *Trichiurus*) has any tooth plates on the basibranchials, and only scattered tooth plates were seen in a few genera of the related gempylids (*Thyrssites*, *Ruvettus*, *Nesiarchus*, *Rexea*, *Prometichthys*), the remaining examined forms being toothless in the area of the basibranchials.

In acanthopterygians, however the basibranchial plate was reduced or lost, it is clear that initially there was little modification of the potentiality for tooth plate formation in the area of the basibranchials (e.g., that of *Pristipomoides*, pl. 87, fig. 2).

Some members of all the major teleostean lineages (e.g., the Osteoglossomorpha, Elopomorpha, Clupeomorpha) are without median basibranchial tooth plates, apparently as a result of secondary reduction. Loss of the primitive basibranchial dentition in each case is probably correlated with some particular improvement or specialization of the feeding mechanism, with the result that the basibranchials themselves no longer participate in seizing and holding large prey. Jaw protrusion and pharyngeal-bone mobility seem to be improvements, and shearing and grinding jaw dentitions are specializations, inversely correlated with basibranchial dentition. The large paired plates (and their median derivatives, e.g., in *Parona*) that in some cases occur over the basibranchials of teleosts could represent a reversal in the general trend toward loss of basibranchial dentition. Functionally, this reversal would mean that the basibranchial area in some cases is secondarily involved in seizing and holding large prey. Seemingly, this reversal has tended to occur in predators that run down and seize their prey; it may therefore be associated with high-speed swimming and the pelagic environment. At least the

¹ A toothed third basibranchial is fairly common in paracanthopterygians (fig. 6B; see also Zander, 1906b; Nybelin, 1957; Rosen and Patterson, 1969) but rare if present at all in Recent acanthopterygians, the only known examples being some centrarchids (e.g., *Ambloplites*, *Archoplites*, *Centrarchus*, *Chaenobryttus*, *Micropterus*; see also Blair and Brown, 1961, fig. 7; Dineen and Stokely, 1956, fig. 12). In some cases the tooth patch gives some indication of being paired (pl. 87, fig. 3), suggesting the possibility of a secondary origin. However, among all centrarchids in which a tooth plate is known, it is fused with its support, in contrast to the condition of the secondarily median tooth plates of remoras, *Pomatomus* and *Parona*. For this reason it is best regarded as a derivative of the basibranchial dentition of primitive teleosts. It is to be concluded therefore that the condition primitive for acanthopterygians was essentially the same as that for lower groups, including both basihyal and basibranchial plates, fused or not with their endoskeletal supports.

secondarily developed basibranchial dentition in such fishes as *Pomatomus*, *Echeneis*, and *Parona* suggests this possibility.

SARCOPTERYGIANS

Based on the above analysis of the median plates of acanthopterygians, it might be expected that the median basibranchial plates also of lower teleosts were derived from paired plates of even more primitive fishes. Therefore, it is not surprising to find that such median plates are absent from all Recent non-teleostean fishes and that those plates that do occur almost without exception are paired (fig. 14; pl. 79, figs. 1, 2; pl. 81, figs. 1-3; pl. 83, fig. 1). The only median plate known in non-teleostean fishes is that of *Latimeria* (pl. 81, fig. 1; Millot and Anthony, 1958, pl. 45B), and it almost insignificantly is tucked in among two pairs of much larger plates and apparently is not invariably present (Smith, 1940, pl. 23). It seems likely that even the condition in *Latimeria* is a secondary one, for no median plates occur in the fossil coelacanths in which basibranchial dentition is well known (Nielsen, 1936; Schaeffer, 1952). In the most primitive coelacanths what the basibranchial dentition was like is unknown, but Nielsen's (1936, pp. 31, 32) observation of several pairs of tooth plates of the large Greenland form suggests that the pattern might have been similar to that of *Polypterus* (pl. 81, fig. 2; in *Calamoichthys*, the arrangement of tooth plates is

similar, but the plates are fused with the supporting basibranchial). In *Polypterus* occur a paired series of tooth plates probably derived from the dermal-element series of the second and third arches. In *Diplurus* occur three pairs of larger tooth plates (fig. 14B; Schaeffer, 1952, fig. 8, pl. 12, fig. 2). It is relatively easy to imagine how the condition in *Latimeria* could have been derived from that of *Diplurus* by the fusion and partial reduction of the posterior tooth plates, and how that of *Diplurus* could have been derived from that of *Polypterus* (fig. 14A) by consolidation of the small plates of arches 2-3. But to interpret coelacanth tooth plates as derivatives of particular arches can be done only tentatively, for in the fossil forms their exact relations with the paired arch-elements are not known, and in *Latimeria* the plates are so large that their primitive relationships are obscured. Provided that they are comparable with those of *Polypterus*, they can be assigned to the dermal-element series of one or both of arches 2 and 3 with reasonable certainty. Thus a probable interpretation of these structures in coelacanths is that shown in figure 14. The large, paired basibranchial plates of *Eusthenopteron* (fig. 3A), if comparable, probably represent tooth plates 2A of coelacanths. If so, tooth-plate consolidation in rhipidistians is advanced beyond the level shown in *Polypterus*, but not to that shown in coelacanths.

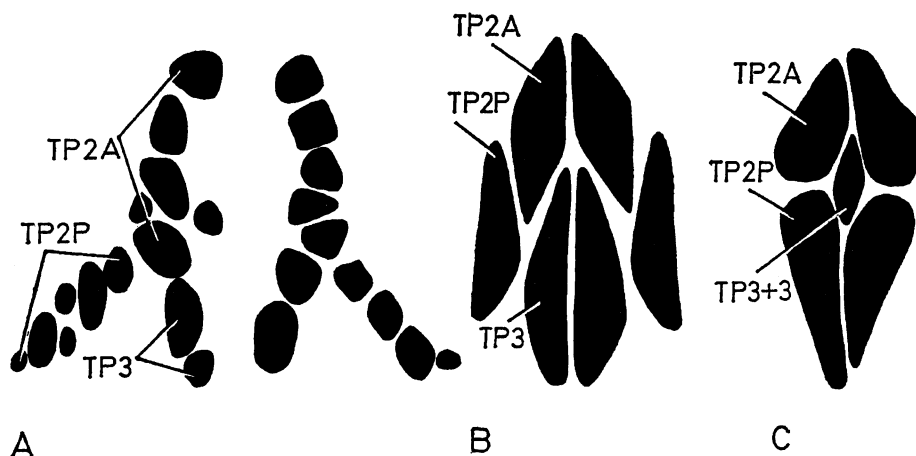


FIG. 14. Basibranchial tooth patches. A. *Polypterus* sp. B. *Diplurus newarki* (modified from Schaeffer, 1952, fig. 8). C. *Latimeria chalumnae*.

CHONDROSTS

Paired tooth plates occur anteriorly on the paired elements of arches 1 and 2 of *Polyodon* (pl. 83, fig. 1), and of arch 1 in *Psephurus* (pl. 79, fig. 1), at least in small specimens of both genera (two large examined specimens of *Polyodon* lacked these plates). In addition, *Psephurus* has very small tooth plates scattered over the basibranchial and adjacent areas; posteriorly, dentition is absent. It is noteworthy also that dorsally, behind the upper jaw and palatal dentition, two pairs of small plates occur in both genera, an anterior pair probably assignable to the dermal-element series of the hyoid arch, and a posterior pair to the series of the first branchial arch (pl. 84, fig. 3). In *Psephurus* also a scattering of very small plates underlies the parasphenoid and adjacent areas.

In adult sturgeons teeth are reduced or absent (Zograf, 1887, 1896; Jakovleva, 1954) although the anterior part of the basibranchial area is in many cases occupied by a peculiar, non-calcified, biting surface. In both *Acipenser* (pl. 88, fig. 1) and *Scaphirhynchus* (pl. 88, fig. 2) this surface is formed of ridges in a pattern suggestive of that of the tooth plates in the same position in *Polyodon*. Dorsally, supported by the endoskeletal part of the upper jaw (see Bugajew, 1930), occurs a similar biting surface likewise composed of ridges in a complex pattern (pl. 84, figs. 1, 2), but not one easily compared with the patterns of tooth patches in *Polyodon* (pl. 84, fig. 3; according to Zograf, 1896, pl. 5, figs. 8, 9, 13, 15, only the most anterior of the upper transverse ridges develops in relation to a tooth patch, one presumably homologous with the palatine tooth patch of *Polyodon*). These biting surfaces are specializations unique to sturgeons and doubtless function in relation to the highly protrusile jaws of these fishes (see Meinel, 1962).¹ The structure of these biting surfaces, particularly the nature of the ridges, has not been investigated in detail, but it would seem that the

ridges in some way must be related both to the ventral and to the dorsal tooth plates found in *Polyodon*. Because it is uncalcified, the substance of the ridges is not comparable with that of the tooth plates, but the pattern of both is about the same, although a secondary increase in the number of ridges certainly seems to have taken place dorsally. During ontogeny how tooth plates develop, how later they are resorbed, and how ridges are formed are not known in much detail (see Jakovleva, 1954).

In sturgeons one further phyletic trend worth noting is the tendency for the surface of the gill arches to become papillate. A similar tendency seems apparent in lungfishes (pl. 89, fig. 2), some herbivorous characins (e.g., *Curimata*), *Electrophorus*, and other teleostean fishes. The exact significance of these papillae is not known, but their occurrence is correlated with a reduced or absent gill-arch dentition. How they, and also the peculiar biting surfaces of sturgeons, functionally could replace tooth plates is not known, but possibly is associated at least in some cases with a tendency toward herbivorous feeding habits.

With respect to the occurrence of paired plates in lower actinopterygians, it is a remarkable fact that even in *Lepisosteus* (pl. 81, fig. 3), in which one would expect to find a single, well-ossified plate (like that in osteoglossomorphs: pl. 80, figs. 1-3), the dermal part of the elongate, tooth-bearing tongue is composed of a paired series of tooth plates. From the remaining lower Recent teleostomes, including the lungfishes (pl. 89, fig. 2) and *Amia* (pl. 79, fig. 2) prominent tooth plates are absent over the anterior basibranchials, although *Amia* has a paired series over basibranchial 6.

Among actinopterygians, the teleosts are unique in having two median tooth plates, a smaller one over the basihyal and a larger one over basibranchials 1-3. If derived through fusion of paired tooth plates, these median tooth plates likely represent an advance in basibranchial structure over the paired condition found in other, and in this respect more primitive, teleostomes.

The long anteroposterior extent of the basibranchial plate in *Elops* makes it difficult to imagine that the plate was derived from the paired dermal-element series of a

¹ It is the protrusile, endoskeletal upper jaw that supports the upper ridge pattern. From this standpoint, sturgeons appear to be significantly more specialized than paddle fishes. In this connection it may be added that not all sturgeons have such ridges (they are absent, for example, from *Acipenser mikadoi*) and that there possibly were fossil "paddle fishes" with protrusile jaws (MacAlpin, 1947, p. 230).

single arch. More probably two or more arches were involved, possibly the same ones (second and third) that produced the basibranchial plates of *Polypterus*, *Latimeria*, and *Eusthenopteron*. If so, the plate of *Elops* could have been derived simply through fusion of basibranchial plates such as those of *Polypterus*. The first arch of *Elops* possibly is involved, but only in the formation of the basihyal tooth plate. In *Hoplias*, paired series of plates extend from the first arch onto the basihyal (pl. 85, fig. 1).

BASIBRANCHIALS

The significance of basibranchial tooth plates in groups of bony fishes cannot be

discussed without reference to their supporting endoskeletal bones. When well developed and ossified, the basibranchials of these fishes are arranged according to two basic patterns: (1) either as a series of elements, ossified or not, so that each of the paired arch-elements articulates with the series between two successive basibranchials; or (2) as a single (possibly in some cases double) element to the side of which articulate all or most of the paired arch-elements.

ACTINOPTERYGIANS

In primitive representatives of all the major groups of teleosts, the basibranchial series is subdivided into three separate

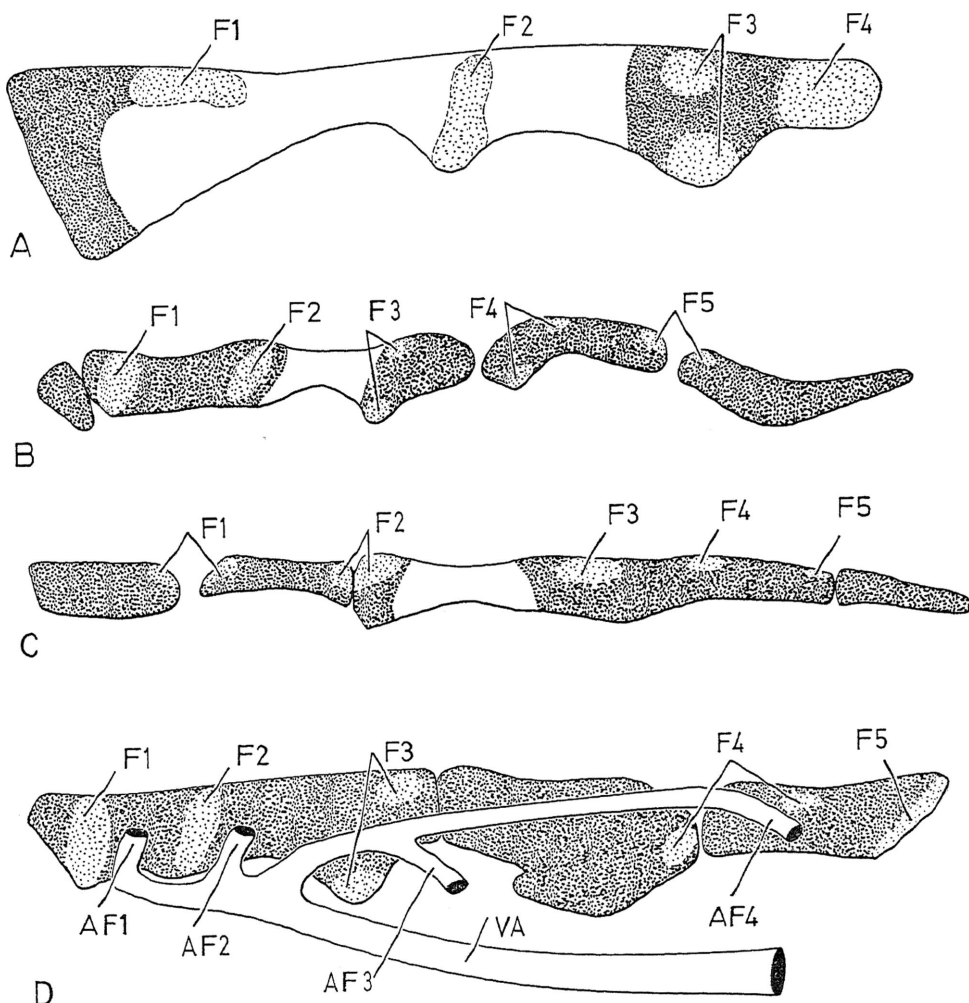


FIG. 15. Basibranchial series, lateral view of left side. A. *Polypterus* sp. B. *Amia calva*. C. *Lepisosteus platyrhinchus*. D. *Polyodon spathula*.

pieces (copulae): (1) the anterior basihyal, which is a single ossification (not invariably separate from the first basibranchial); (2) a middle piece, including the ossified basibranchials 1-3; and (3) a posterior element, almost invariably cartilaginous. The paired hyoid elements articulate with the basibranchial series between the basihyal and basibranchial 1; the paired elements of branchial arch 1, between basibranchial 1 and basibranchial 2; the elements of arch 2, between basibranchials 2 and 3; the elements of arch 3, between basibranchial 3 and the posterior cartilaginous element; and the elements of arch four and arch 5, with the posterior element, arch 4 anteriorly along its sides, and arch 5 posteriorly. In some cases the posterior element ends at the level of arch 5 and in other cases it extends farther

backward. In *Amia* and *Lepisosteus* (fig. 15B, C) there is no separate basihyal, but there are a small, independent first basibranchial (cartilaginous), only one ossification in the series, and one or two cartilaginous posterior elements. In sturgeons and paddlefishes, there likewise is no separate basihyal, and in the small specimens examined no ossification in the basibranchial series, which is subdivided as in *Polyodon* (fig. 15D).¹ The fossil actinopterygians known in this regard likewise lack a separate basihyal, but some

¹For *Acipenser*, van Wijhe (1882, pl. 15, fig. 2) showed two small ossifications, one (basibranchial 4 according to the present terminology) between the paired elements of arch 3 and arch 4 and one (basibranchial 5) between arch 4 and arch 5 (for chondrosteian gill-arch structure, see also Bridge, 1879; Parker, 1882; Iwanzov, 1887; Imms, 1904; Kurz, 1924; Sewertzoff, 1928; Stengel, 1962; Meinel, 1962).

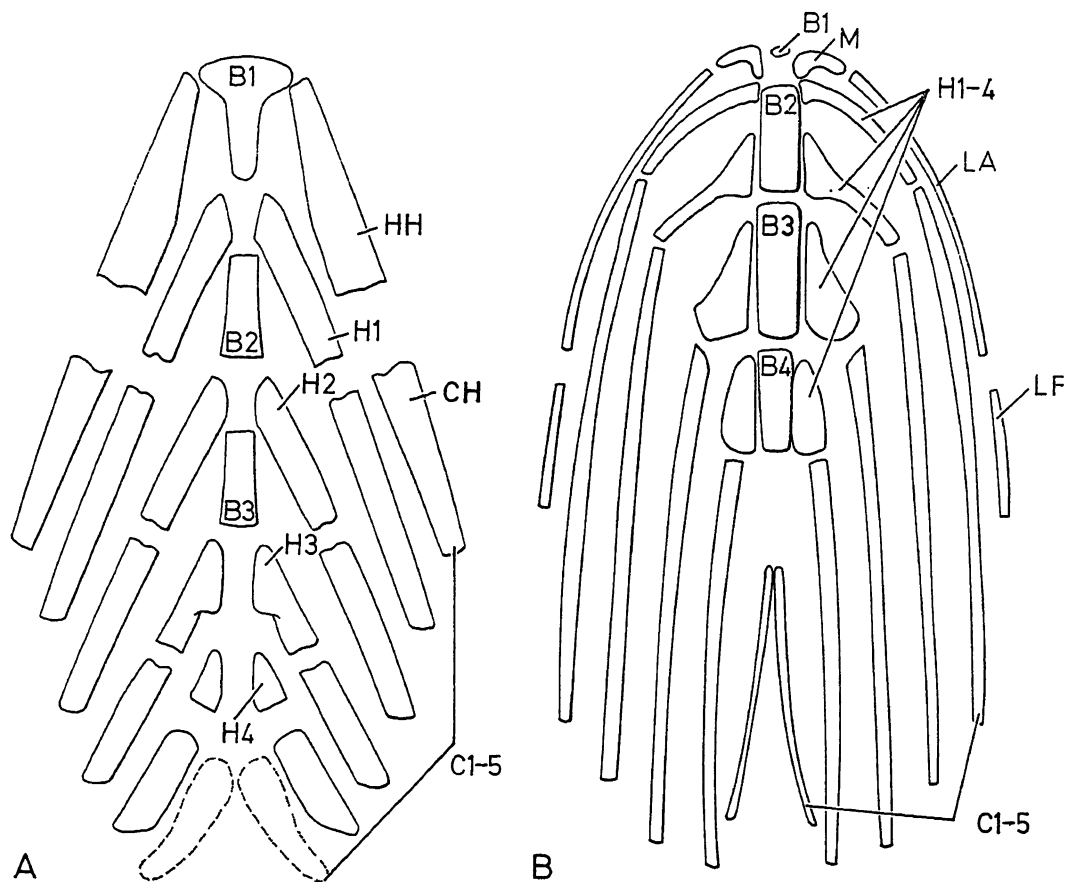


FIG. 16. Gill arches, ventral ossified parts, ventral view. A. *Acanthodes bronni*. B. *Pteronisculus stensioei* (modified from Nielsen, 1942, fig. 45).

forms have a series of from three to four basibranchial ossifications (fig. 16B; see also Stensiö, 1921, fig. 66; 1925, fig. 26; Nielsen, 1942, 1949). This pattern is similar but not identical to that known also in acanthodians (fig. 16A).

SARCOPTERYGIANS

A different pattern occurs in *Polypterus* (figs. 3C, 15A), rhipidistians (fig. 3A, B), *Latimeria* (Smith, 1940, pl. 24; Millot and Anthony, 1958, pl. 46), and tetrapods (Gaupp, 1905) in which there is typically only a single basibranchial element, with most or all of the paired arch-elements articulating with it.¹ From all these forms a separate basi-hyal apparently is absent, although in *Eusthenopteron* the "sublingual rod" of Jarvik in reality possibly is one. So far as known, all dipnoans lack a well-developed basibranchial skeleton, but in *Neoceratodus* occur a basi-hyal and two basibranchial rudiments, all cartilaginous (personal observations; see also Sewertzoff, 1927, fig. 8; Schaeffer, 1968, fig. 1).

ELASMOBRANCHIOMORPHS

Among elasmobranchiomorphs the condition of the basibranchials is variable, ranging from several, small elements in sharks to a few, large elements in rays, with a varied assortment in chimaeras.²

¹ In *Polypterus* there is only one basibranchial element, in both the embryo and the adult (Allis, 1922, pl. 8, figs. 16-17; Daget, 1950, p. 121; Daget, Bauchot, Bauchot, and Arnould, 1964, figs. 24, 27-29; Devillers, 1958, fig. 432; Pehrson, 1947, fig. 5; van Wijhe, 1882, pl. 15, fig. 7; and personal observations), despite some statements to the contrary (Sewertzoff, 1927, fig. 9; see also Jarvik, 1954, p. 23). In *Eusthenopteron*, in which, according to Jarvik (1954), two ossifications occur, three arches including the hyoid articulate with the anterior element, the larger of the two.

² (Allis, 1923a, pl. 13, figs. 35, 36; van Bemmelen, 1886, pl. 11, fig. 16; Braus, 1906, fig. 1; Cole, 1896, pl. 2, fig. 2; Daget, 1948, figs. 1, 6; Daniel, 1915, pl. 4, fig. 11; 1916, fig. B; 1934, fig. 50; Dean, 1904, pl. 1, fig. 7; van Deinsse, 1916, figs. 1, 2, 16-20; Denison, 1937, fig. 7; Devillers, 1958, figs. 376, 377; Edgeworth, 1935, fig. 168; El-Toubi, 1949, fig. 9; 1952, figs. 1, 3, 5-7; El-Toubi and Hamdy, 1959, pl. 1, fig. 5, pl. 4, fig. 5, pl. 5, fig. 5; Fürbringer, 1903, pl. 17, figs. 18-21, pl. 18, figs. 24, 28, 29, 37; Garman, 1885, pl. 9; 1899, pl. 2, fig. 6, pl. 5, fig. 2; 1904, pl. 12, figs. 1, 2, pl. 13, figs. 1-3; 1913, pl. 51, figs. 2, 3, pl. 59, fig. 6, pl. 62, fig. 3, pl. 64, figs. 1-3, pl. 65, figs. 1-3, pl. 66, fig. 2, pl. 67, figs. 1, 3, pl. 68, figs. 1, 2, 4, pl. 69, figs. 2-4,

COMPARATIVE BASIBRANCHIAL STRUCTURE

In the literature there is much confusion and no agreement regarding the terminology of basibranchial elements in fishes. Little is known of their basic structure and of their considerable variation. For example, it is not known whether there was a separate basibranchial for each arch of the most primitive fishes, with a subsequent phyletic trend toward fusion, or whether the opposite was the case.

ACTINOPTERYGIANS

Afferent arterial canals in actinopterygians are formed in many cases by the double articulation of arch 3 and arch 4 with the basibranchial series, and accommodate the posteriorly directed roots of afferent branchial arteries 3 and 4 (Nelson, 1967a).³ The presence of afferent arterial canals in arch 3 of *Polypterus* (fig. 15A) and commonly in arches 3-4 of actinopterygians would seem

pl. 70, figs. 2, 4, pl. 71, figs. 2-4, pl. 72, fig. 2, pl. 73, figs. 1-4, pl. 74, fig. 2, pl. 75, fig. 2; Garrick, 1954, fig. 3; Gegenbaur, 1872, pl. 14, figs. 1-3, 6, pl. 16, fig. 1, pl. 17, figs. 1, 2, pl. 18, figs. 1-6, pl. 19, figs. 1-4, pl. 20, fig. 1; Gibian, 1913, pl. 4, figs. 1-6; Goodey, 1910, pl. 43, fig. 6; Hamdy, 1961, figs. 1-4; Haswell, 1885, pl. 1, fig. 10, pl. 2, fig. 2; Hawkes, 1905, figs. 1, 2; Helbing, 1904, figs. 15, 16, 23; Hoffman, 1914, pl. 10, figs. 1-3; Holmgren, 1940, figs. 68, 82, 87, 90, 96, 110, 117, 123, 137, 138, 143, 144, 155, 158, 161, 164, 170, 180; 1942, fig. 34; Hosford, 1920, figs. 1, 2; Hubrecht, 1878, pl. 8, fig. 4; Jaquet, 1897, pl. 6, figs. 9, 10; 1900, pl. 5, fig. 201; Luther, 1909, fig. 12; Metschnikoff, 1880, pl. 24, fig. 8; Molin, 1860, pl. 6, figs. 2, 4, 6, pl. 8, fig. 3, pl. 11, fig. 1, pl. 12, fig. 5; Parker, 1878, pl. 36, fig. 4, pl. 37, fig. 2, pl. 38, fig. 1, pl. 40, figs. 4, 5, pl. 41, fig. 3, pl. 42, fig. 4; Rabinerson, 1925, figs. 1, 2; Reis, 1897, pl. 1, figs. 2, 3; Ridewood, 1899, fig. 1; Schauinsland, 1903, pl. 18, fig. 129; Sewertzoff, 1927, fig. 1, pl. 29, fig. 8; Tchang, 1950, fig. B; Wells, 1917, pl. 2, fig. 6; White, 1892, pl. 1, figs. 1, 2, pl. 2, fig. 3).

³ The canals are developed in much the same way in sturgeons, paddlefishes (fig. 15D), *Amia* (fig. 15B; pl. 90, figs. 2-5), and representatives of most lower teleostean groups (Allis, 1897, p. 648; 1922, p. 232, 264; Bridge, 1879, p. 710; Danforth, 1912, figs. 4, 5; Dulzetto, 1950, fig. 4; Thys van den Audenaerde, 1961, fig. 21; van Wijhe, 1882, pp. 227, 284, 285; Woskoboinikoff, 1910, figs. 13, 14, 17, 21; pl. 2, figs. 24, 25). Among Recent forms both *Latimeria* and *Lepisosteus* lack canals, and they are secondarily reduced or lost in many advanced teleosts. In *Latimeria*, the canals might secondarily have been reduced in relation to the loss of independent hypobranchials. Whether they occurred in any rhipidistian is not known.

to be an important similarity bridging the apparent gap between the two basic types of basibranchial series. If so, it is necessary to decide which of the two basic types of ossification patterns is primitive and which is advanced, in short, whether there occurred a phyletic trend toward multiplication or alternatively consolidation of ossification centers. For teleosts much information suggests that in primitive forms there occurred a basihyal ossified in its posterior part and three basibranchials, consisting of three ossification centers in a single cartilage. These ossifications in the various teleost lineages were modified in various ways and in some cases were lost in part or completely. However modified among teleosts, they seem not in any case to have been combined into a complex, larger ossification like that of *Polypterus* and other sarcopterygians.

Therefore it might be argued that the large element in *Polypterus* did not arise as a result of fusion of separate ossifications or ossification centers, that primitively it was single, and consequently that the phyletic trend has operated in the direction of subdivision. In *Polypterus* the single element when viewed from the side is partly subdivided into three ossified areas by the cartilaginous surfaces articulating with hypobranchial 1 and hypobranchial 2 (fig. 15A; see also Allis, 1922, pl. 8, fig. 16, pl. 24, fig. 54). One can imagine how constriction of this single element during evolution could have produced the three basibranchial ossification centers (B1-3). The fact that among actinopterygians an endoskeletal basihyal is known only in teleosts suggests that at least this element arose by subdivision of a larger element such as that of *Polypterus*.¹

Thus, it seems possible that both the number of ossification centers and the number of independent elements (copulae) secondarily were increased. Other observations could be marshaled to support these two

hypotheses: (1) that basibranchial structures in some cases become secondarily subdivided, for in characids an extra median, or in some cases paired, cartilage commonly occurs anterior to the basihyal, probably having arisen by segmentation (fig. 7B; Bertmar, 1959, figs. 38-39); (2) that when the basibranchial series is subject to reduction, secondarily separate rudiments in some cases are associated with arches ordinarily without them, for in eels a number of such rudiments seem to have been generated by the reduction of basibranchials 1-3 (Nelson, 1966, figs. 17-19, 30, 34), and in *Aulostomus* similar rudiments by the reduction of the posterior, normally cartilaginous element (fig. 17A; for some other fishes, see Allis, 1903, figs. 29, 30; Günther and Deckert, 1959, fig. 16; Kadam, 1961, figs. 23, 24); (3) that basibranchials arise embryologically not by means of fusion of separate elements contributed by the various arches, but by subdivision of independently formed, larger rudiments into smaller²; finally (4) that in one or a few cases additional ossifications are produced secondarily within or closely adjacent to the basibranchial series.

One example of a secondary basibranchial ossification might be the "fourth" basibranchial of the Triassic actinopterygian *Australosomus*. In describing the basibranchials, Nielsen (1949, fig. 40) noted four ossifications, the most posterior being peculiarly deep, with two large canals through it. The facts available in 1949 did not allow Nielsen to interpret this element with certainty, but there is little doubt that the canals were afferent arterial canals housing

¹ Indeed it is a remarkable fact that an endoskeletal basihyal seems to be lacking even in *Lepisosteus*, in both the embryo and the adult, the long series of tooth plates being supported only by dense connective tissues (van Wijhe, 1882, pl. 16, fig. 10; Veit, 1911, pl. B, fig. 14, pl. C, fig. 20; Hammarberg, 1937; and personal observations). What might be the curious rudiment called a basihyal by Hammarberg (fig. 12), however, is difficult to say.

² (Aziz, 1960, fig. 1; Bamford, 1948, fig. 12; Berrill, 1925, figs. 11, 14, 15; Bertmar, 1959, figs. 20, 21, 30, 31, 33, 38, 39; Bhargava, 1958, figs. 3, 6, 8, 10, 14, 15, 20; Böker, 1913, pl. 27; Daget and d'Aubenton, 1957, figs. 21, 24; De Beer, 1927, figs. 24, 30, 41; Hsueh, 1934, figs. 7, 14, 19, 20, 23; Kadam, 1958, figs. 3, 6; 1961, figs. 8-10; Kindred, 1921, figs. 9, 10, 14; Mackintosh, 1923, figs. 6, 9; Marathe and Bal, 1956, fig. 6; 1957, figs. 3, 7, 11, 18; Marathe and Suterwala, 1963, figs. 4, 11, 17; Norman, 1926, fig. 35; Omarkhan, 1950, figs. 4, 7, 8; Ramaswami, 1945, pl. 1, fig. 1, pl. 2, fig. 2, pl. 3, fig. 3; Sewertzoff, 1928, pl. 7, figs. 26-28; Srinivasachar, 1953, figs. 18, 22; 1958b, figs. 3, 6, 9; Swinnerton, 1902, pl. 28, figs. 6, 7, 14-16, pl. 29, fig. 22; Veit, 1911, pl. B, fig. 14, pl. C, fig. 20; Wells, 1923, fig. 5; Woskoboinikoff, 1910, pl. 2, figs. 17-21, pl. 4, figs. 46, 47, 49.)

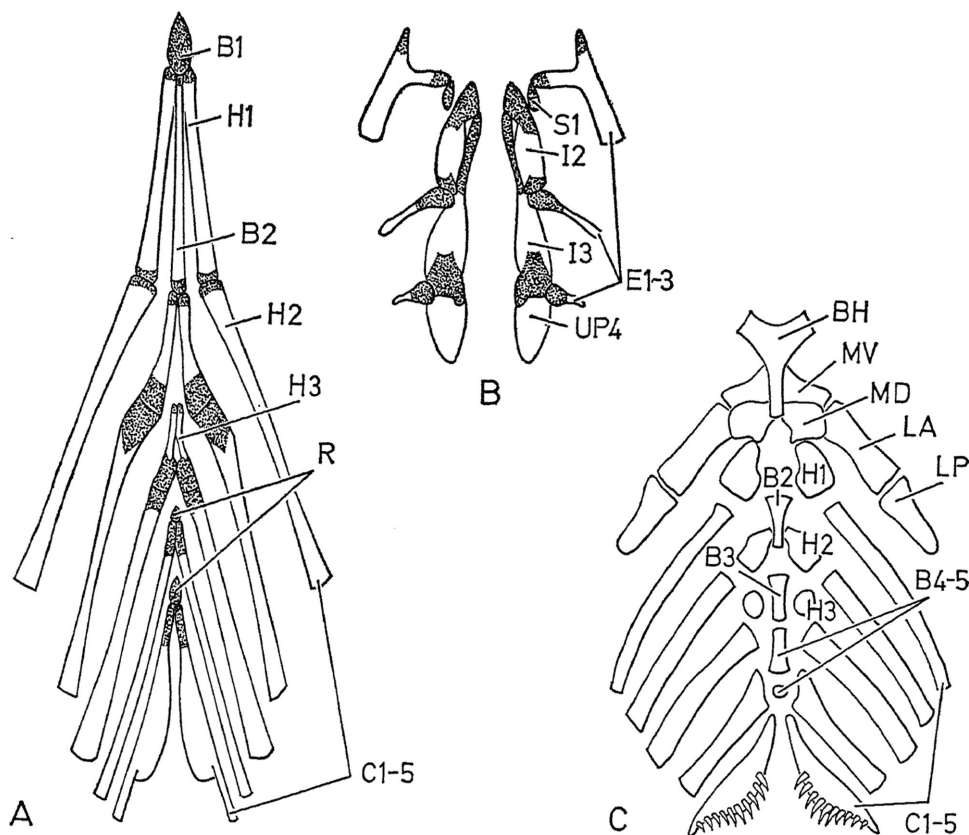


FIG. 17. Gill arches. A, B. *Aulostomus chinensis*. A. Ventral parts, ventral view. B. Dorsal parts, dorsal view. C. *Nemachilus pulcher*, ventral ossified parts, dorsal view.

posteriorly directed, fourth afferent branchial arteries. Nielsen (1949, p. 128) identified this structure as "either a specialized posterior basibranchial ossification or possibly such an ossification which has become fused with the hypobranchials of the fourth branchial arch." Indeed, the fourth afferent canals known in other fishes are formed with the participation of the fourth hypobranchials (as in *Amia*), rudiments of them (as in *Misgurnus*, fig. 18D), or, on the fourth ceratobranchials, the cartilaginous articular areas which sometimes are said to represent fused-on fourth hypobranchials. Thus it is possible to imagine that the element of *Australosomus* did include the structural equivalents of fourth hypobranchials. If one assumes that primitively there were independent fourth hypobranchials, then it follows that a secondary fusion could have taken place. Relative to the

conditions among Recent fishes, however, this would be an unusual example of fusion between ossified endoskeletal elements, or one leading to the same result. One alternative to this explanation is that the fourth hypobranchials perhaps separated from, rather than fused with, the posterior basibranchial of such a fish as *Australosomus*.¹

A more likely interpretation is suggested by the similarity in basibranchial structure

¹ Little is known of the origin of hypobranchials, but it is conceivable that they originally were produced by secondary segmentations of one or more larger median elements, possibly independently in different groups of fishes. Among elasmobranchs the peculiarities of the ventral parts of the gill-arch endoskeleton seem not to have arisen as the result of fusion of primitively independent elements. By secondary segmentation of a median structure possibly arose also the most antero-ventral paired elements of the hyoid arch (the so-called hypohyals), a possibility suggested by a comparison of *Acanthodes* and *Pteronisculus* (fig. 16A, B).

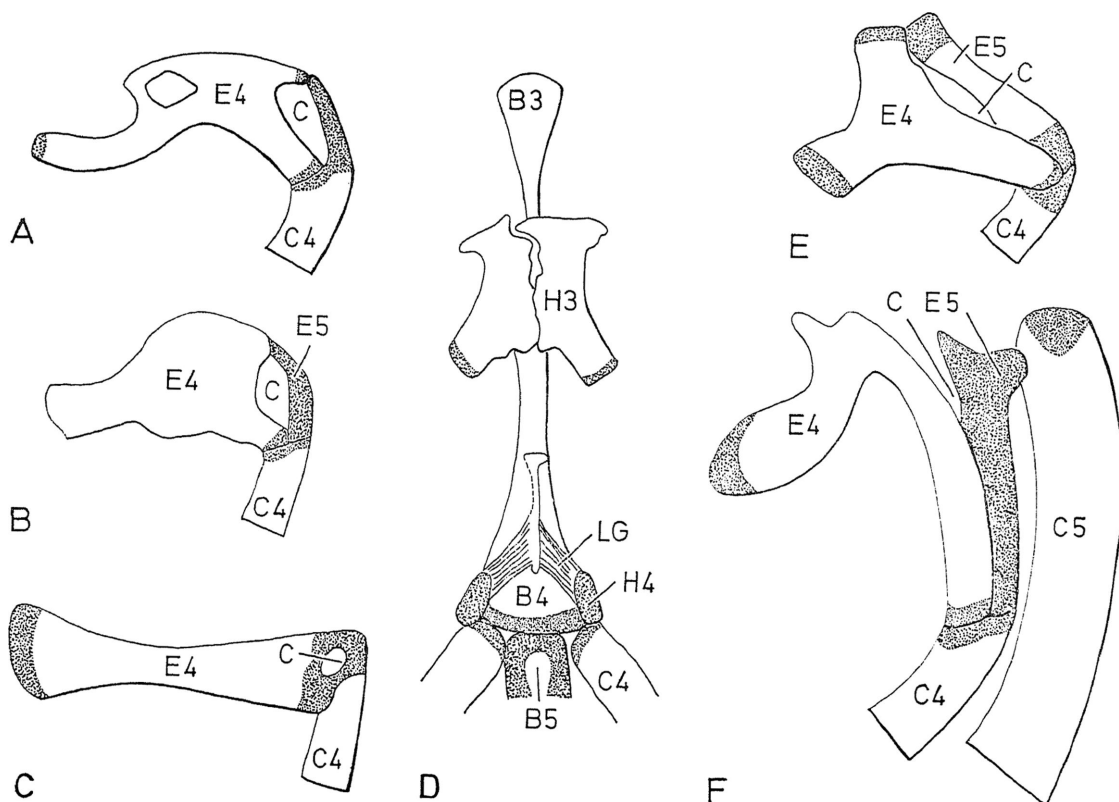


FIG. 18. A. *Misgurnus anguillicaudatus*, posterodorsal gill-arch elements, lateral view of left side. B. *Homaloptera caldwelli*, as in A. C. *Crossostoma davidi*, as in A. D. *Misgurnus anguillicaudatus*, some ventral gill-arch elements, ventral view. E. *Eigenmannia lineata*, as in A. F. *Catostomus commersoni*, as in A.

between *Australosomus* and *Polyodon*. In both, the paired, ventral arch-elements are very long, and the articulations between the anterior arches and the basibranchial series are peculiarly concentrated.¹

From *Polyodon*, basibranchial ossification centers are absent (see also Bridge, 1879, p. 709), but the hyoid and arch 1 articulate close together on the basibranchial series.

¹ Thus in *Australosomus* (as also in *Pteronisculus*, fig. 16B; Nielsen, 1942, fig. 45; *Saurichthys*, Stensiö, 1925, fig. 26; and probably also in *Birgeria*, Stensiö, 1921, fig. 66) in which occur a series of ossified basibranchials, the most anterior is shown to be situated between arch 1 and arch 2, rather than between the hyoid and arch 1, as is the rule in other fishes having ossified basibranchials. The most anterior element consistently is called "copula 1" by these authors, but according to the present terminology it is the second basibranchial. Consequently, an additional element (basibranchial 1), one situated between the hyoid and first branchial arch, could have existed in these forms. Both the rudiment of *Pteronisculus* considered by Nielsen (1942, fig. 45)

The absence of comparable ossification centers from *Polyodon* poses a problem in interpreting the condition in *Australosomus*. To the writer it seems that the most anterior ossified basibranchial in *Australosomus* (Nielsen, 1949, fig. 37) is a second basibranchial, comparable with that in *Acanthodes* (fig. 16A) and in actinopterygians generally, and that a first basibranchial probably is secondarily reduced. If so, in *Australosomus* the element with canals would be a fifth basibranchial comparable with the most posterior element of the basibranchial series of *Polyodon* (fig. 15D). In sturgeons there are ossification centers corresponding in position

and the more prominent element of *Elonichthys* considered by Watson (1925, fig. 29) to be a basihyal are better considered a first basibranchial. Doubtless a similar condition occurred also in *Centrolepis* (Patterson, personal communication) for which Gardiner (1960, fig. 9) illustrated a "basihyal."

to fourth and fifth basibranchials (van Wijhe, 1882, pl. 15, fig. 2; Iwanzov, 1887, pl. 1, fig. 8). No definite canals occur in the element of *Polyodon*, but the fourth artery passes backward in a lateral groove in the fifth basibranchial before reaching the posterior of the two articulations of the ceratobranchials of the fourth arch.

Ossified fourth and fifth basibranchials are known in other fishes only in some teleosts (Ostariophysi), in which both possibly arose secondarily. There is no evidence that separately ossified fourth and fifth basibranchials are very primitive structures among vertebrates; therefore, they tentatively may be regarded as of secondary origin also in lower actinopterygians.

A final example of "extra" ossifications associated with the basibranchial series is provided by the peculiar sublingual ossifications of some cyprinoids. In cobitids such as *Cobitis* and *Misgurnus* there are two ossifications in a cartilage fitting between and articulating with the ventrohyals (fig. 19B,

D). In others, such as *Barbatula*, two additional, nodular ossifications occur as paired elements on each side of the dorsomedian one (fig. 20C). In homalopterids and some catostomids occurs a single large ossification also fitting between the ventrohyals (fig. 20A, B; Ramaswami, 1952c, fig. 6A-B; 1952d, p. 529; Weisel, 1960, fig. 7; Branson, 1962, figs. 68-69).¹

The peculiar basihyal of homalopterids (see also Ramaswami, 1948, fig. 26; 1952c,

¹Weisel termed this ossification a "supplementary basihyal," but other authors have considered it either part of the basihyal (e.g., Ramaswami, 1952c, p. 505) or a complete basihyal (Branson, 1962, p. 122, but for Branson's "first basibranchial" read "basihyal"). But the ossification can be neither a basihyal, partly or wholly, nor a first basibranchial because a basihyal is invariably present as a separate element above the sublingual, and, although a first basibranchial is absent from homalopterids and cobitids, in some catostomids one occurs posterodorsal to the sublingual. In apparent agreement with Weisel (1960), the writer regards the sublingual ossifications as new structures peculiar to these cyprinoid groups. So far as known, they do not occur in other fishes, including cyprinids.

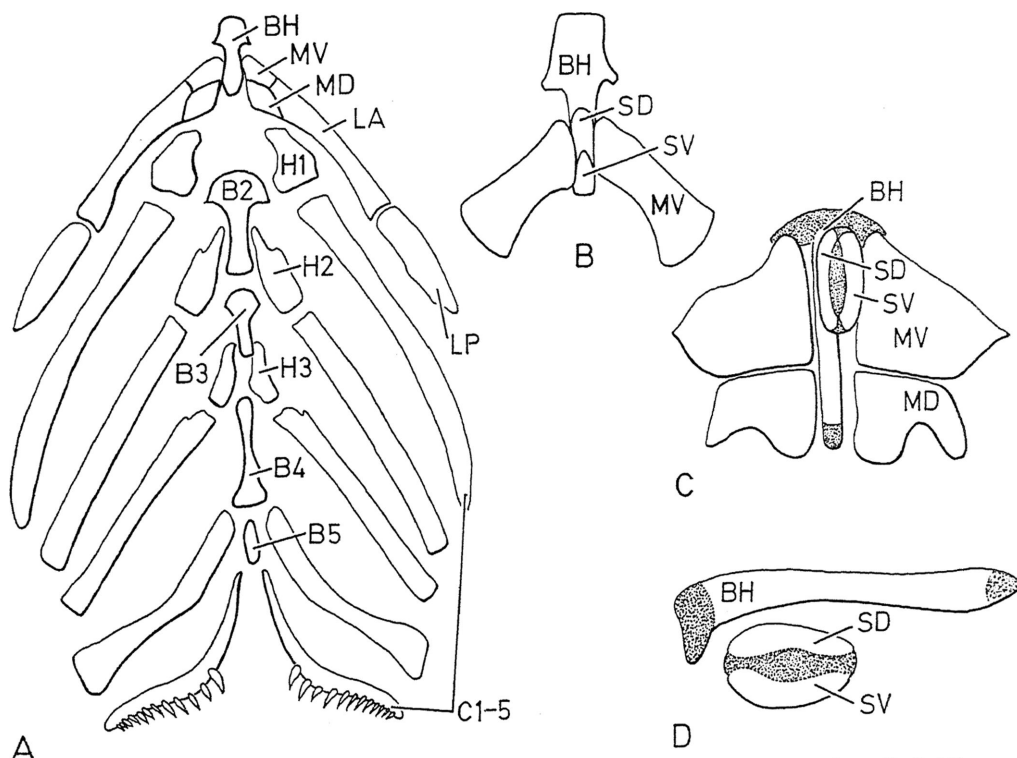


FIG. 19. A, B. *Cobitis taenia*. A. Gill arches, ventral ossified parts, dorsal view. B. Sublingual and associated bones, ventral view. C, D. *Misgurnus anguillicaudatus*. C. Sublingual and associated bones, ventral view. D. Lateral view of left side.

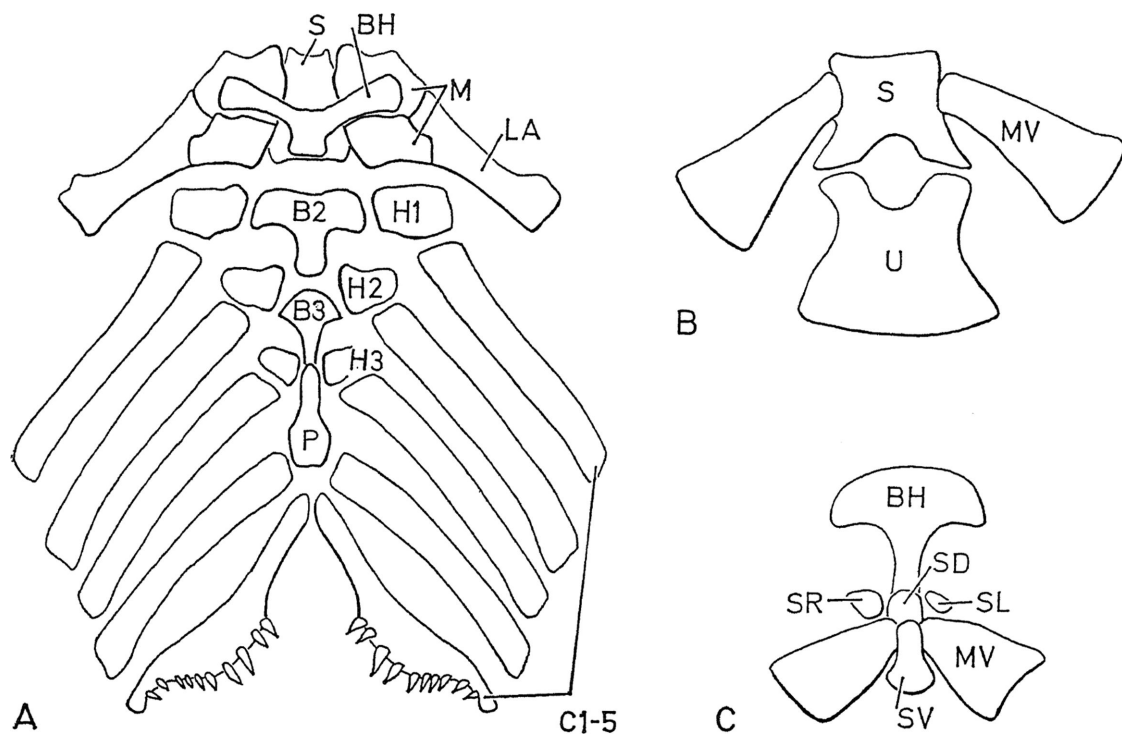


FIG. 20. A, B. *Crossostoma davidi*. A. Gill arches, ventral ossified parts, dorsal view. B. Sublingual and associated bones, ventral view. C. *Barbatula* sp., sublingual and associated bones, ventral view.

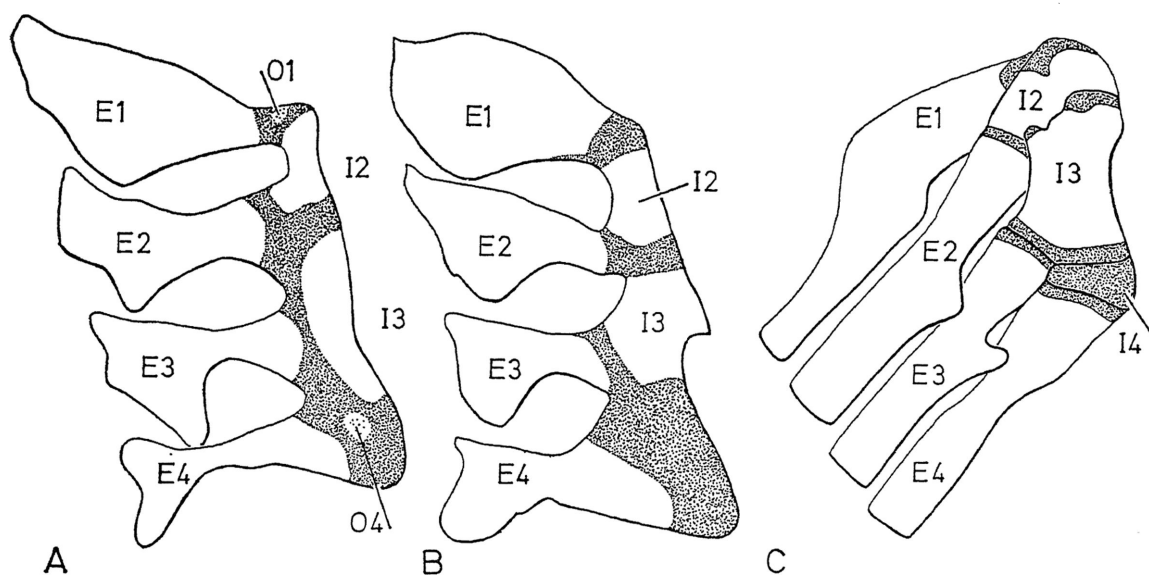


FIG. 21. Gill arches, dorsal parts, dorsal view of left side. A. *Protomyzon griswoldi*. B. *Homaloptera caldwelli*. C. *Cyprinus carpio*.

fig. 6; 1952d, p. 529) deserves some comment, for so far as known it is of a form unusual in fishes, being widely forked anteriorly (for gobiids, see Takagi, 1950). This condition is foreshadowed in some cobitids in which the basihyal anteriorly is either less forked (like that of *Nemachilus*, fig. 17C; see also Ramaswami, 1953, p. 335) or simply broadened, like that of *Misgurnus* (fig. 19C, D).

To the writer the above-mentioned peculiarities of cyprinoids suggest that homalopterids are most closely related to cobitids, particularly those of the subfamily Nemachilinae. In any case, the theory of Hora (1952, p. 407) and Ramaswami (1952c, p. 514; 1952d, p. 535; 1953, p. 344; see also Silas, 1952) concerning the polyphyletic origin of homalopterids is not supported by gill-arch structure, for all homalopterids known are both similar and peculiar in these respects, not only ventrally but dorsally as well (fig. 21A, B), and they differ markedly from cyprinids (cf. fig. 21C; see also Das and Deftari, 1967, fig. 7; Girgis, 1952, fig. 8; Holstvoogd, 1965, fig. 12A-B; Khanna, 1961, pl. 4, figs. 1-6, pl. 5, figs. 1-5, pl. 6, figs. 1-4; Ramaswami, 1955a, fig. 9; 1955b, fig. 17; Saxena and Khanna, 1968, fig. 13). There is no gill-arch evidence to suggest an independent origin of the Gastromyzoninae from the Cyprinidae. Rather to be suspected is that the cobitids and homalopterids are most closely related to each other, and are related more closely to catostomids than to cyprinids, for these groups share not only the sublingual bones, a reduced or absent first basibranchial, but a single row of lower pharyngeal teeth. All these characters likely are advanced over the conditions in cyprinids.

It is true, however, that the lower pharyngeals of catostomids are enlarged, as are those of cyprinids. But it seems that all cyprinoids are basically alike in lower pharyngeal structure, for the lower pharyngeal bones "bite against" not the upper pharyngeals (which are toothless in all cyprinoids in which their condition is known), but the pharyngeal roof posterior to them, which is a feature unique to these fishes. Of course, reduction to a single row of pharyngeal teeth possibly occurred independently in catostomids and cobitids and homalopterids, although presently there is no direct evidence suggesting

that this resemblance is due to parallel evolution. Perhaps as far as gill-arch structure is concerned, the sublingual bones are the strongest evidence in favor of a catostomid-cobitid-homalopterid relationship.

With respect to the lower pharyngeal teeth of cyprinoids, there has been some controversy as to whether one or more rows of teeth are primitive (see Chu, 1935, p. 172; Vaneecov, 1939, pp. 490-491; Ramaswami, 1955a, pp. 129, 152; 1957, p. 302; Weisel, 1960, p. 127; 1967, p. 54). Nevertheless, there is every reason to believe that multiple rows of conical teeth are primitive for any given group of teleostome fishes, for pharyngeal teeth ultimately are to be derived through assimilation and consolidation of tooth plates (not well-differentiated gill-rakers as Weisel, 1960, p. 127, assumed) and the fusion of these with their endoskeletal supports. Further consolidation and specialization of tooth units are to be expected, and specialized teeth of any sort can be interpreted only as end products of these phyletic tendencies, unless there is some overwhelming body of evidence that shows that the trends have operated in the reverse direction. Such a reversal in the trends toward consolidation and specialization has never been demonstrated among fishes, neither on the gill arches nor on the jaws (cf. Myers, 1958, p. 29; Alexander, 1964, p. 169; and Roberts, 1967, pp. 239-242, whose evidence indicates that conical teeth really are primitive for characins).

Following the above line of argument leads to the view that in the basibranchial series all aspects of segmentation are secondary, including multiplication of ossification centers as well as actual segmentation. This view would seem to go far in explaining the variability actually observed among teleostomes. Reduction of ossification in the basibranchial series of dipnoans, sturgeons, paddlefishes, *Amia*, and *Lepisosteus* could then be regarded as the result of trends paralleling those already observed in various teleostean lineages. The variations in the pattern of the actual segmentation of the basibranchial elements could be interpreted as secondary modifications related to certain functional aspects of the branchial apparatus in the particular forms concerned.

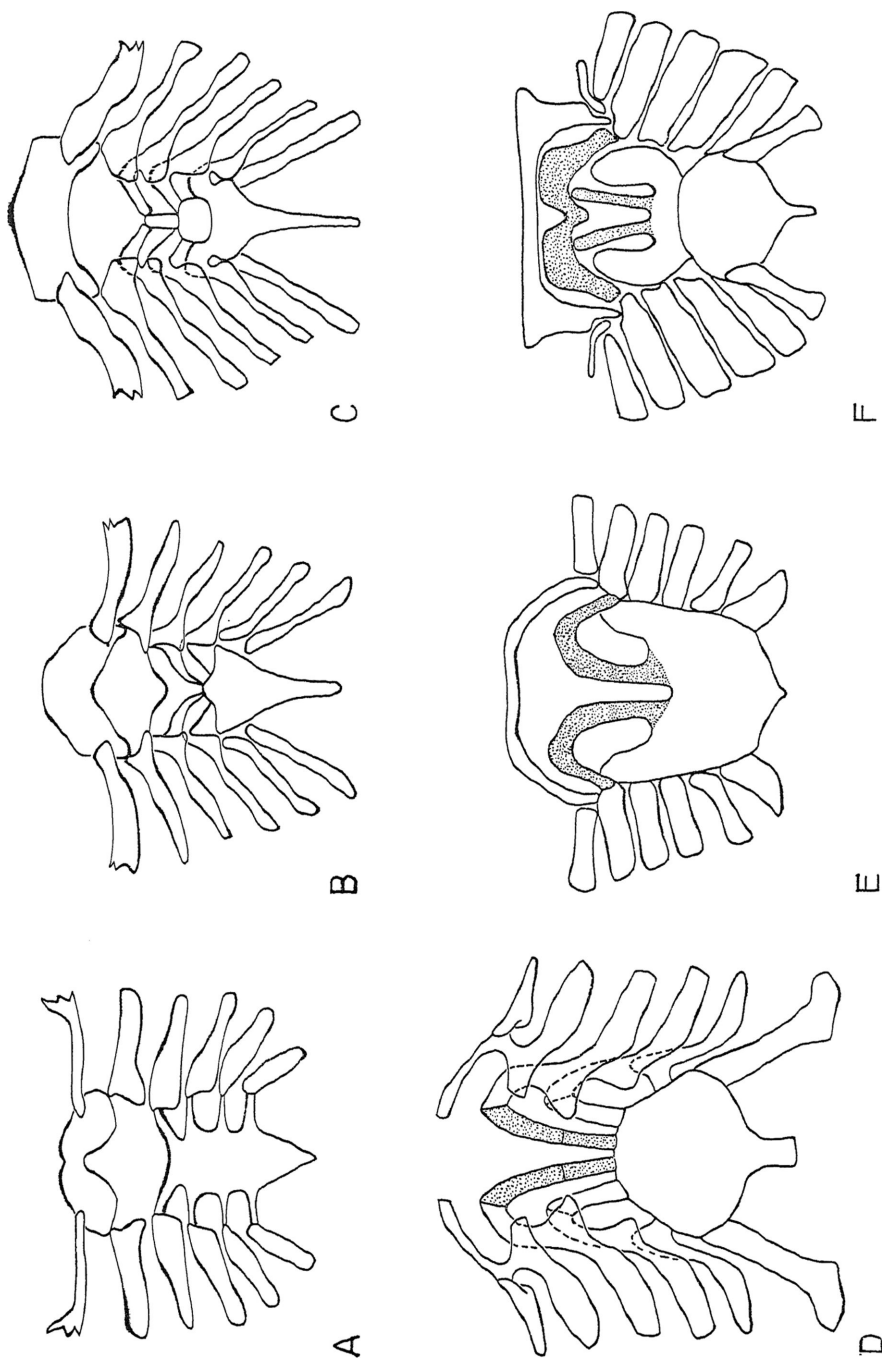


FIG. 22. Gill arches, ventral view. A-C. *Elmopterus spinax*, 30-mm., 43-mm., 55-mm. larvae (after Holmgren, 1940, figs. 82, 90, 96). D-F. Three species of rays (*Narcacian*, *Rhinobatus*, *Rhynchobatus*, modified from Garman, 1913, pl. 65, figs. 1, 2, pl. 67, fig. 1), with homologous parts stippled.

ELASMOBRANCHIOMORPHS

A detailed account of the basibranchial structure of elasmobranchiomorphs is beyond the scope of the present paper, but a brief discussion of this subject here is worthwhile. As mentioned above, in sharks each basibranchial usually is attributed to the arch in front, and there is developmental evidence that indicates that some basibranchials are segmented from the bases of the posteriorly directed hypobranchials (fig. 22A-C; see also Gibian, 1913; Holmgren, 1940). In addition, it has often been said that both hypobranchials and pharyngobranchials of elasmobranchiomorphs are posteriorly directed, that the arches therefore are Σ -shaped, and that this character distinguishes them as a group (De Beer, 1937, p. 407).

Generally overlooked are the facts that in all elasmobranchiomorphs the most anterior basibranchial, whether associated with or derived from either the hyoid, the first branchial arch, or both, is anterior to these arches; that among chimaeras probably all the hypobranchials are anteriorly directed; and that even in sharks and rays hypobranchials possibly are anteriorly directed in one or more of the anterior arches.

From these facts it is evident that the gill arches of elasmobranchs are poorly understood and that further work is required to demonstrate their basic organization, especially that of the basibranchial complex.

In elasmobranchiomorphs it is not known whether the basibranchials primitively were independent elements, or whether their segmental subdivision is a secondary development. If, as suggested above, basibranchial subdivision occurs only secondarily in teleostomes, there is reason to suppose subdivision occurs only secondarily in elasmobranchs also. It is not surprising, therefore, to find that the basibranchials are not subdivided into a segmented series early in the ontogeny of sharks and rays (fig. 22A-C; see also Holmgren, 1940) or in adult rays (fig. 22D-E; see also Garman, 1913). But that this really represents the condition primitive for adult elasmobranchs is not known.

In sharks and rays the basibranchial series is divided into anterior and posterior divisions with a large space between them: the

anterior division includes a single element (the so-called basihyal), and the posterior division includes the remaining basibranchials. There is no reason to assume that this subdivision is anything but a secondary development peculiar to sharks and rays. In chimaeras the basibranchial complex is not so subdivided, nor is it among teleostomes. Therefore, it is meaningful to ask, how in sharks and rays did the basibranchials become subdivided in this way?

The most likely explanation is that the subdivision occurred by means of a secondary reduction and loss of part of the basibranchial series, more exactly, a basibranchial that was once situated between the paired ventral ends of arch 1 and arch 2, interconnecting the anterior and posterior divisions of the basibranchial series. That such an element in fact did exist is suggested by the occurrence in this position of a rudiment in some Recent and possibly some fossil species (fig. 23A, C; see also Gegenbaur, 1872, pl. 19, fig. 3; Koken, 1889, fig. 4; Fritsch, 1895, fig. 215, pl. 96, fig. 1; Jaekel, 1895, fig. 1; Reis, 1897, pl. 1, figs. 2-3; Fürbringer, 1903, pl. 18, fig. 24). With the addition of such an element, the basibranchial complex of elasmobranchs so closely approaches that of teleostomes that direct comparisons are possible. From this point of view it appears that the basibranchials of elasmobranchs and primitive teleostomes are organized in the same way, with a basibranchial, whether independent or not, situated between the ventral ends of the arches up to the hyoid but not beyond. It therefore is reasonable to number the basibranchials in the same way, regardless of how embryologically they develop.¹ For elasmobranchs the basibranchials here are numbered as in teleostomes according to the arch behind, in order to facilitate dealing with the elements at the anterior end of the series. Consequently, for sharks, the basibranchial between arch 2 and arch 3 is basibranchial 3; the next anterior element (rudiment, in some forms only) between arch 2 and arch 1 is

¹ It is possible that some of the independent basibranchials of teleostomes in ontogeny develop from the arch behind, whereas those of elasmobranchs develop from the arch in front. Such a difference in ontogenetic patterns would suggest that the basibranchial series underwent segmentation independently in both groups.

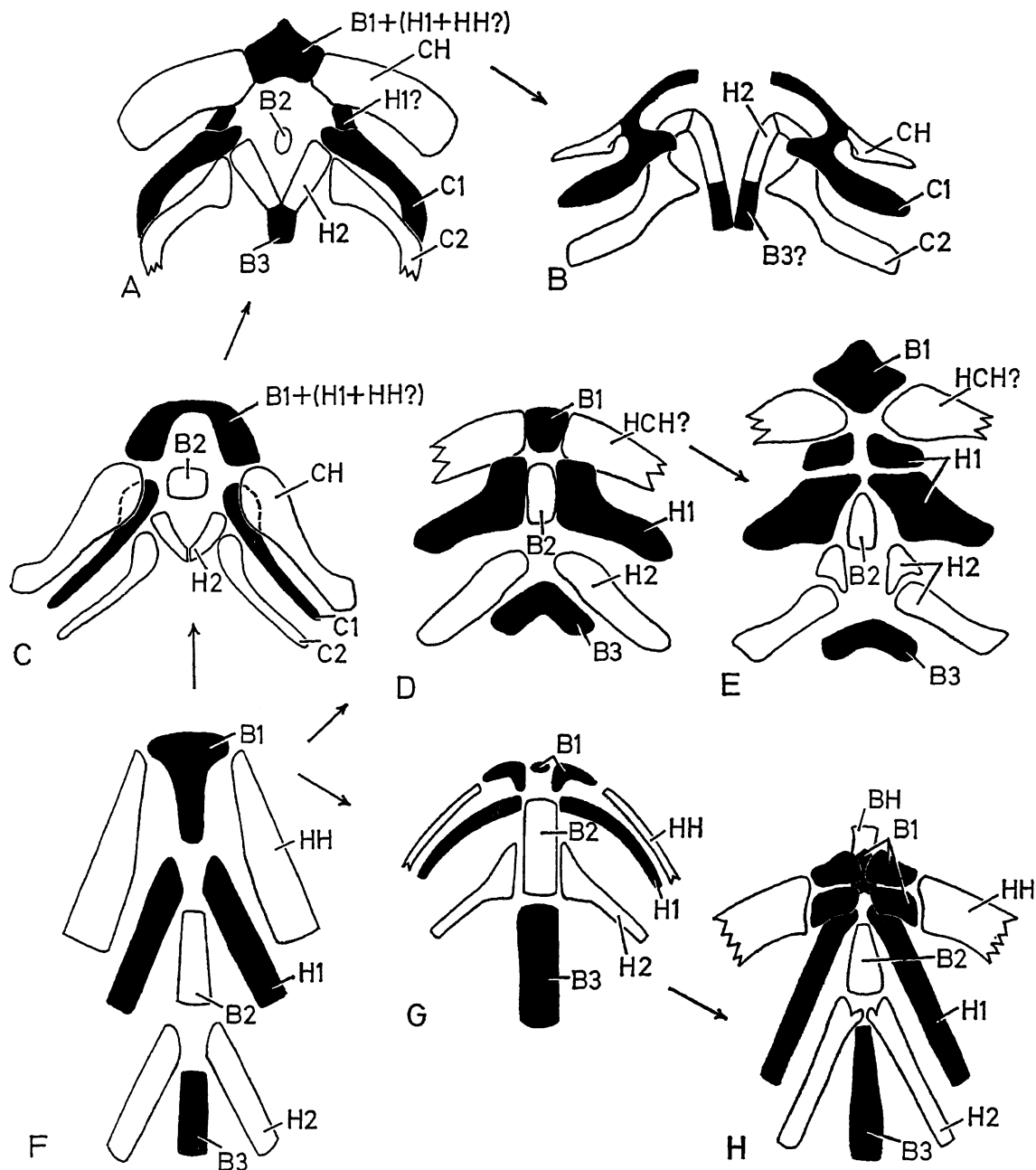


FIG. 23. Anterior basibranchial and associated bones of some fishes, ventral view; parts of first and third arches black. A. *Cestracion* sp. (modified from Gegenbaur, 1872, pl. 19, fig. 3). B. *Narcacion* sp. (modified from Garman, 1913, pl. 67, fig. 1). C. *Pleuracanthus* sp. (a possible interpretation modified from Koken, 1889, fig. 4; Fritsch, 1895, fig. 215, pl. 96, fig. 1; Jaekel, 1895, fig. 1; Reis, 1897, pl. 1, figs. 2, 3). D. *Callorhynchus* sp. (modified from Schauinsland, 1903, pl. 18, fig. 129). E. *Chimaera monstrosa* (modified from Devillers, 1958, fig. 377). F. *Acanthodes bronni*. G. *Pteronisculus stensioei* (modified from Nielsen, 1942, fig. 45). H. *Elops hawaiiensis*. Arrows indicate direction of probable phyletic trends.

basibranchial 2; and the most anterior element is basibranchial 1, a basihyal or an element representing both. On present evidence (e.g., that of Holmgren, 1940; and the fact that an independent basihyal does not seem to be developed in primitive teleostomes) the most anterior element probably represents at least a basihyal and first basibranchial. In any case, there is no reason to believe that an independent basihyal, comparable with that in teleosts, occurs in elasmobranchs. There is the possibility also that the anterior basibranchial of elasmobranchs includes the equivalent of a hypohyal and a first hypobranchial (see fig. 22A). It should be noted, however, that small cartilages often occur adjacent to the anterior basibranchial, and that some of these possibly represent hypal elements (fig. 23A). At the present time it is difficult to evaluate the nature and significance of all the cartilaginous rudiments described in the branchial region of elasmobranchs (see Goodrich, 1930, pp. 404-406; De Beer, 1931a, pp. 629-630; 1937, pp. 410, 418-419). Possibly they all are secondary developments with as yet unknown morphological and systematic significance. In rare cases first "hypobranchials" seem developed enough to be credible (Garman, 1913, pl. 51). In contrast well-developed hypohyals seem uniformly to be lacking in Recent elasmobranchs. Among fossil forms well-developed hypohyals have been described in xenacanthids (Jaekel, 1895, fig. 1; 1925, fig. 17). There is disagreement, however, concerning the paired nature of these elements (Koken, 1889, fig. 4). It seems that from their position they supported the tongue and, if so, probably are comparable with the most anterior basibranchial of Recent forms (fig. 23C). Whether they actually were paired in xenacanthids therefore is doubtful, although consistent with the idea that the most anterior basibranchial includes equivalents of hypohyals (see De Beer, 1937, p. 410).

All the above-mentioned problems at the present time cannot be resolved without an exhaustive restudy of elasmobranch material. It is evident that the visceral endoskeleton of elasmobranchs usually has separate elements combined in various ways into larger structures, whether primarily or secondarily.

Thus in rays, what appear to be equivalents of the second hypobranchials are included in widely different structural patterns representing a type of interspecific variation not shown in teleostomes (fig. 22D-F). Possibly such variation eventually will be explained in terms of ontogenetic modifications of an early formed, mesenchymatic, gill-arch complex, continuing without a break between elements from one arch to another. Such a condition might be directly comparable with that of the visceral skeleton of cyclostomes, which so far has defied successful detailed comparison with the visceral skeleton of gnathostomes (see Woskoboinikoff, 1910, 1935, 1937; Sewertzoff, 1916, 1927; Balabai, 1935, 1937; Jarvik, 1954, 1964; Jollie, 1968). From this viewpoint, however, the large basibranchial elements of rays (perhaps also the undivided elements of other fishes) seem to have resulted from tendencies to retain embryonic conditions in the adult, rather than from complex processes of secondary fusion, as often are assumed to have occurred (e.g., by Garman, 1913; Stensiö, 1963a, fig. 84).

PHYLETIC TRENDS

It is possible to arrive at an interpretation of phyletic trends in the basibranchial structure of fishes (fig. 23). For this scheme the condition in acanthodians is accepted as the most primitive type. Acanthodians are the oldest known gnathostomes and the only fishes known to have two prootic arches segmented in a way comparable with that of the branchial arches, with both the mandibular and hyoid including at least four paired elements. Especially noteworthy in *Acanthodes* is the ventral segmentation of the mandibular and hyoid each into two paired elements of large size, which correspond so closely to hypobranchials and ceratobranchials that there is little reason to doubt their serial homology (see Reis, 1890, figs. 1, 2; 1894, fig. 1; and references on jaw structure cited below). In these respects the viscera apparatus of acanthodians appears to be more primitively organized than that of any other gnathostome group (see below, and also Nelson, 1968b).

Compared with acanthodians, fossil and Recent chondrosts (and presumably holosts

as well) are advanced in having the most anterior basibranchial apparently reduced and subdivided into three parts, including one median and one paired element. If so, teleosts are further advanced in having two paired elements instead of one, and an independent basihyal. How these elements originated is not known, but the hypothesis is suggested that they originated by means of further secondary segmentation.

Compared with acanthodians, sharks are advanced in having equivalents of hypohyals and first hypobranchials apparently included in the most anterior basibranchial, and the remaining hypobranchials posteriorly directed. From most forms basibranchial 2 is absent. Conditions in rays are variable but basically the same as those in sharks. The most anterior basibranchial of sharks and rays could be thought of as having arisen through a process of consolidation of separate elements. This process might have been the immediate cause of an anterior shift of the ceratobranchials, with the result that the first ceratobranchials partly underlie the ceratohyals. With a forward movement of the other ceratobranchials, the hypobranchials could have become posteriorly directed if their medial ends, presumably attached to the basibranchials, were not free to move anteriorly.

Compared with acanthodians, chimaeras are hardly more advanced. Independent hypohyals are absent, but well-developed first hypobranchials and first basibranchials occur. Whether equivalents of hypohyals are included either in the ceratohyals or in the most anterior basibranchial is not known. All chimaeras have the basibranchials separated from one another, and some forms have the anteriorly directed hypobranchials apparently subdivided.

Gill arches of rhipidistians, coelacanth, *Polypterus*, and lungfishes are difficult to interpret because of the few ossification centers or reduced basibranchials. In the hyoid arch, three ventral, paired elements are described for *Eusthenopteron* (Jarvik, 1954, figs. 8, 9) and are comparable only with those of actinopterygians. Two paired elements are known for *Latimeria* (Millot and Anthony, 1958, pl. 41), *Polypterus* (Allis, 1922, pl. 8), and lungfishes (personal observation). Ex-

actly what these elements are is difficult to determine on present evidence.

At the present time it is not possible to assess the functional significance of the various types of basibranchial segmentation, but the type common in teleosts deserves some mention. So far as known, in all teleosts having the basibranchial skeleton developed to a significant degree, a division occurs in the basibranchial series between the third ossified basibranchial and the posterior cartilaginous element. Probably in most teleosts a certain degree of flexion occurs at this point during feeding, especially if the mouth is opened wide and the buccopharyngeal cavity greatly expanded. In advanced teleosts, commonly at least in acanthopterygians, the posterior cartilaginous element becomes reduced and antero-dorsally displaced, or lost altogether. When still present, with the paired elements of the posterior (3-5) gill arches it forms a structural complex capable of sliding back and forth to a limited degree over the elongate shaft of the third basibranchial ossification. Tchernavin (1938, 1948, 1953) recognized the functional importance of this mobility, and considered the basibranchial series at this point to be divided into anterior and posterior parts, which he termed "copulae," using in a new sense a term usually considered synonymous with "basibranchial." The present writer is in complete agreement with the analysis and conclusion of Tchernavin, but wishes to add that an enhanced mobility is developed in this area only in teleosts, and in these only when the third hypobranchial has lost or loosened its connections (those forming part of the dorsal and ventral walls of the afferent arterial canals; see above) with the basibranchial series. These modifications allow the third hypobranchials together with the other posterior arch elements more or less freely to slip back and forth over the third basibranchial. Presumably these modifications constitute some sort of functional advance, possibly associated with an increased potential of lower pharyngeal-bone mobility. If so, they probably are correlated with the muscular modifications (those concerning the forward lengthening of the rectus communis) discussed elsewhere (Nelson, 1967f).

THE DERMAL SKELETON VERSUS THE ENDOSKELETON

The preceding account is based on a clear distinction between the dermal skeleton and the endoskeleton of the gill arches, with the acknowledgment that such a distinction becomes useless in some instances (see also Jollie, 1968; Moss, 1968). With respect to the gill arches of Recent fishes, two are worth being discussed in this connection, both of which seem to involve the transformation of dermal elements into endoskeletal ones. The first is the series of modifications of the fourth upper pharyngeal tooth plate, which, according to the above analysis, in some characins and possibly some catfishes and some gonorynchiforms (Swinerton, 1903, fig. K; Thys van den Audenaerde, 1961, fig. 21; Greenwood, Rosen, Weitzman, and Myers, 1966, fig. 7) is toothless and to varying degrees wrapped around the cartilaginous fourth infrapharyngobranchial (a somewhat similar condition occurs in some clupeids, according to Ridewood, 1905b, p. 468; and Nelson, 1967b, fig. 7).¹

In some cyprinoids (mainly if not exclusively catostomids, cobitids, and homalopterids [figs. 17C, 18D, 19A, 20A; see also Branson, 1962, p. 124; Ramaswami, 1948, fig. 26; 1952a, fig. 13; 1952b, fig. 4; 1952c, p. 529, fig. 6; 1953, p. 335]) and possibly in some siluroids (Srinivasachar, 1958a, fig. 10), a similar transformation possibly has taken place from a tooth plate or plates overlying the fourth and fifth basibranchials into ossified fourth or fifth endoskeletal basibranchials (for gonorynchiforms, see Swinerton, 1903, fig. J; d'Aubenton, 1961, figs. 9, 10; Greenwood, Rosen, Weitzman, and Myers, 1966, fig. 7). At the present time there is no known series of

intermediates between these two types of skeletal elements (only *Amia* is known to have tooth plates so far posteriorly over the basibranchial series; pl. 79, fig. 2, pl. 90, fig. 1), and the "endoskeletal" basibranchials involved clearly include ossifications within the cartilage, not simply a layer of perichondral bone possibly formed of a reduced tooth plate. Such endochondral ossification centers seem to occur in a somewhat vestigial form in various areas in the gill-arch skeleton of the Ostariophysi, e.g., in the area of infrapharyngobranchials 1 and 4 of the homalopterid *Protomyzon* (fig. 21A). Similar "vestigial ossification centers" have been noticed also in the anterior, cartilaginous articular area of the fourth ceratobranchial (ossification centers in the position of fourth hypobranchials) in the related *Crossostoma davidi*. It is difficult, if not impossible, to account for all these phenomena simply by presumed reductions of dermal bones, even though this process sometimes seems to be involved. In the opinion of the writer, none of them definitely is a primitive, "holdover" ossification of the gill-arch endoskeleton. All are interpreted most satisfactorily as features peculiar to the Ostariophysi and the presumably related Gonorynchiformes.

REDUCTIONS OF THE ENDOSKELETON

Fusions between endoskeletal pieces of the gill arches have frequently been said to occur, in order to account for the absence of elements from some arches, for one reason or another believed to be secondarily modified. This line of reasoning is based on the assumption that some formula of independent elements is basic to all the visceral arches (van Wijhe, 1882; Woskoboinikoff, 1910; Schmalhausen, 1923, 1950; Allis, 1925a; Corsy, 1933; Holmgren, 1940, 1942, 1943; Bertmar, 1959; Jarvik, 1954; Bjerring, 1967). This view in its extreme form would mean that in some early vertebrate all the visceral arches were segmented in the same way, that this pattern was a common heritage of all descendent vertebrate groups, and that such variation as occurs is due to secondary losses, fusions, or other modifications (Sewertzoff, 1931, fig. 24). The extent to which this purely archetypal assumption can be usefully applied to studies of the vertebrate

¹ In adult catfishes, however, this element when previously described always has been called a pharyngobranchial, and has never before been considered a possibly modified tooth plate (Bamford, 1948, fig. 12C; Gauba, 1962, pl. 6; 1966, fig. 5; 1967, fig. 16; Hashmi, 1957, fig. 22A, B; Holstvoogd, 1965, fig. 10a, b; Khanna, 1961, pl. 1, figs. 1-4, pl. 2, figs. 1-4, pl. 3, figs. 1-6; Joseph, 1960, figs. 7, 8; Koschkaroff, 1906, fig. 33; McMurrich, 1884, pl. 2, fig. 4; Mahajan, 1966, figs. 20, 21; Nawar, 1954, fig. 5; Rastogi, 1963a, pl. 8; 1963b, pl. 8; 1963c, fig. 5; Saxena, Moitra, and Kumar, 1964, fig. 6; Srinivasachar, 1956, fig. 6; 1957, fig. 3; 1958a, fig. 10; 1958b, figs. 6, 9; 1961, figs. 9, 18; Tilak, 1963a, fig. 22; 1963b, fig. 5; 1964, figs. 24, 27, 40; 1965a, fig. 20; 1965b, fig. 24).

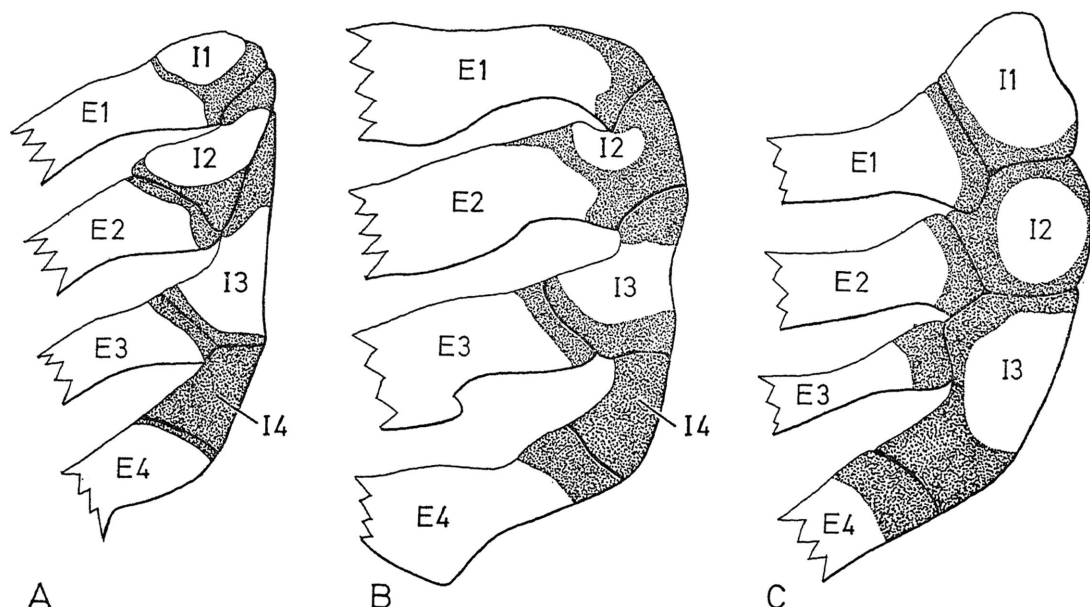


FIG. 24. Gill arches, dorsal view of left side. A. *Sternopygus macrurus*. B. *Gymnotus carapo*. C. *Electrophorus electricus*.

head remains to be determined. Thus among fishes there invariably seems to be some anteroposterior gradient in the segmentation of the endoskeletal gill arches, with the anterior arches tending to be larger and more complexly segmented than the posterior. It is possible that this tendency was manifest even in the earliest vertebrates. Whatever the case, there is little doubt that, in the history of some Recent fish groups, certain endoskeletal gill-arch elements have been secondarily reduced or lost altogether. So far as is known, such losses among Recent teleostomes do not occur through fusions of ossified elements (but for prootic arches, see below). A normal sequence of events seems to be an initial loss of ossification, resulting in an independent cartilaginous element, and its gradual reduction with loss of the resulting rudiment or its fusion with the cartilaginous articular areas of an adjacent ossified element.

Such seems to have been the history of the fifth epibranchial in many groups of teleosts. It does in some cases occur as an ossified element, although known as such only on one side of one specimen of the gymnotid *Eigenmannia lineata* (fig. 18E). More often it is discernible as an independent cartilage associated with the fourth epibranchial as in

Homaloptera (fig. 18B).¹ In many cases it seems secondarily to fuse into the cartilaginous articular areas of either the fourth epibranchial or ceratobranchial and, in so doing, encloses the most posterior efferent artery in a canal (fig. 18A, C; see also Nelson, 1967e). In no case does it seem to have been incorporated into the ossified part of the epibranchial, as some authors have suggested to explain the large dorsal process of the fourth epibranchial (Weitzman, 1962, p. 35, but for Weitzman's fourth and fifth "ceratobranchials" read "epibranchials"). A fifth epibranchial is present also in cyprinids and catostomids (fig. 18F), which have the fifth ceratobranchial arching dorsally far beyond its usual extent, a condition that has suggested to some authors that the part added

¹ (For its occurrence in other fishes, see d'Aubenton, 1961, figs. 9, 10; Bertmar, 1961, figs. 1-4; 1962, fig. 6; Daget, 1959, fig. 7; 1960, p. 47; 1961, fig. 5; 1962a, fig. 5; 1962b, fig. 8; 1965, fig. 10; Heim, 1935, figs. 4, 5, 7, 8; Holstvoogd, 1965, figs. 3A, B, 7B, 9A, B; Nelson, 1967e, figs. 1-3; Rastogi, 1964, fig. 5; Teichmann, 1951, fig. 6B; Weitzman, 1967a, p. 530; Woskoboinikoff, 1910, pl. 1, fig. 10. This element is not to be confused with the secondary cartilage sometimes called a fifth epibranchial; see, e.g., Chapman, 1944a, p. 319; Gegenbaur, 1878, figs. 10, 11, 13; Monod, 1949, figs. 26, 28-30; 1963, fig. 40; Ridewood, 1904a, p. 80; 1905b, pp. 459, 477, fig. 135B; 1905c, p. 367, fig. 1; Sagemehl, 1887, pl. 18, fig. 3.)

came with a fusion with the fifth epibranchial (Hubendick, 1942; Branson, 1962), and to others that the bones concerned are epibranchials only (Girgis, 1952; Bali, 1956).

One or more infrapharyngobranchials have been reduced in many teleostean groups. Segmentation in some cases is lost first, followed by the loss of an ossification center, as seems to have happened to pharyngobranchial 1 in *Sternopygus* and *Gymnotus* (fig. 24A, B), and possibly pharyngobranchial 2 of some eels (Nelson, 1966, figs. 12, 18). In other cases the absence of ossification seems to have preceded the loss of segmentation, as seems to be shown by the comparison of pharyngobranchial 4 of *Gymnotus* and *Electrophorus* (fig. 24B, C), and that of *Mormyrus* and *Gymnarchus* (Nelson, 1968a, figs. 9, 10), and also of pharyngobranchial 1 in *Bodianus* and *Scarus* (Nelson, 1967c, figs. 3C, 4). These are probably fairly common reductions in teleosts, and many more examples no doubt could be found. It is noteworthy that a pharyngobranchial when undergoing reduction in some cases appears to be incorporated into the epibranchial of the same arch (e.g., *Sternopygus*), and in others into the pharyngobranchial of a different arch (e.g., *Amia* and *Gymnotus*), a circumstance that suggests that the pharyngobranchials are interarcual rather than arcual structures (see Woskoboinikoff, 1910, 1914a, 1914b, 1935, 1937).

Recently a great deal has been written of suprapharyngobranchials and their significance in fishes. In Recent teleosts ossified suprapharyngobranchials are known only in the first arch of elopids and alepocephalids, although cartilaginous rudiments are known for the second arch of elopids, and the first arch of albulids and aulostomids. Such information as is available suggests that among teleosts these elements were reduced, first by loss of ossification and then by reduction, loss, or fusion of the resulting cartilaginous rudiment (for a discussion of suprapharyngobranchials in other fishes, see Nelson, 1968b).

Reduction of the epibranchials is relatively rare, e.g., epibranchial 4 in *Aulostomus* (fig. 17B), epibranchials 1-3 of *Cyema* (Nelson, 1966, table 1), and most of the epibranchials of *Polypterus* (van Wijhe, 1882, pl. 15, fig. 7; Allis, 1922, pl. 8, fig. 17), *Protopterus*, and *Lepidosiren* (Kisselewa, 1929, figs. 15,

21), and little is known of the process of reduction in these forms.

Ceratobranchials likewise are seldom reduced; the only examples known to the writer are the fifth ceratobranchials of *Polypterus*, *Calamoichthys*, and some eels. The eels show the reduction of this element in stages. Apparently in anguillid eels loss of ossification is followed by reduction and the complete loss of the element, while the lower pharyngeal tooth plates originally supported by it shift to the fourth ceratobranchial.

Reduction of the hypobranchials is relatively more common. The third hypobranchial in eels apparently first lost its ossification, then subsequently fused with the cartilaginous part of the adjacent ceratobranchial. A similar process seems to have taken place in the fourth hypobranchial in the immediate ancestors of the teleosts. This element in *Amia* and *Lepisosteus* is ossified, but it is not known to be ossified in any teleost. It is preserved as a cartilaginous rudiment in some adults of the Ostariophysi (e.g., *Misgurnus*, fig. 18D) and has been reported as a transitory rudiment in embryos of other teleosts. The fate of the fourth hypobranchial in teleosts seems to have been to fuse with the cartilaginous articular area of the adjacent ceratobranchial, forming at least the ventral wall of the afferent arterial canal.

Variation in basibranchial structure is discussed above in relation to the basibranchial tooth plates. It would seem that, where reduction of purely endoskeletal elements can be traced in related species, the same general steps are followed, leading to loss of ossification, reduction to the level of a cartilaginous rudiment, and ultimately to loss or fusion between cartilages. There is no known example of simple fusion between separate bones or ossification centers. This is in marked contrast to the ontogenetic and phyletic trends of the dermal skeleton. This circumstance suggests that the fusions known to occur between bones of the gill arches (the toothed fifth ceratobranchials of some atherinomorphs and labroids [and apparently also of some gobioids; see Gosline, 1955, p. 162], and the toothed third infrapharyngobranchials of some exocoetids) are due to the involvement of the dermal skeleton.

THE PROOTIC ARCHES

ON THE BASIS OF WHAT IS KNOWN about the dermal skeleton of the gill arches, one may suppose that the other toothed surfaces of the buccopharyngeal cavity arose in a similar way, by consolidation of tooth plates primitively supported by the visceral endoskeleton. For the prootic arches one may suppose also that the dermal elements probably were organized in paired series along the gill slits, and that only through secondary fusion of such plates did median plates arise. Of these matters little can be added here to the discussion of Jarvik (1954, 1960), who interpreted the toothed bones of the palate of *Eusthenopteron* as dermal derivatives of particular arches (the vomer, dermopalatine, and ectopterygoid of the premandibular, the endopterygoid and parasphenoid of the mandibular, and the paraotic dental plates of the hyoid). In actinopterygians the posterior extension of the parasphenoid was said to involve fusion between the parasphenoid and paraotic plates (perfectly good "paraotic plates" seem to occur in *Polyodon*; pl. 84, fig. 3), and Jarvik therefore concluded that their parasphenoid is of a "complex" nature, formed of dermal elements of both the mandibular and hyoid arches.

Jarvik considered some of the toothed palatal bones (vomer and parasphenoid) primitively to have been supported by serial homologues of infrapharyngobranchials. From the regular arrangement of the toothed bones of *Eusthenopteron*, Jarvik inferred that the supporting parts of the cranium include these visceral components, and in some cases serial homologues of suprapharyngobranchials. Thus, the parasphenoid was thought to have arisen through the fusion of tooth plates originally supported by paired infrapharyngomandibulars, which were said to form at least part of the trabeculae cranii and, in adults, part of the parasphenoid.

For any theory concerning the prootic arches, the most important consideration is their number. Current theory favors three: premandibular, mandibular, and hyoid, but the existence of a premandibular arch remains questionable (Jarvik, 1954, pp. 71-72; Jeffries, 1968, pp. 299-310). Consequently the

dermal elements of the palate cannot be attributed to specific arches with certainty. But if the vomer is premandibular in origin, the parasphenoid might be mandibular, or mandibular and hyoid. If, in contrast, the vomer is mandibular, all the parasphenoid might be hyoid. It is possible that through detailed embryological studies of Recent fishes (e.g., of *Elops*, which has a very primitive arrangement of these plates, according to Nybelin, 1968) this problem eventually could be solved. At present, however, Jarvik's conclusions are supported elsewhere mainly by Bertmar's (1959, 1963) studies on the embryology of the chondrocranium of a characin.

The idea of a visceral (or ectomesenchymatic) contribution to the braincase is not new (Platt, 1893, 1898; Allis, 1923b, 1925b; De Beer, 1931b, 1947; Hörstadius, 1950), but never before have separate homologues of both infrapharyngobranchials and suprapharyngobranchials been so ardently searched for within the braincase itself (see also Bertmar, 1959, 1963, 1965; Stensiö, 1963a; Miles, 1964, 1965; Bjerring, 1967). This approach rests on the assumptions of uniformly segmented visceral arches and of primitively separate infrapharyngobranchials and suprapharyngobranchials.

In the opinion of the writer neither of these assumptions can be accepted without qualification. Thus, in gnathostomes the anterior arches tend invariably to be more complex, and only some teleostomes are known to have independent suprapharyngobranchials, and these only in branchial arches 1 and 2 (see references in Nelson, 1968b). Particularly intriguing are the observations that in adult coelacanth (*Latimeria*; see below), acanthodians (*Acanthodes*; see below), and chimaeras (see De Beer and Moy-Thomas, 1935), and in early ontogenetic stages of other fishes (Bertmar, 1959, pp. 308-331) only a single pharyngohyal is known (disregarding rudiments likely to be of secondary origin; see Holmgren and Stensiö, 1936, fig. 263). Because of the presence of the pharyngohyal, it has been suggested (De Beer and Moy-Thomas, 1935, p. 307) that in the history of

the chimaeras the hyoid arch never was suspensory. For *Acanthodes*, Miles (1964, 1965), in contrast, has attempted to show that, despite the presence of a pharyngohyal, the hyoid arch was suspensory (and acanthodians not aphetohyoid), the hyomandibula presumably fitting into a groove on the medial side of the quadrate, and through the pharyngohyal articulating with the braincase. It is true that the pharyngohyal is of a form different from that of the pharyngobranchials, lacking a dorsal process and two anterior articular surfaces (pl. 91). Furthermore, it is anteriorly directed, not posteriorly as the pharyngobranchials seem to be (Nelson, 1968b). These differences suggest a functional significance for the pharyngohyal different from that of the pharyngobranchials, one possibly involving contact with the braincase and jaw suspension. In chimaeras, in contrast, the pharyngohyal is not particularly different in shape and orientation from the pharyngobranchials (De Beer and Moy-Thomas, 1935, fig. 1). But *Acanthodes* has hyoidean gillrakers (Watson, 1937; Miles, 1964; see also Nelson, 1968b), the groove in the palatoquadrate does not match very well the outline of the hyomandibula (Miles, 1968, fig. 1A), and the posterior ends of the hyomandibula and quadrate typically are not preserved in close proximity (pl. 91). These observations suggest that the hyomandibula and quadrate possibly were not intimately associated, that the hyomandibula was not suspensory, and that the hyoidean gill slit was open, at least partially. Consequently, whether or not the acanthodians really were aphetohyoid remains an unresolved issue, at least from the standpoint of visceral-arch structure (see also Heyler, 1962, p. 45; Novitskaya and Obruchev, 1967, p. 267).

Significant complications arise when, for logical consistency, the search for gill-arch homologues within the braincase requires a secondary origin (Miles, 1964; 1965, p. 239) for elements such as the "pharyngohyal" of *Acanthodes* (Reis, 1895, pl. 4, figs. 2, 4, pl. 5, figs. 1, 2; 1896, pl. 6, figs. 1, 2; Dean, 1907, fig. 12; Jaekel, 1925, figs. 12, 14; Miles, 1964, fig. 1; 1965, fig. 1; Nelson, 1968b, fig. 3) and *Latimeria* (Millot and Anthony, 1958, p. 53). It is difficult to believe in a secondary origin

of these elements simply to satisfy the theory that in gnathostomes the pharyngohyal is fused with the braincase. The upper jaw of *Acanthodes* (and that of coelacanth and actinopterygians) presents a similar problem, for it contains what appears to be at least one pharyngomandibular—the "metapterygoid."¹ Bertmar's (1959, p. 336) belief in the secondary segmentation in the upper jaw of *Acanthodes* is noteworthy but does not resolve the problem. Jarvik (1954, p. 99) supposed that a pharyngomandibular ("suprapharyngomandibular") fused with the epimandibular to form part (processus ascendens palatoquadrati) of the upper jaw (there seems to be reliable evidence that fusions of this type have occurred in at least the prootic arches of early actinopterygians; Nielsen, 1942, p. 143). Possibly the type of pharyngohyal of *Acanthodes* and *Latimeria* in a similar way became fused with the epihyal and produced the type of hyomandibula found in other fishes. Whatever the case, it should be emphasized that separate infra-pharyngeal and suprapharyngeal elements possibly never existed in the prootic arches, if, as has been suggested elsewhere (Nelson, 1968b), independent suprapharyngobranchials arose as secondary modifications associated with the crowding together of the gill arches under the cranium, hyoid arch, and associated dermal bones.

If the metapterygoid and pharyngohyal really are serial homologues of pharyngobranchials, any visceral contribution of the prootic arches to the endocranium probably involves elements with no serial homologues among the gill arches. In this connection may be mentioned the fact that the first branchial arch in some clupeids, apparently through fusion of paired rudiments, secondarily has produced a median cartilage of considerable size and functional significance as a support

¹ (For *Acanthodes*, see, e.g., Reis, 1895, pl. 4, fig. 5, pl. 5, figs. 1, 2; 1896, pl. 6, figs. 1, 2, 5; Jaekel, 1899a, fig. 1; 1899b, fig. 1; 1906, fig. 8; 1925, figs. 6, 14; 1927, figs. 6, 8; Dean, 1907, fig. 12; Watson, 1937, figs. 18, 20, pl. 13, fig. 2; Miles, 1964, fig. 1; 1965, fig. 1. For coelacanth, see, e.g., Stensiö, 1921, figs. 26, 50, 52, 53; 1937, fig. 18; Watson, 1921, figs. 1-3; Moy-Thomas and Westoll, 1935, fig. 3; Smith, 1940, figs. 6-8, 11, 13, 17, 18, pls. 21, 22, 25, 27, 28; Lehman, 1952, fig. 9; Schaeffer, 1952, fig. 6; Jarvik, 1954, fig. 15. For actinopterygians, see, e.g., Nielsen, 1942, p. 143.)

for dermal elements (Nelson, 1967b). It seems possible that farther anteriorly similar modifications could have produced for the vomer and parasphenoid endoskeletal supports without posterior serial homologues. It may be mentioned further that the regular arrangement of the toothed elements of the palate of fishes such as *Eusihenopteron* (Jarvik, 1954) and *Elops* (Nybelin, 1968) cannot be taken to mean that the plates are the serial homologues of particular upper pharyngeal plates of the branchial arches, or that the endoskeleton supporting the plates includes homologues of infrapharyngobranchials. It can be taken to mean only that the elements primitively were associated with paired dermal-element series, probably supported by some part of the visceral endoskeleton. An instructive example of variation in the gill arches concerns the most anterior "upper pharyngeals" of engraulids which have prominent tooth plates supported by, and in some cases fused with, the first epibranchials (pl. 82, figs. 4, 5). Some species have, in addition, one or more median plates

supported by the anterior end of both epibranchials. Whether one chooses to call them "epibranchial" or "pharyngobranchial" plates, it would be erroneous to infer, from the regular arrangement of these and the enlarged plates (supported by infrapharyngobranchials) of the posterior arches, that the endoskeletal parts supporting all of them are serial homologues. Therefore, without knowledge of their endoskeletal supports, there possibly is no real basis for the assumption of serial homology between individual plates of different arches. In such cases serial homology is best restricted to the entire dermal-element series.

With respect to the endoskeleton, therefore, it can be suggested only that pharyngobranchials in primitive gnathostomes possibly were single, with serial homologues in the mandibular and hyoid arches, that the prootic arches possibly included additional endoskeletal elements, and that some of these might have become secondarily incorporated into the braincase.

INTERRELATIONSHIPS OF MAJOR FISH GROUPS

ELASMOBRANCHIOMORPHI

ALL ELASMOBRANCHIOMORPHS in which the gill arches are known have the pharyngobranchials posteriorly directed. Whether this character is primitive or advanced is not known, but some authors have assumed that it is advanced relative to the condition in teleostomes, which have the pharyngobranchials anteriorly directed. If so, the character is important and suggests a relationship between sharks, rays, chimaeras, and probably acanthodians. The pharyngobranchials of acanthodians are peculiarly complex, however, in having a double articulation with the epibranchial in front, a prominent dorsal process, and a posterior articular surface (pl. 91; Nelson, 1968b), features otherwise absent from the pharyngobranchials of elasmobranchiomorphs.

In sharks and rays, the dermal gill-arch skeleton consists of "placoid scales." In chimaeras the dermal gill-arch skeleton is reduced, but placoid scales occur on the outside of the body (Patterson, 1965, p. 114). Regardless of their distribution, these non-growing scales probably are a character advanced relative to the growing scales and tooth plates of other fishes. If so, they and the characters mentioned above suggest a relationship between sharks, rays, and chimaeras, and are consistent with the placement of these forms in the group Elasmobranchiomorpha.¹ Acanthodians have growing scales on the outside of the body, but, except for well-developed gillrakers, a dermal gill-arch skeleton seems to be absent. From the standpoint of gill-arch structure, there-

¹ In recent years the term Elasmobranchiomorpha has been used for a taxon including sharks, rays, chimaeras, and all their supposed fossil relatives, especially the arthrodires (Stensiö, 1963a, p. 410). As here conceived, the term Elasmobranchiomorpha does not depend on a particular theory of the relationships of any fossil group. Thus, Recent chimaeras, if they are more closely related to Recent sharks and rays than to other Recent fishes, are to be classified with sharks and rays. That arthrodires, or any other fossil group, can be conceived of as holocephalan ancestors does not change this requirement and has no necessary bearing on the validity of the concept of the Elasmobranchiomorpha.

fore, the relationships of acanthodians are relatively obscure.

Sharks and rays have some of the hypobranchials or their equivalents posteriorly directed and the basibranchial series divided into two main parts. Both of these are probably advanced characters, suggesting that sharks and rays are more closely related to each other than either group is to chimaeras and acanthodians, in which the gill arches retain the relatively more primitive condition of both structures. If so, gill-arch structure is consistent with the division of the Elasmobranchiomorpha into two subgroups: Elasmobranchii, including sharks and rays, and Holocephali, including chimaeras. Thus, the Elasmobranchii and Holocephali emerge as sister-groups (Hennig, 1966). If so, it follows that they should be coordinate taxa, and coincidentally that they must be of the same absolute age.

Gill-arch structure of arthrodires is not sufficiently well known to warrant comment (Ørvig, 1962; Gross, 1962b, 1963, 1965; Stensiö, 1963a).

TELEOSTOMI

With the exceptions of dipnoans and brachiopterygians, primitive representatives of all other major teleostome groups have independent suprapharyngobranchials in arch 1 or arch 2, a character possibly advanced relative to that of elasmobranchiomorphs (Nelson, 1968b). With the exception of dipnoans, all other teleostome groups (infraclasses, as treated below) include primitive members with variously consolidated tooth plates most prominent over the basibranchial series. This character, too, probably is advanced relative to that of elasmobranchiomorphs. If so, these characters may be said to suggest a relationship between rhipidistians, coelacanth, brachiopterygians, and actinopterygians and are consistent with the tentative placement of these forms in the group Teleostomi.

SARCOPTERYGII

Latimeria, *Polypterus*, and *Calamoichthys* have only one large basibranchial ossification

with which the paired arch-elements articulate, and upon which lies a prominent system of paired basibranchial tooth plates. Among rhipidistians and tetrapods, too, there seems to be but a single basibranchial (although two possibly occurred in *Eusthenopteron*), and at least some of the fishes had paired basibranchial tooth plates. Doubtless the very large tooth plates of *Latimeria* represent a specialized condition (compared, for example, with the several plates of brachiopterygians), but whether the over-all basibranchial structure of *Latimeria* and other sarcopterygians is primitive or advanced relative to that of actinopterygians is difficult to say. The single basibranchial ossification center through subdivision could have given rise to the many centers in fossil and Recent actinopterygians, or alternatively could represent those of actinopterygians fused. At present there seems to be no evidence favoring fusion, and the phyletic trend therefore tentatively may be assumed to involve subdivision; this would agree at least with the ontogenetic trend observable in other fishes. Possibly the trend toward subdivision is related to a general narrowing of the head and a phyletic trend from a platybasic to a tropibasic cranium (Stensiö, 1963b). If primitive, the single basibranchial of coelacanth, brachiopterygians, and at least some rhipidistians and tetrapods cannot be considered evidence that these form a monophyletic group, even though this character sharply distinguishes them from actinopterygians. Whatever the case, it is difficult from the standpoint of gill-arch structure (and others, e.g., Daget, Bauchot, Bauchot, and Arnoult, 1964; Jarvik, 1968a, 1968b; Kerr, 1968; Pfeiffer, 1968) to consider *Polypsterus* an actinopterygian (cf. Goodrich, 1908, p. 770; 1928, p. 91; Daget, 1950, pp. 157-169; Gardiner, 1967a, p. 189; Nieuwenhuys, 1967; but for comparison with lungfish and coelacanth forebrains, which in some ways also are actinopterygian-like, see Nieuwenhuys, 1965; Nieuwenhuys and Hickey, 1965). Resemblances in gill-arch structure between various sarcopterygians (such as the reduced dorsal elements of dipnoans, coelacanth, and brachiopterygians), although certainly involving advanced conditions, are suggestive but not entirely con-

vincing. Consequently, no definite scheme of interrelationships of these forms can be advanced from the standpoint of gill-arch structure (the difficulties of this problem from other standpoints have been demonstrated by Gross, 1962a; Stensiö, 1963b; White, 1965; Jarvik, 1967a, 1968a, 1968b; Schaeffer, 1968).

Rhipidistians and tetrapods generally are admitted to be related, and, if they are, they can be included in a restricted group Choanata, after Säve-Söderbergh (1934). It is suggested here that Romer's (1955) term *Sarcopterygii* be used for the Choanata and any Recent non-actinopterygian fish groups related to them. Thus dipnoans, coelacanth, and brachiopterygians (which incidentally lack choanae; Panchen, 1967), if related to choanates, could be combined with them in a group coordinate with the Actinopterygii (see also Stensiö, 1963b, p. 116). Admittedly, the relationships of dipnoans, coelacanth, and brachiopterygians are not very well established, and all of these and the choanates possibly do not form a monophyletic group. For example, brachiopterygians might really have come from early actinopterygians; coelacanth, independently from early teleostomes; and dipnoans, from early elasmobranchiomorphs. But the probability seems rather great that the choanates are more closely related to one or more of these three Recent groups of fishes than to any others. Consequently, the group *Sarcopterygii*, as here emended, appears to represent a meaningful systematic concept even though at present somewhat imprecise. Until it is shown that dipnoans definitely have their relationships elsewhere, there is no reason why they cannot be left within the *Sarcopterygii*, temporarily occupying the status of an infraclass along with the other sarcopterygians of uncertain relationships. From this standpoint the *Sarcopterygii* and Actinopterygii emerge as sister-groups.

ACTINOPTERYGII

With the basibranchial series subdivided into several ossification centers and usually into at least two separate elements, actinopterygians differ markedly from sarcopterygians (except dipnoans that have the basibranchials reduced or absent). But it is not

certain that the subdivided condition is advanced relative to that of sarcopterygians, for a subdivided pattern occurs also in the anterior arches of some elasmobranchiomorphs (other resemblances between some Recent actinopterygians and elasmobranchiomorphs have been noted; references cited in MacAlpin, 1947, p. 228, but are here not commented on, except for the remark that a renewed investigation of these matters may be necessary before the basic division of the gnathostomes into elasmobranchiomorphs and teleostomes can be accepted with confidence).

A character of potentially greater significance is the presence of three paired elements in the hyoid arch below the interhyal. The most ventral of these (the so-called hypohyal) possibly has arisen as an independent element within the teleostomes. Whether it occurs in any or all sarcopterygians presently is not well established, but its occurrence in actinopterygians is widespread. Among teleosts its position is occupied by two elements (the so-called dorsal and ventral hypohyals). The relation between these and the single element of other actinopterygians is unknown. It is suggested above that both the single and double elements segmented from the basibranchial series, and that the double element possibly originated by subdivision of the single one.

CHONDROSTEI

Recent chondrosts show some diversity in gill-arch structure, but probably can be characterized by the biting surfaces supported by the ventral parts of one or more of the anterior arches. These primitively are paired tooth plates supported by hypobranchials in paddlefishes, but in sturgeons they are transformed into peculiar systems of ridges without apparent calcification. If the tooth plates and non-calcified ridges are comparable in form if not in substance, they would appear to be a character unique among Recent fishes, for prominent dentition restricted to the "tongue" otherwise occurs only over the basibranchial series.

HOLOSTEI

Recent holosts together with teleosts are the only fishes known to possess highly

movable upper pharyngeal bones or their functional equivalents. In both *Amia* and *Lepisosteus* these are composed of prominent patches of tooth plates not directly assignable to the dermal-element series of one or more arches. In this respect, the upper pharyngeal tooth patches do not appear to be very primitively organized. Indeed, the consolidation of tooth plates into the large patches of the type found in *Amia* and *Lepisosteus* is unique among fishes, for upper pharyngeal plates otherwise appear as continuations of the dermal-element series of particular arches. Thus in holosts the tooth plates are of uncertain homology with respect to their arch or arches of origin, but this similarity in itself is suggestive of a relationship, however remote, between the two surviving genera of holostean fishes. That either of them is more closely related to teleosts than to the other is not supported by gill-arch evidence (cf. Gardiner, 1961, fig. 79; 1967b, fig. 8). In both *Amia* and *Lepisosteus* the paired upper pharyngeal tooth patches seem to be derived from the dermal-element series at least of the third and fourth arches. It is true that these are the same arches that produce the upper pharyngeal dentition of many specialized teleosts, but not that of ostariophysans, which is derived from the fourth and possibly fifth arches.

Because a movable upper pharyngeal dentition does not occur in other fishes, the question of its potential systematic significance is raised. This question requires considerably more study, particularly of the muscles and possibly also of the nerves of the branchial apparatus, before it can be answered in detail. It seems certain, however, that the pharyngeal dentition of specialized teleosts is of several types, each of which has developed independently in a distinct evolutionary lineage. No doubt a long process of phyletic development lies behind the pharyngeal apparatus also of Recent holosts. These independent developments in holosts and teleosts, apparently involving processes of both parallel and convergent evolution, make it desirable to consider the probable condition for the most primitive members of the lineages leading to the Recent holosts and teleosts. For holosts little information is available on the subject, but one may suppose

that the dermal elements were primitively arranged in rows associated with the dorsal parts of the arches, possibly not different from the condition in *Elops*. No doubt the dermal pharyngeal skeleton of early chondrosts and sarcopterygians also tended to be arranged in rows of tooth plates along the upper parts of the endoskeletal arches. So far as known the upper pharyngeal dermal skeleton of these forms never was consolidated into the large plates or patches like those that occur posteriorly in the pharynx of holosts and even primitive teleosts such as *Elops*. Consequently the presence of a consolidated upper pharyngeal dentition may be said to suggest a relationship between Recent holosts and teleosts, and support their placement in the taxon Neopterygii of Regan (1923, p. 458; 1929, p. 305), one coordinate with the Chondrostei (see also below).

TELEOSTEI

If considered adequately represented by certain primitive members of the major subgroups, the teleosts are unique among fishes in that they have four paired elements ventrally in the hyoid arch below the interhyal, an independent basihyal, median basihyal and basibranchial tooth plates,¹ and consolidated upper pharyngeal tooth plates associated usually with arches 2-4 (possibly also arch 5 and certainly in some cases arch 1). So far as known, the condition of all these characters is advanced over that of holosts, chondrosts, sarcopterygians, and elasmobranchiomorphs. If so, from the standpoint of gill-arch structure the teleosts probably are the best-defined major group of fishes, with little indication of polyphyly, i.e., that some Recent teleosts are most closely related not to other Recent teleosts but to Recent holosts or chondrosts (for discussion of this problem, see Gosline, 1965; Greenwood, Rosen, Weitzman, and Myers, 1966; Patterson, 1967c). It may be added here that, when fossil forms are considered, the basic problem is obscured when the viewpoint shifts from the difficulties of identifying the fossils to a consideration of possible ancestor-descendant sequences. Thus some authors

would consider the teleosts "polyphyletic" if they diverged in more than one lineage from "pholidophoroids," in the same way that "mammals" by some (e.g., Romer, 1965, p. 152) are believed to be polyphyletic because they diverged in independent lineages from "reptiles." In the opinion of the writer this polyphyletic dilemma represents hardly more than a breakdown in logic, the fallacy of which has been nicely discussed by Brundin (1966, pp. 11-45).

With gill-arch characters it so far has proved impossible to divide the teleosts into subgroups of related fishes. However, the distinctive upper pharyngeal dentition (with tooth plates fused with infrapharyngobranchials 2-3 and epibranchial 3 and an independent fourth tooth plate) of primitive myctophiform, paracanthopterygian, and acanthopterygian fishes suggests that at least these form part or all of one monophyletic subgroup the members of which informally have been called "neoteleosts" (Rosen and Patterson, 1969). The condition of all these characters is advanced over that of primitive teleosts, as indicated by the fusion of the tooth plates with their endoskeletal supports. Also, it appears probable that the fourth tooth plate of myctophiforms, paracanthopterygians, and acanthopterygians arose through the fusion of the fourth and fifth plate of primitive teleosts.² The interrelationships of the remaining teleosts, consisting chiefly of the "isospondylous" fishes and some of their "derivatives" (Gosline, 1961, p. 39) so far are as obscure from the standpoint of gill-arch structure as from others and cannot be considered here.

² Other advanced characters of the gill-arch dentition eventually may be found to have systematic significance. These include the toothed second epibranchial of ophidiids and batrachoidids, and the toothed fourth ceratobranchial of atherinids such as *Menidia*, amblyopsids, and cyprinodontoids (see, e.g., Gosline, 1963b, p. 34). The ceratobranchial teeth of these fishes apparently represent fused gillrakers of the anterior series, rather than tooth plates primitively situated above the gillrakers. Fusion of gillrakers with the fourth ceratobranchials probably has occurred independently in atherinids, cyprinodontoids, and percopsiforms. At least percopsids, aphredoderids, and some atherinids with a well-developed, dermal gill-arch skeleton do not have gillrakers fused to the fourth ceratobranchials, even though prominent tooth plates (or consolidated gillrakers?) in some cases occur in this position (pl. 92, figs. 1, 2).

¹ A median basibranchial plate is known in some non-teleostean actinopterygians, but in them a separate basihyal plate is lacking (see Nielsen, 1952, 1955).

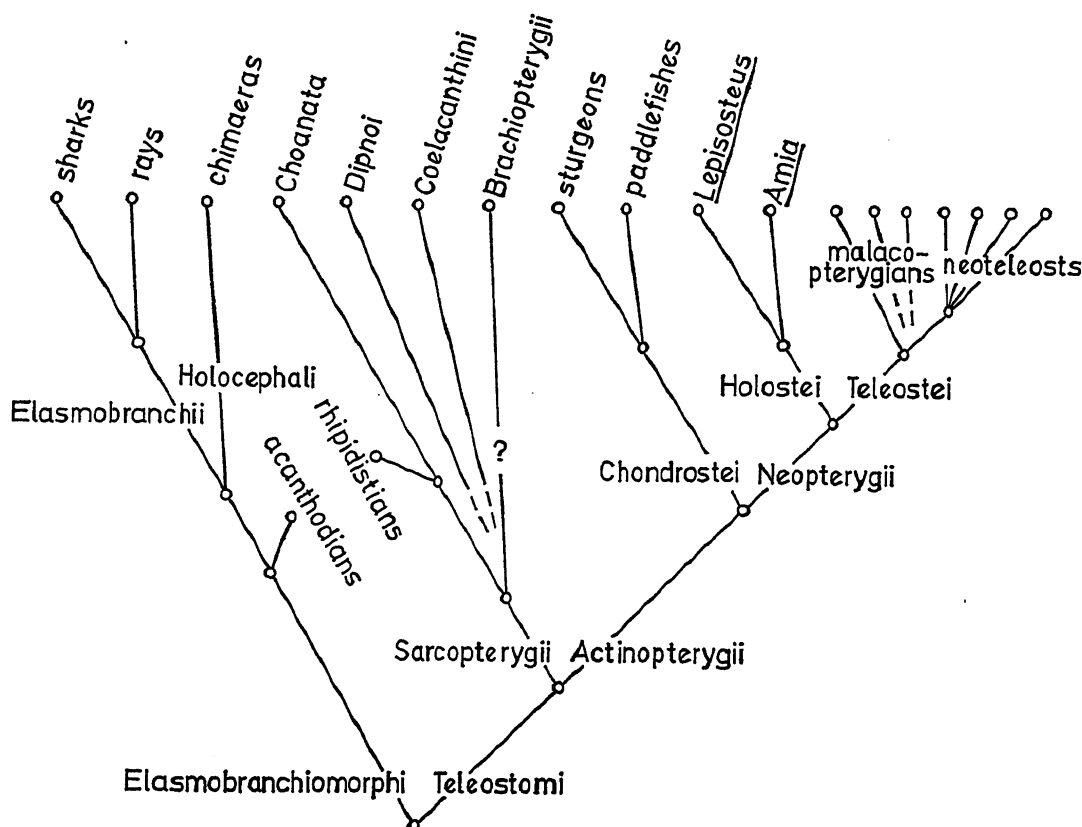


FIG. 25. Relationships of some groups of Recent vertebrates, based chiefly on a consideration of gill-arch structure.

Based on these considerations of gill-arch structure, relationships among the fishes possibly are as depicted in figure 25. From this standpoint it may be emphasized that the Recent Chondrostei, Holostei, and Teleostei emerge as monophyletic groups, with holosts and teleosts more closely related to one another than either is to chondrostei. If so, the Holostei and Teleostei are of equal age, and the group including holosts and teleosts is of an age equal to that of chondrostei. It follows that the usual discussion of actinopterygian relationships, involving the progression from chondrosteian through holosteian to teleostean levels of organization, requires rethinking in so far as it concerns the phyletic interrelationships of fishes. To the present author, the conceptual model of such a progression through levels of organization is suitable for a discussion of phyletic trends of variation for particular structures, but is

not suitable for relationships of fishes. For these, current concepts have been strongly influenced by studies on fossil actinopterygians, including attempts to demonstrate ancestor-descendant sequences (Gardiner, 1961, 1963, 1967a, 1967b). This approach usually involves hardly more than a discussion of possible phyletic trends against a background of the stratigraphic distribution of fishes. Indeed, in many cases this is all that is attempted (Gardiner, 1961, p. 333). Consequently, considerable revision in the definition and alignment of fossil groups of actinopterygians is to be expected and, needless to say, will be required before much can definitely be said about the relationships of many of the fossil groups, as well as of the absolute ages of the groups represented in the Recent fauna.

A great deal of the discussion of actinopterygian evolution in terms of levels of

organization overlooks the fact that the categories Chondrostei, Holostei, and Teleostei originally were proposed to express relationships between Recent fishes (Müller, 1846a, pp. 31, 83; 1846b, pp. 33, 43; 1846c, pp. 523, 532). The Actinopterygii generally are accepted as a monophyletic group, and there is general agreement (often not clearly stated) that the Recent Chondrostei, Holostei, and Teleostei also are monophyletic groups. To the knowledge of the writer, no one recently has attempted to show that sturgeons and paddlefishes are not more closely related to each other than to any other Recent fishes (but see Nielsen, 1955). For teleosts various authors have been struck by the resemblances between certain characins and *Amia*, but very few have gone so far as to suggest that some teleosts are most closely related to *Amia*, sturgeons, or, for that matter, any other fishes except other teleosts (cf. Bertmar, 1962, fig. 12, whose argument rests chiefly on an irrelevant consideration of some primitive characters retained in characins). The relationships of *Amia* and *Lepisosteus* seemingly have been more seriously questioned (e.g., by Westoll, 1944, p. 95, and more recently by Gardiner, 1960, fig. 79; 1967a, fig. 8, whose argument rests

on a supposed independent origin of both semionotids and parasemionotids from palaeoniscoids [1960, p. 338], with the derivation of furids and pholidophorids from parasemionotids, amiids from furids, teleosts from pholidophorids, and lepisosteids from semionotids [1960, fig. 79]. In a more recent treatment, the pattern of derivation is even more complex [1967a, fig. 8]). Gardiner (1960, pp. 357–362) considered a number of differences between semionotids and parasemionotids to justify the conclusion that amiids are more closely related to teleosts than to lepisosteids, and later (1963, p. 317) added that the single nostril of semionotids supports the concept of separate ancestries for semionotids and amioids. In the writer's opinion such comparisons of advanced versus primitive conditions of single structures do not bear directly on the problem of relationships. But regardless of whether *Amia* is most closely related to *Lepisosteus* or to the teleosts, the Neopterygii probably are to be subdivided into two groups, one (Holostei) including at least *Lepisosteus*, and the other (Teleostei) including the "teleosts" and probably fossil groups such as leptolepids and pholidophorids.

CLASSIFICATION OF VERTEBRATES

IT HAS LONG BEEN APPARENT that the higher classification of vertebrates requires revision so that it may be brought into agreement with modern conceptions of vertebrate history (Säve-Söderbergh, 1934). To suggest a scheme of classification that is more or less consistent with vertebrate phylogeny is simple enough, for there is little real disagreement about the interrelationships of the major Recent groups, although some persons would not classify tetrapods with their nearest relatives among "fishes"; birds and mammals, with their nearest relatives among "reptiles"; teleosts, with their nearest relatives among "holosts." In contrast, here it is assumed that the main purpose of a phyletic classification is to express such relationships. Matters such as the size of "gaps" separating groups, different "rates" of evolution, and divergence, size, and diversity of "taxa" are not considered, for in the opinion of the writer they are irrelevant to the purpose at hand. More serious problems, which prevent ready acceptance of any particular scheme, concern the treatment of fossil groups and the rank given to higher categories such as the Aves and Mammalia.

The classification of fossil groups poses special problems (Hennig, 1966, pp. 192-193) to the extent that it has been suggested that they possibly have no place in a classification of Recent forms (Brundin, 1966, p. 21). The high ranks assigned to some categories of vertebrates have been criticized, especially by entomologists who find comparisons between taxa such as orders of insects and orders of mammals absurd by any standard except anthropomorphism (Brundin, 1966, p. 19). Indeed, it seems that the arrangement of vertebrate classes clearly "favors" the birds and mammals, and has little relation to currently accepted theories of vertebrate evolution.

Concerning the relationships of the major groups of vertebrates, the writer can add relatively little to the conception of Säve-Söderbergh (1934, fig. 5), one unlikely to be radically altered by future work. With the addition of gill-arch evidence of the fishes it seems even more secure and worthy of con-

sideration. Consequently it is appropriate here to attempt a provisional classification, one in which the major vertebrate groups are better coordinated along phyletic lines. To achieve this end it is assumed that "sister-groups" should be coordinate taxa (Hennig, 1966). Also, the two included fossil groups are treated in a special way, each given a rank coordinate with that of the most closely related sister-groups of the Recent fauna (the fossil groups thus are not given strictly formal recognition as sister-groups). The necessary lowering of the relative ranks of groups of mammals is eased somewhat by the recent introduction into fish systematic literature of additional levels of higher "taxa," such as "division," "cohort," and "series" (Greenwood, Rosen, Weitzman, and Myers, 1966; Greenwood, Myers, Rosen, and Weitzman, 1967; Rosen and Patterson, 1969).

For these purposes it is necessary to outline only the major groups, but two of these, the Sarcopterygii and the Actinopterygii, are further subdivided to the ordinal level so that groups of equivalent rank may be compared (see list below). The names used are ones already proposed in the literature, but no claim is made for their nomenclatorial propriety, and no effort is made to render their endings uniform. There admittedly are some areas of uncertainty. Thus, in addition to the problems mentioned below, rhipidistians eventually may have to be distributed among choanate subgroups if tetrapods are "diphyletic" (Jarvik, 1942, 1960, 1962, 1963, 1965, 1966a, 1966b, 1968b), and doubtless the alignment of teleostean supraordinal taxa will be further modified when their interrelationships become understood.

The tetrapod groups (fig. 26) include the Batrachomorpha and Reptilomorpha of Säve-Söderbergh (1934), the Sauropsida and Mammalia (=Theropsida of Goodrich [1916]), and the Archosauria (including birds) and Lepidosauria as listed by Romer (1956, p. 474).

Both the Batrachomorpha and the Sauropsida have been considered polyphyletic, with anurans considered more closely related to sauropsids and mammals than to urodeles

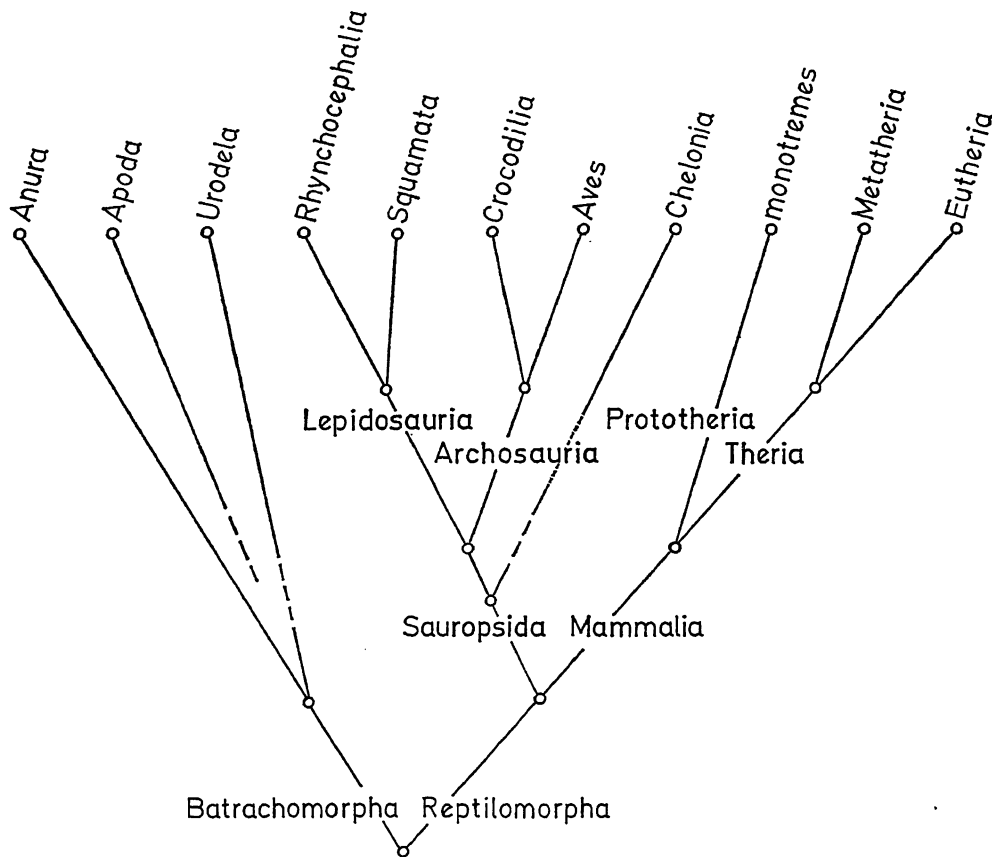


FIG. 26. Relationships of some groups of choanate vertebrates, based on a study of the literature.

(e.g., by Jarvik, 1968b; see also Huene, 1948, 1956), and lepidosaurs and archosaurs more closely related to mammals than to chelonians (e.g., by Olson, 1947). Whatever merit is contained in these arguments, there is little agreement about the relationships of the three groups of Recent "amphibians" and little more about those of chelonians. In contrast, there is better agreement that lepidosaurs and archosaurs (including birds) are monophyletic sister-groups, and that sauropsids (with the possible exception of turtles) and mammals (including "mammal-like reptiles") also are monophyletic sister-groups. In the opinion of the writer, only areas of agreement such as these can form the basis of any phyletic classification of tetrapods. Accordingly, there seems little point in isolating either urodeles or chelonians in taxa of very high rank simply

because their relationships are obscure. Rather, they are better left among batrachomorphs and sauropsids, respectively, until their relationships are better understood.

Many persons doubt that phyletic relationships can be expressed in a classification; others would disagree that relationships among Recent organisms can form a basis for phyletic classification, or they would insist that fossils be given primary if not exclusive consideration in a determination of the major divisions of any classification dealing with them. About these matters there is room for honest difference of opinion. Here it is assumed that classification must express relationships. Fossils here are not given primary consideration (nor even formal sister-group recognition), for the writer can see no reasonable way that such can be done and is unaware of any non-arbitrary attempt ever

to do so. That fossil groups can be fitted into a phyletic classification is shown, however, by the above consideration of two exclusively fossil groups of fishes (acanthodians and rhipidistians), the relationships of which are adequately expressed within a formal classification based on living forms. It seems desirable that exclusively fossil groups could be aligned in alternative ways without disrupting the main outlines of a phyletic classification, and for this reason the rank for purely fossil groups here is determined in a way neither arbitrary nor artful but different from that for Recent groups (see above). The result is a classification the main outlines of which are determined by the generally acknowledged interrelationships of the major groups represented in the Recent fauna, and are independent of the problems created by fossil groups, both those of which the relationships are obscure and the many awaiting discovery.

It may be added that the difficulties inherent in the study not only of fossil fishes but of fossil tetrapods prompts some persons to abandon the few systematic concepts about which there really is widespread agreement. Thus it is remarkable that *Diadectes*, for example, simply because its

relationships are obscure, can be considered to have an important bearing on the validity of the sauropsid-theropsid concept of Goodrich (1916), as Olson (1966) believed. Further, even if chelonians are to be removed from the Sauropsida, it is impossible to agree that Goodrich's position would be "with little or no support" (Olson, 1966, p. 224) or that "Parrington (1958) made a strong case against the sauropsid-theropsid dichotomy" (Olson, 1966, pp. 223-224), when Parrington (1958, p. 114) in fact found it necessary to terminate his review of reptile classification with the following: "Judged from the evidence available today, therefore, the dichotomy of the amniotes amounts to no more than the development from primitive, captorhinomorph stock of two dominant lines of reptiles, the Synapsida and the Diapsida, leading to the mammals and birds respectively." This statement, which might have been made 50 years ago by Goodrich, really is a paraphrase of: "[The Reptilia] includes a main stem leading from the Stegocephalian type to a central point of divergence of two main branches, one giving rise to the Birds, the other to the Mammals" (Goodrich, 1916, p. 261).

Order Insectivora

SUMMARY

STUDY OF ADULT GILL-ARCH DENTITION of Recent and some fossil fishes suggested that the condition primitive for gnathostomes included numerous dermal elements, initially small but capable of growth. During evolution these small units apparently were organized into specialized structures of several types, through processes involving fusion between initially separate dermal elements, and in some cases fusion between the dermal skeleton and visceral endoskeleton.

Advanced types of gill-arch dentition were found to characterize most of the major groups of fishes. These types, combined with characters of the gill-arch endoskeleton and related muscles, provided a basis for discussion of the phyletic interrelationships of all major fish groups represented in the Recent fauna. Concerning relationships, conclusions reached are in essential agreement

with those of earlier workers. In addition, the basic branching of the gnathostomes appears to be consistent with the sister-group model of Hennig. On the basis of this agreement and consistency it was possible to propose a revised higher classification of fishes, proceeding from the assumption that sister-group relationships among Recent organisms must be expressed in the main outlines of a phyletic classification.

Because it is generally agreed that tetrapods are related to rhipidistian fishes, it was possible to extend the classification to include the major groups of Recent tetrapods. The final result was a revised higher classification of the superclass Gnathostomata in which the major groups are arranged not arbitrarily but according to their probable phyletic interrelationships.

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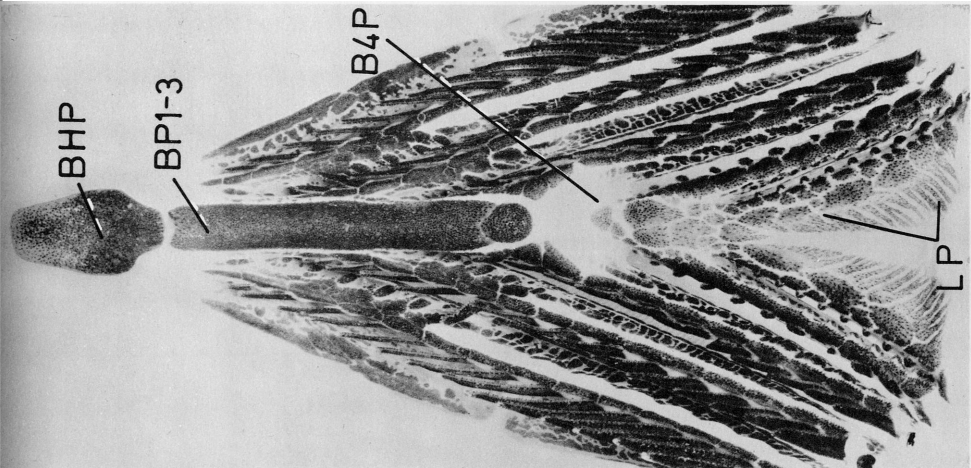
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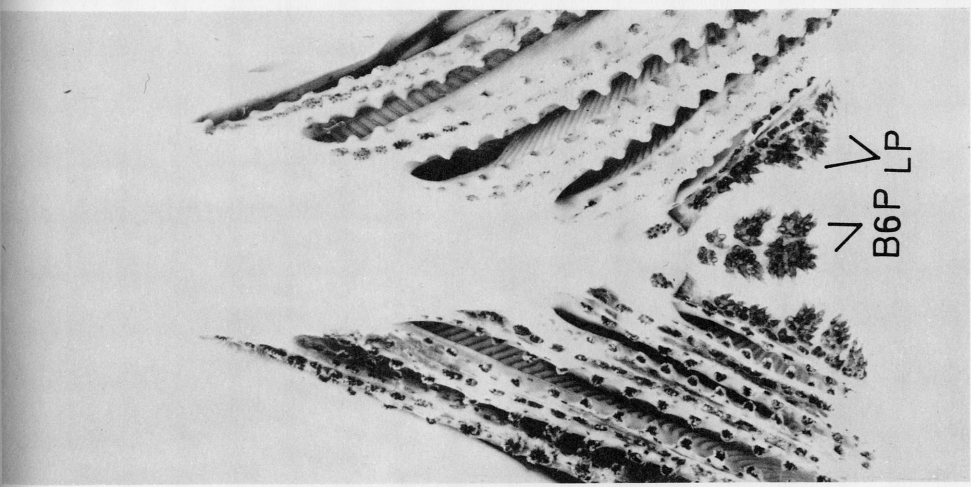
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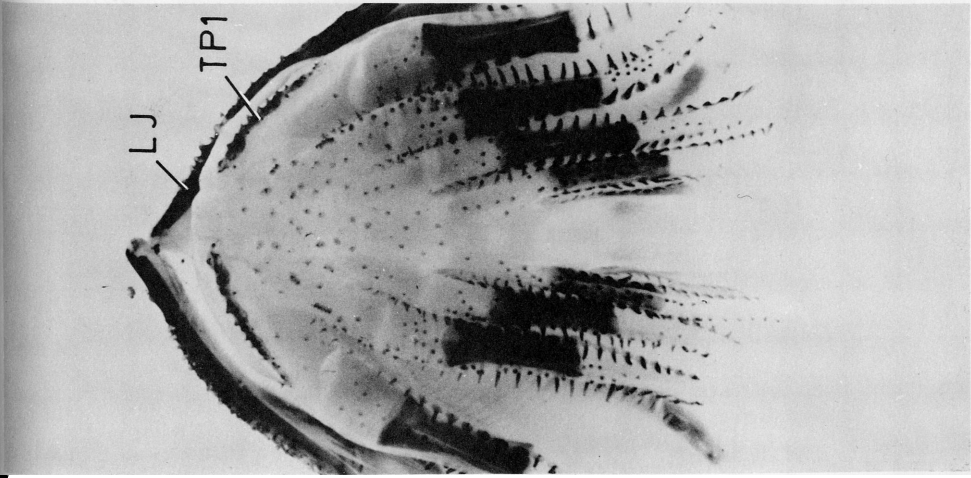
PLATES 79-92



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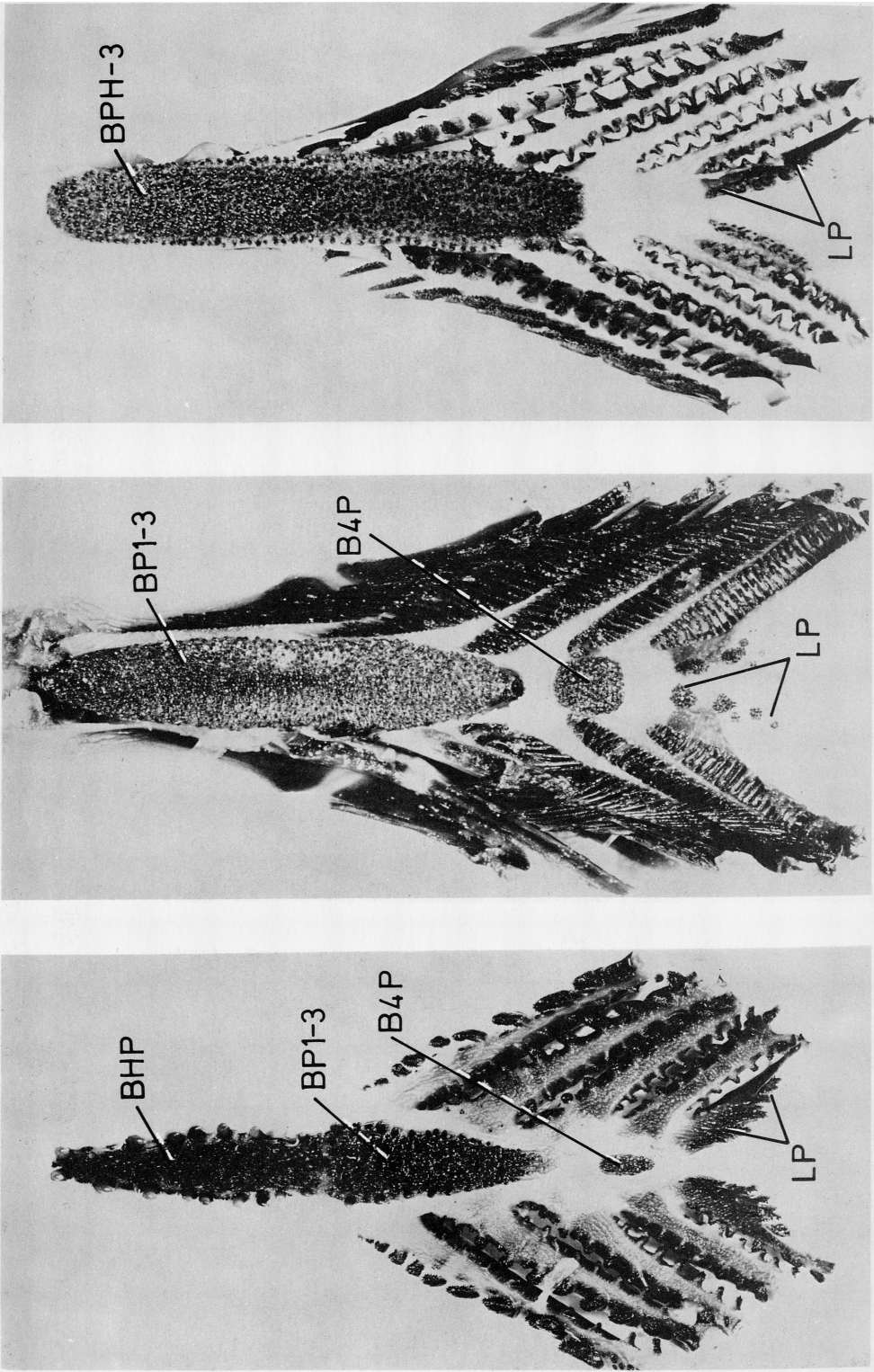


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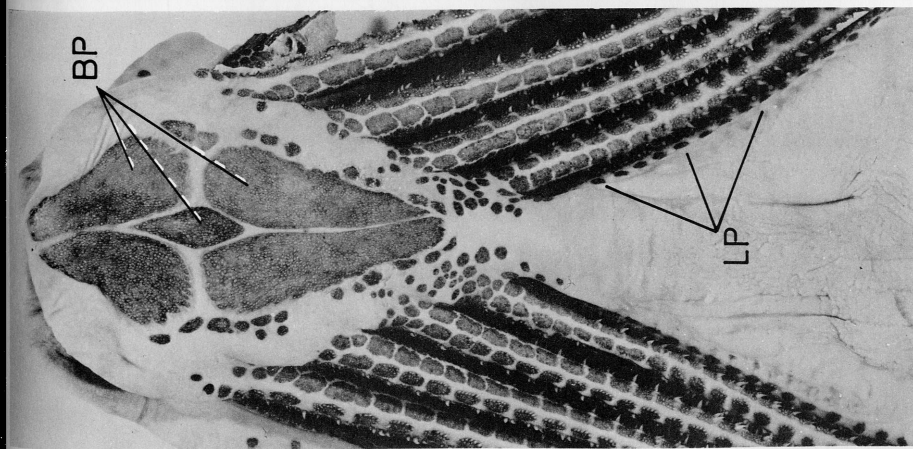


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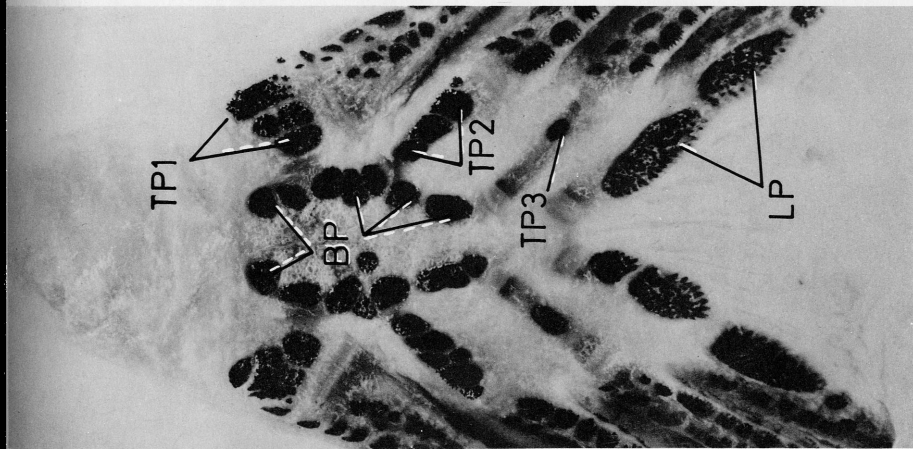
Gill arches, ventral parts, dorsal view of the alizarin-stained dermal skeleton. 1. *Psephurus gladius*. 2. *Amia calva*. 3. *Elops saurus*



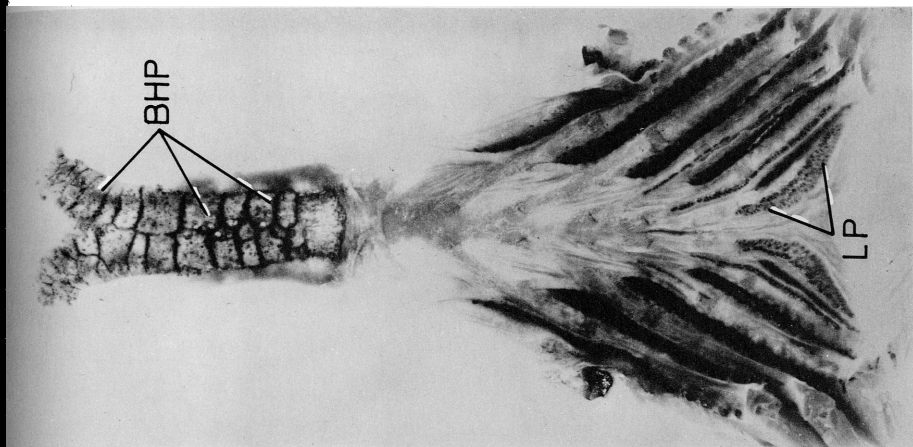
Gill arches, ventral parts, dorsal view. 1. *Hiodon alosoides*. 2. *Arapaima gigas*. 3. *Osteoglossum bicirrhosum*



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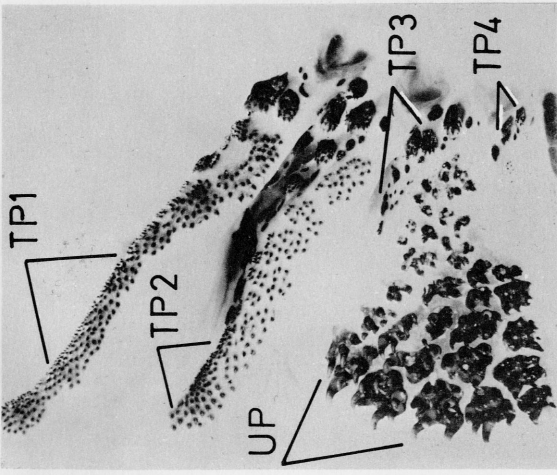


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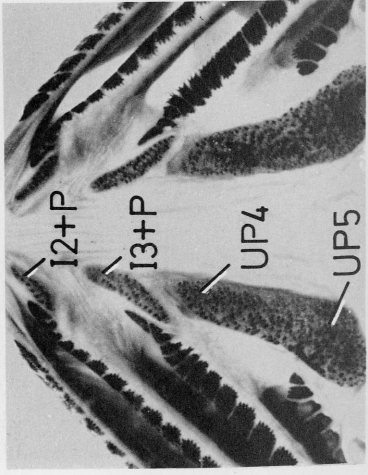


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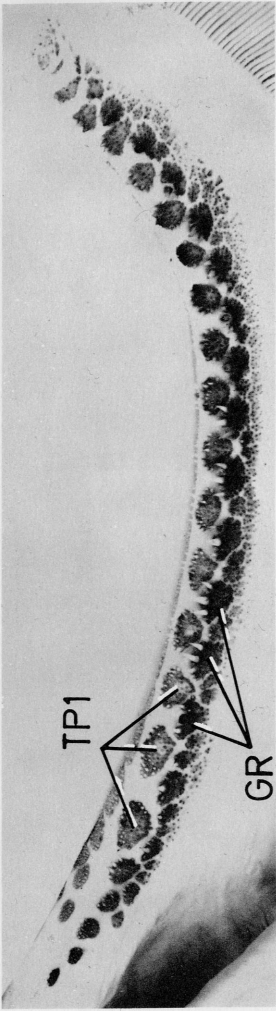
Gill arches, ventral parts, dorsal view. 1. *Latimeria chalumnae*. 2. *Polypterus* sp. 3. *Lepisosteus platyrhincus*



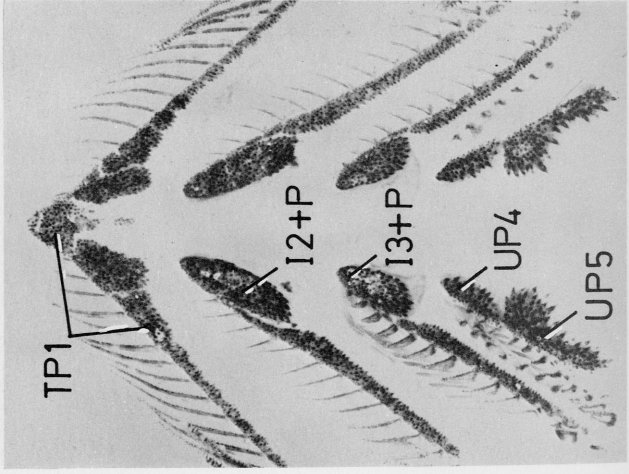
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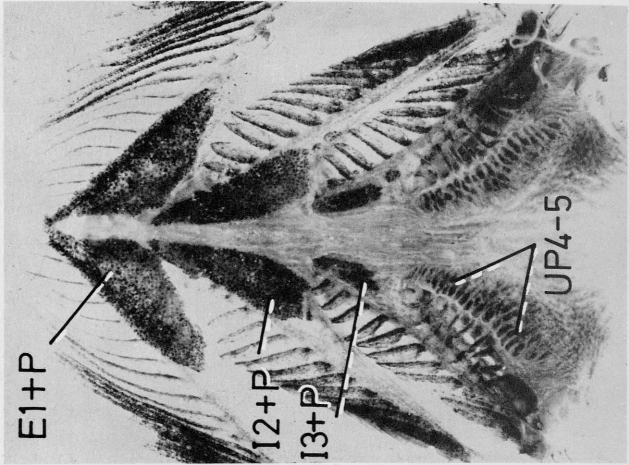
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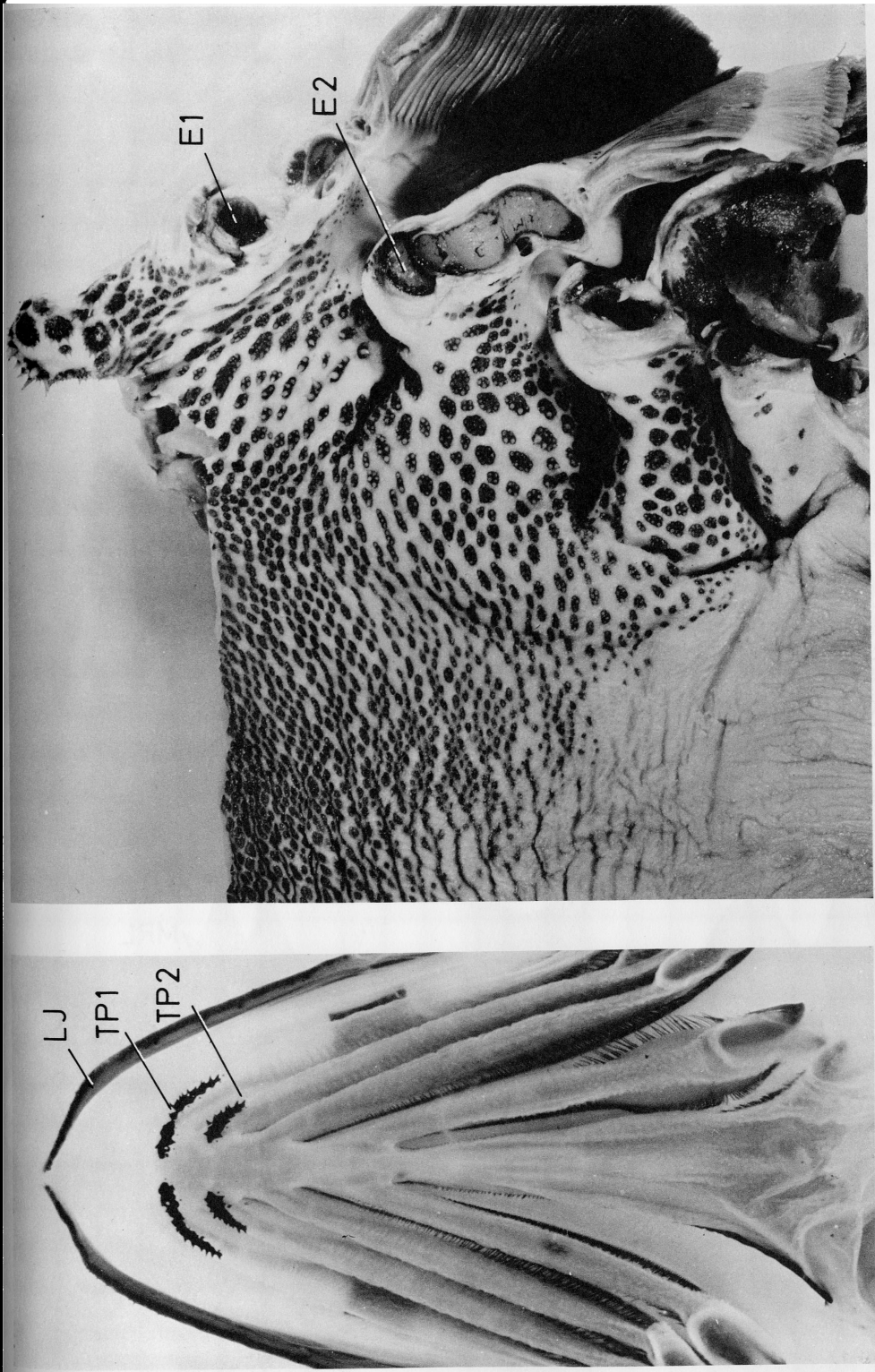


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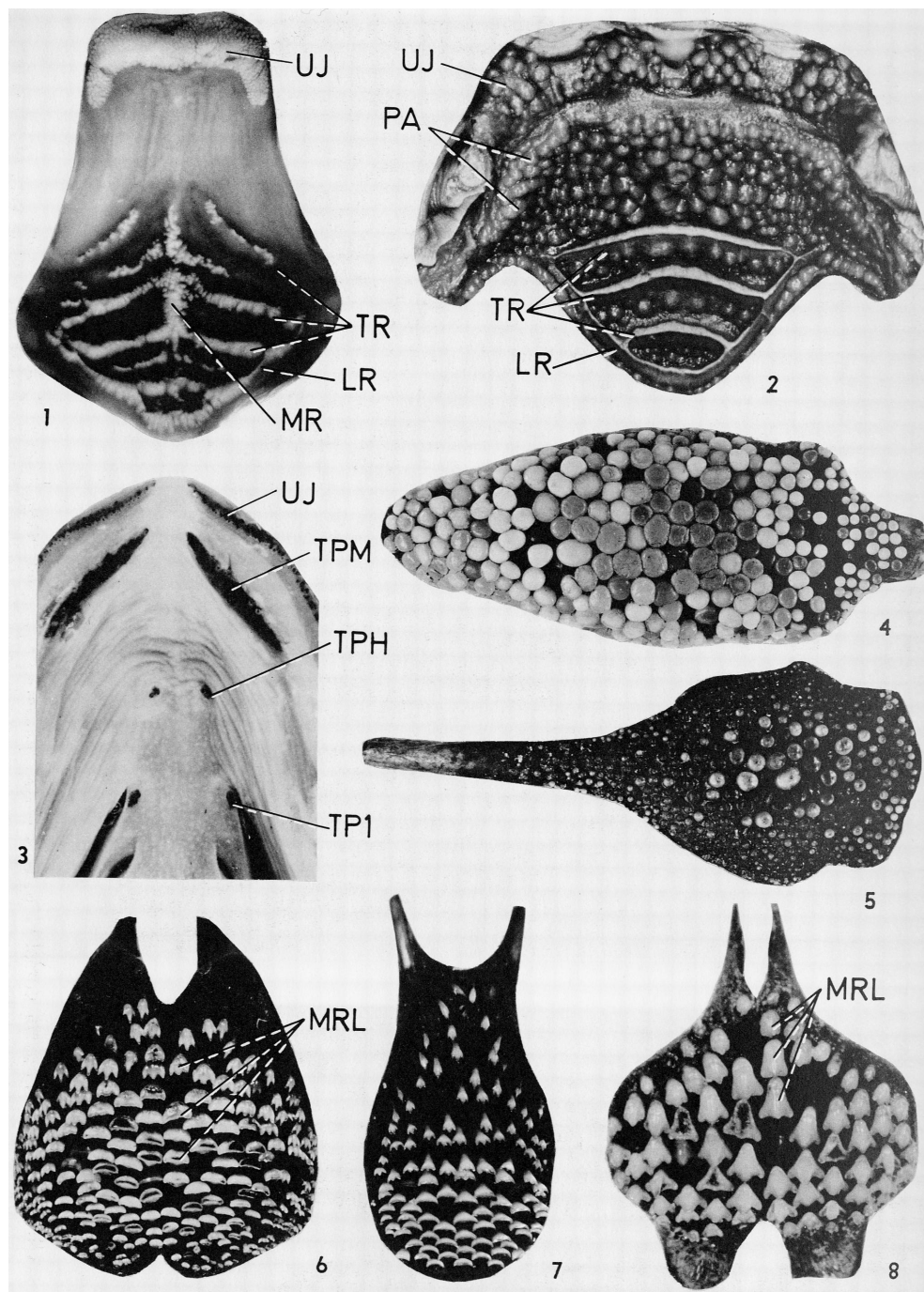


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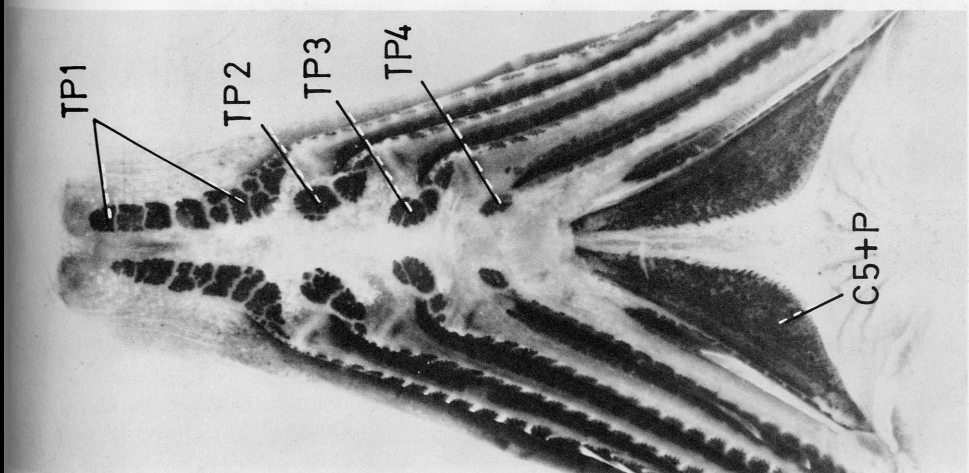
1. *Amia calva*, upper pharyngeal tooth plates, ventral view of left side. 2. *Latimeria chalumnae*, first ceratobranchial, anterior view of left side. 3. *Hoplias malabaricus*, roof of pharynx, ventral view. 4. *Pterengraulis atherinoides*, roof of pharynx, ventral view. 5. *Anchoa hepsetus*, roof of pharynx, ventral view



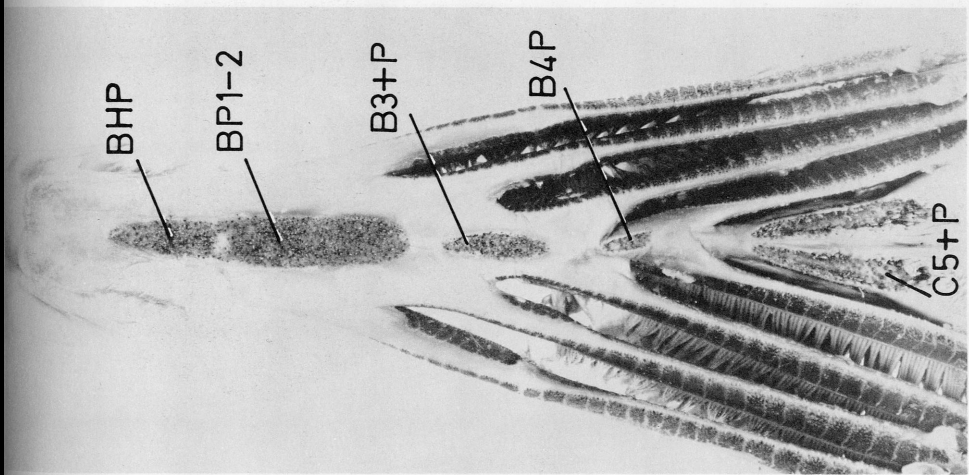
1. *Polyodon spathula*, gill arches and jaws, ventral parts, dorsal view. 2. *Latimeria chalumnae*, roof of pharynx, ventral view of left side



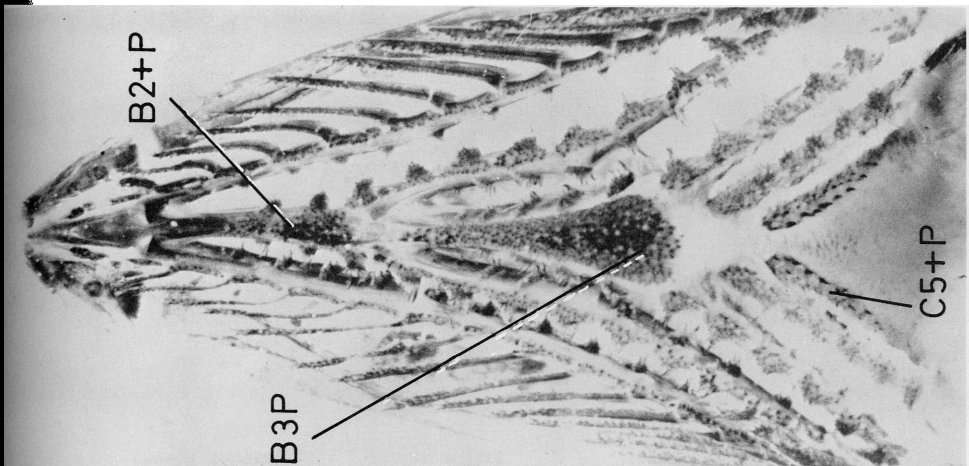
1. *Acipenser oxyrhynchus*, upper jaw and palate, ventral view. 2. *Scaphirhynchus platyrhynchus*, upper jaw and palate, ventral view. 3. *Polyodon spathula*, upper jaw and palate, ventral view. 4. *Albula vulpes*, basibranchial tooth plate, dorsal view. 5. *Pristolepis fasciata*, basihyal, dorsal view. 6. *Exocoetus volitans*, left and right third infrapharyngobranchials, ventral view. 7. *Chriodorus atherinoides*, fused third infrapharyngobranchials, ventral view. 8. *Zenarchopterus* sp., left and right third infrapharyngobranchials, ventral view.



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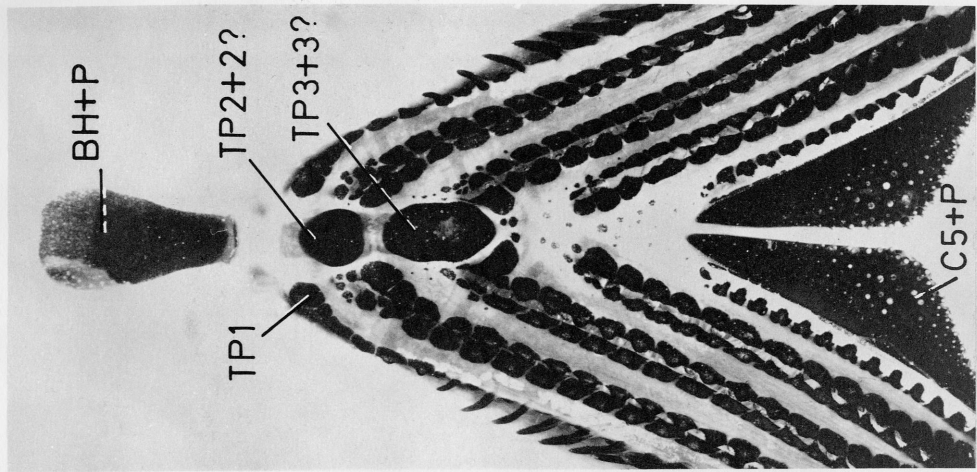


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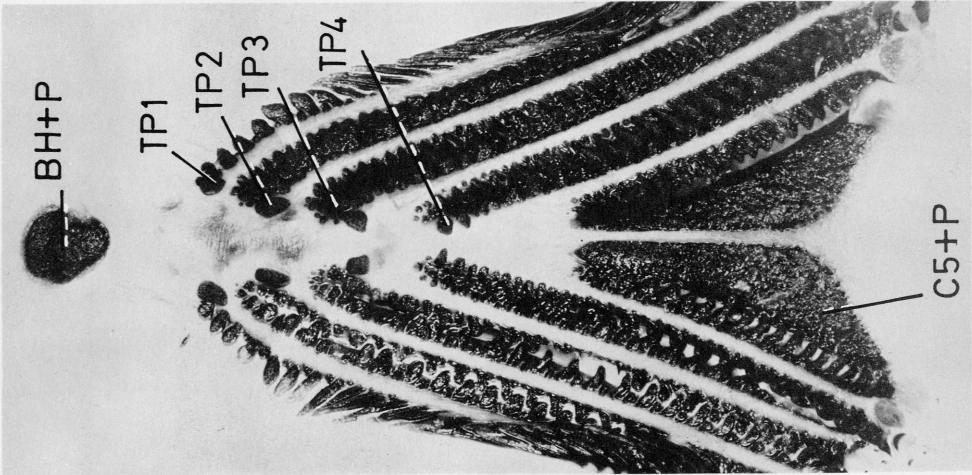


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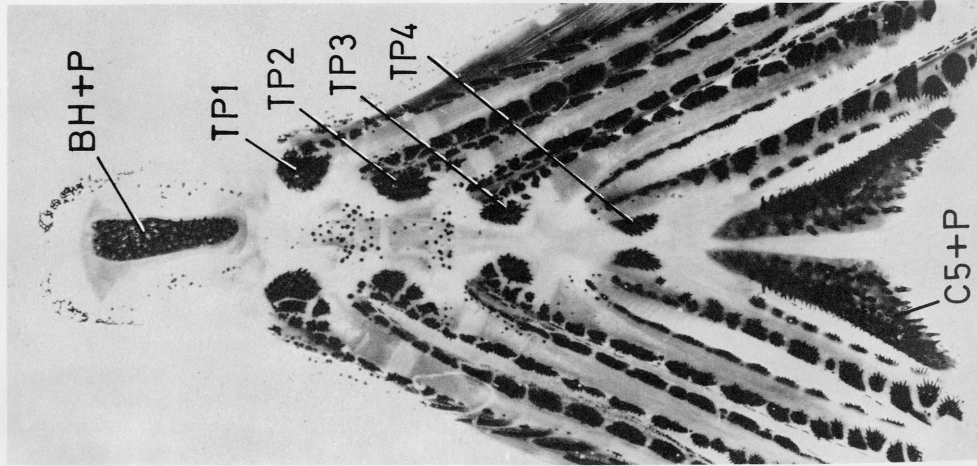
Gill arches, ventral parts, dorsal view. 1. *Hoplias malabaricus*. 2. *Esoc masquinongy*. 3. *Mycophum affine*



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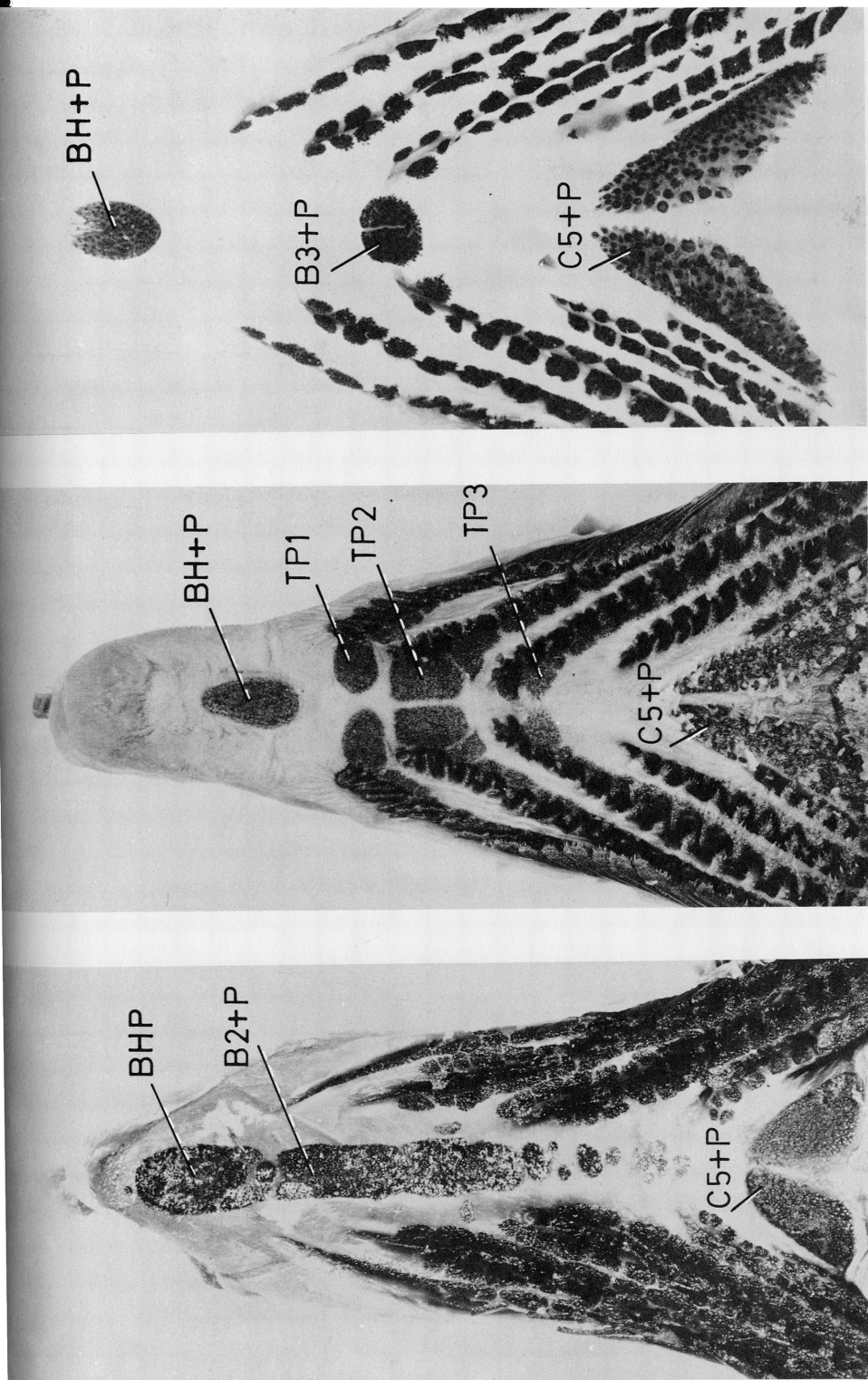


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Gill arches, ventral parts, dorsal view. 1. *Rachycentron canadum*. 2. *Remora remora*. 3. *Echeis naucrates*

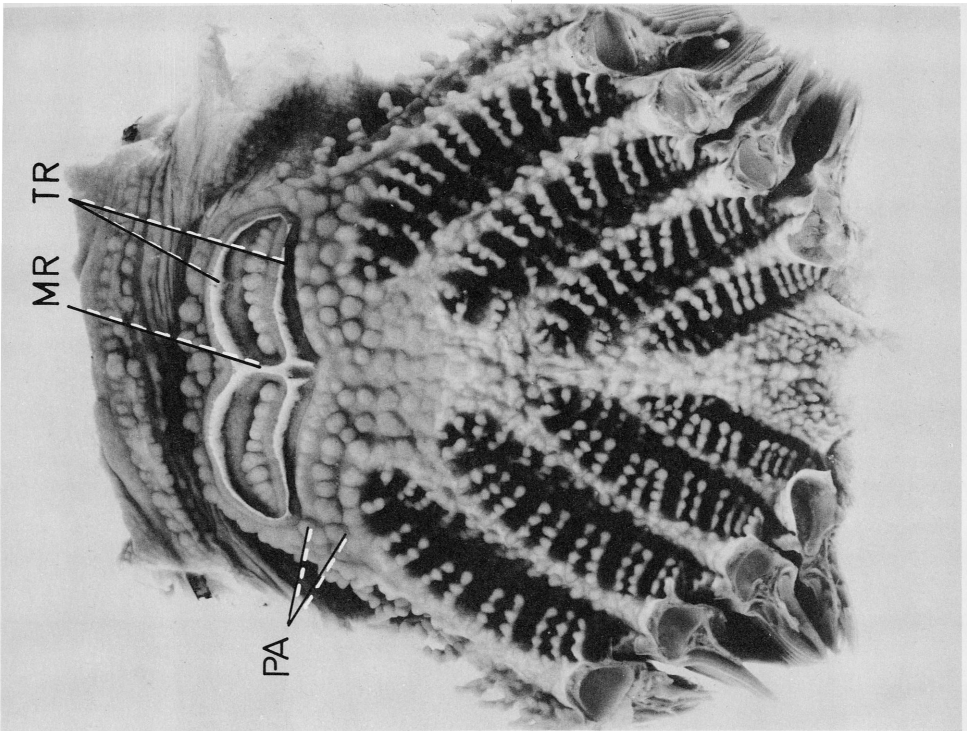


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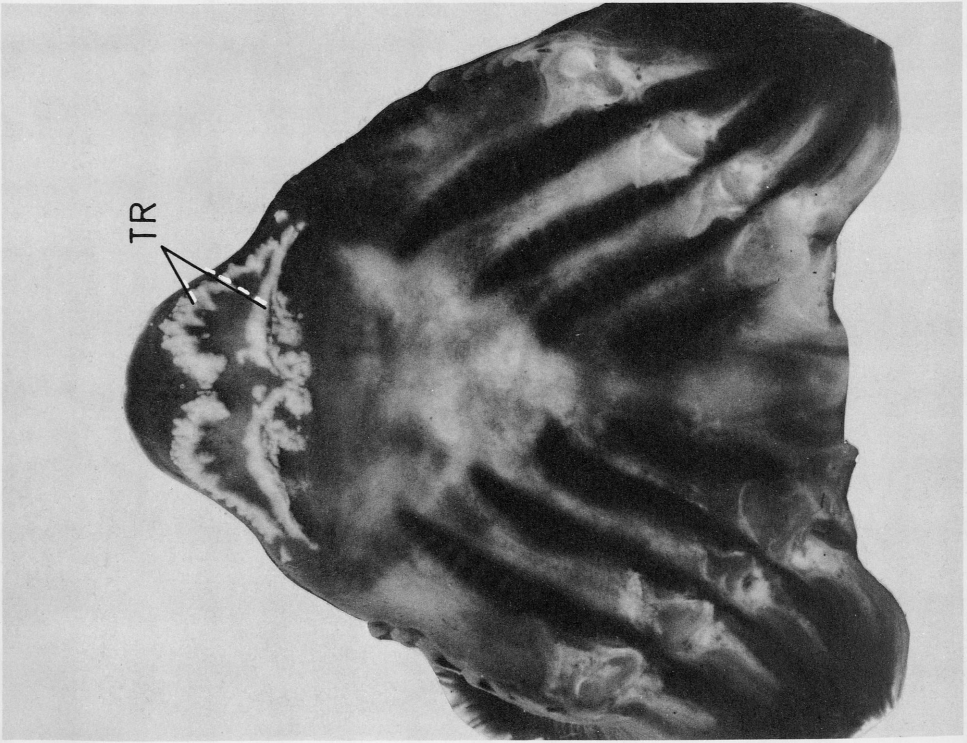
2

1

Gill arches, ventral parts, dorsal view. 1. *Polymixia japonica*. 2. *Pristipomoides sieboldi*. 3. *Chaenobrytus gulosus*

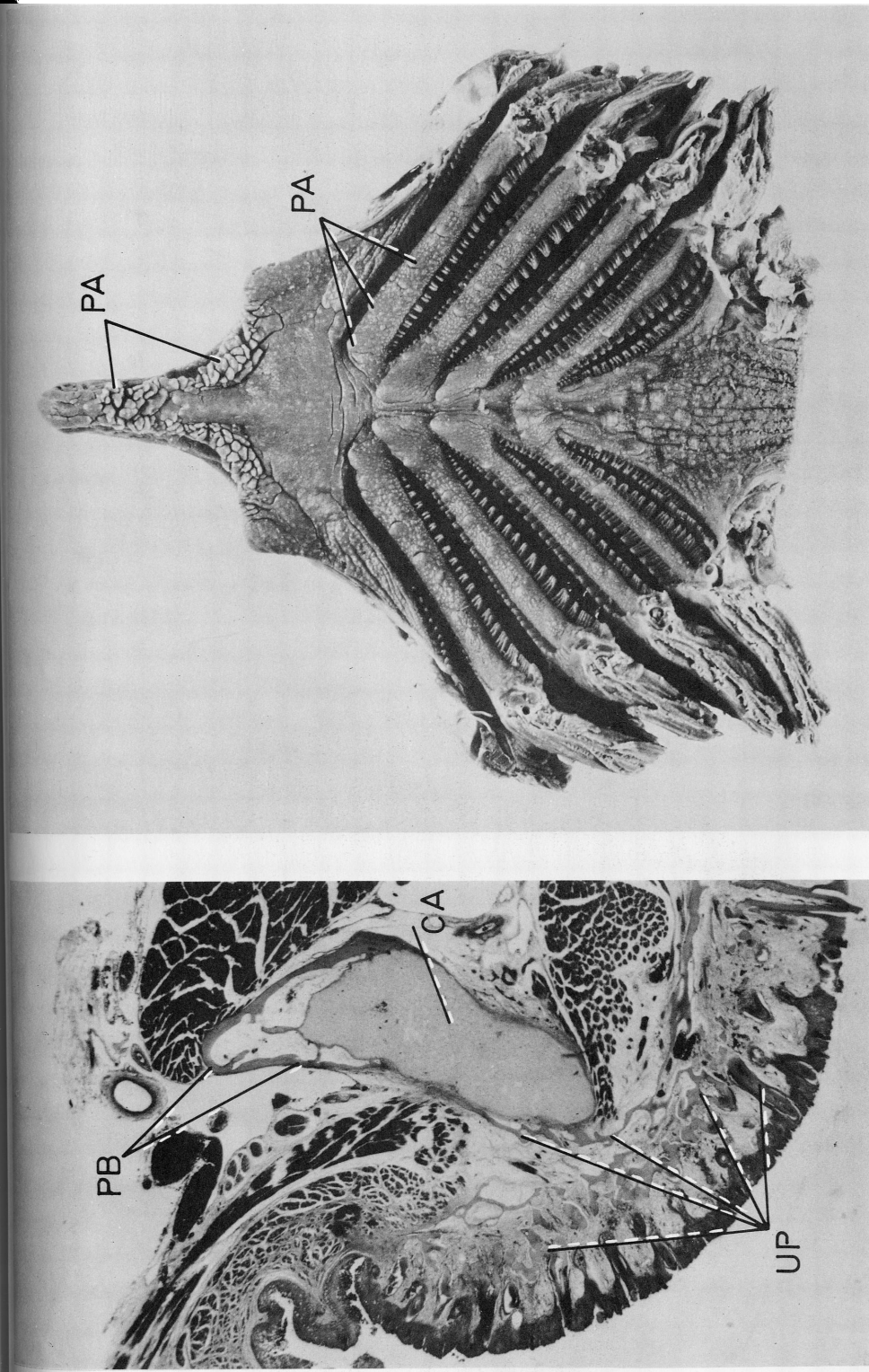


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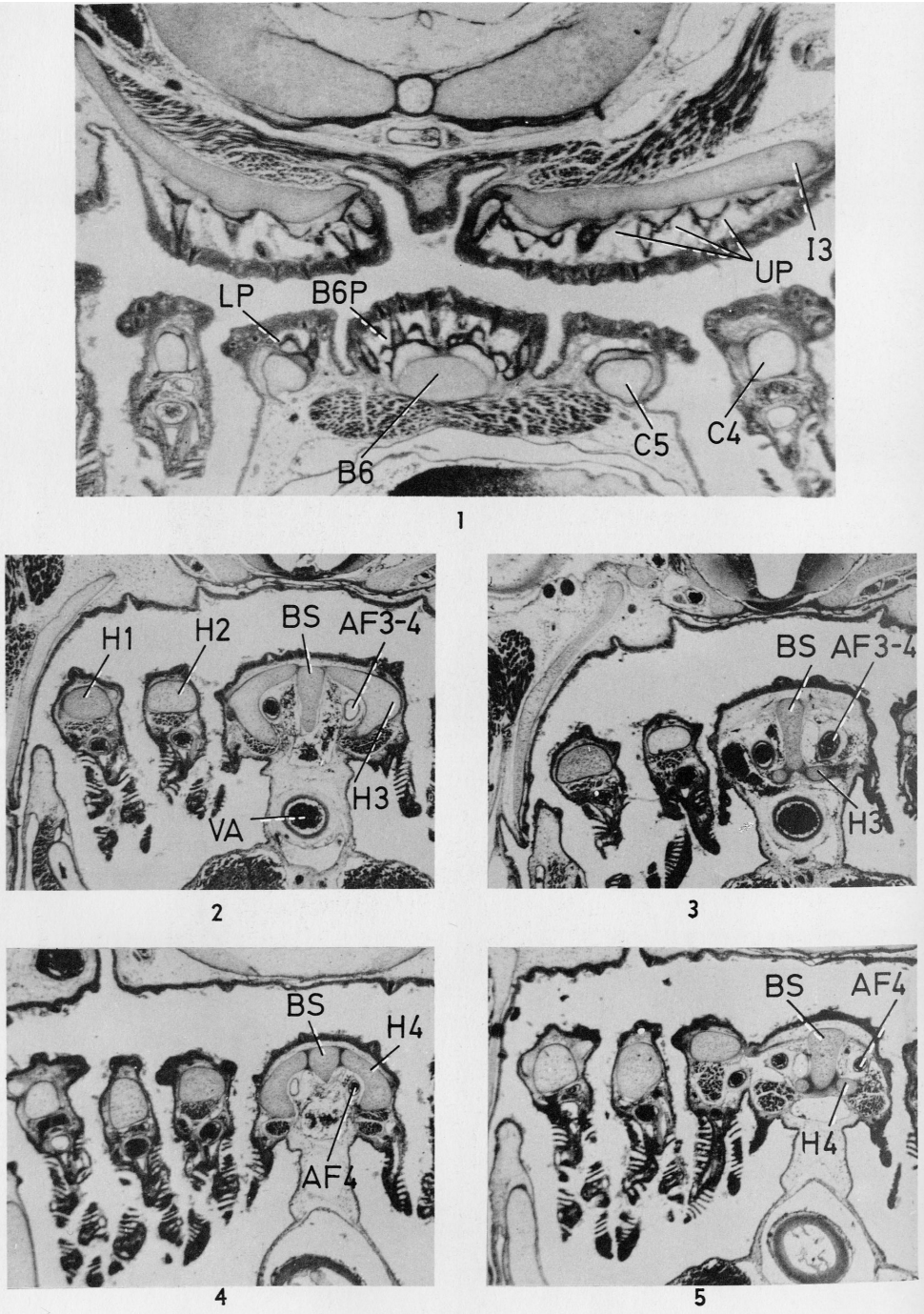


1

Gill arches, ventral parts, dorsal view. 1. *Acipenser oxyrinchus*. 2. *Scaphirhynchus platyrhynchus*



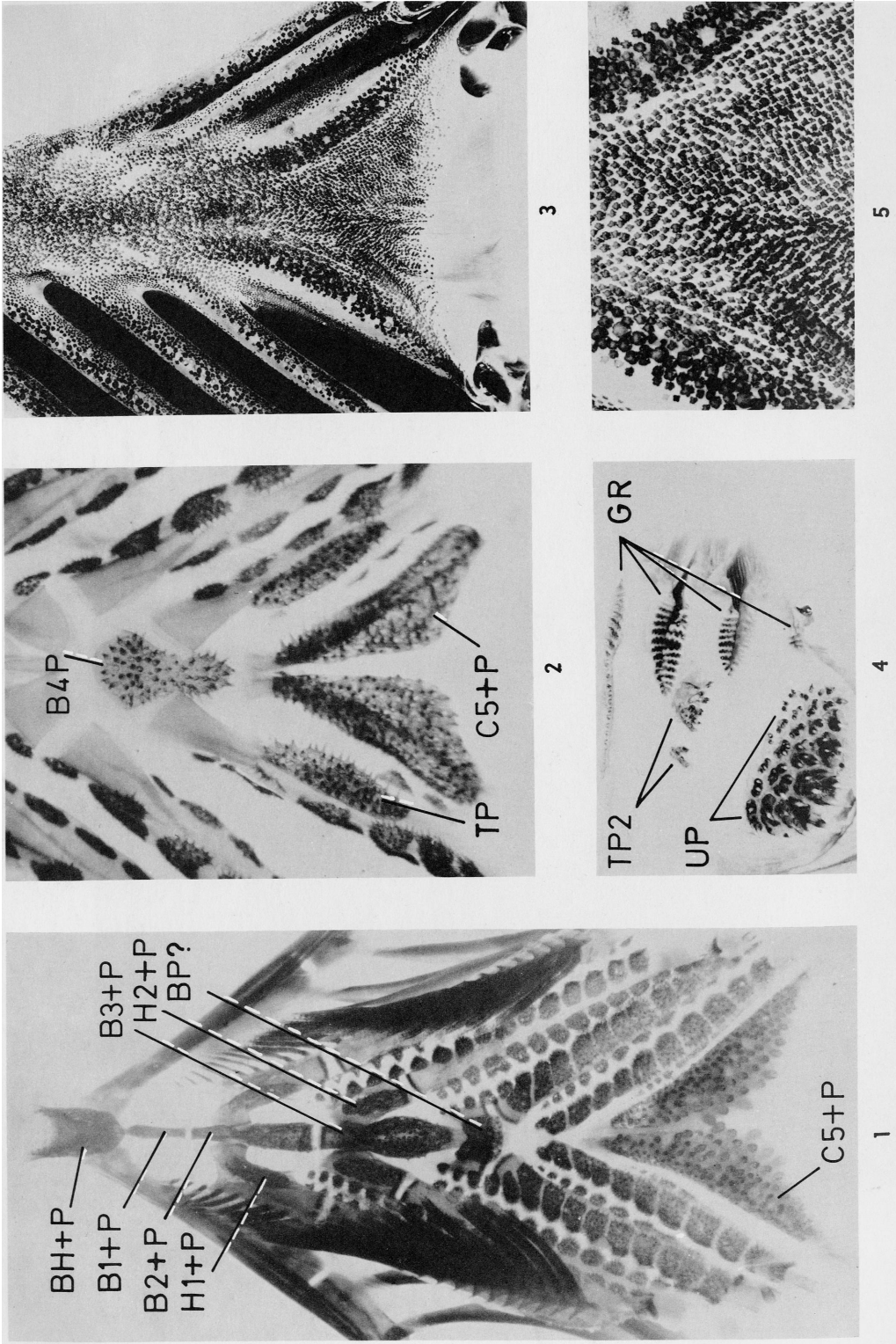
1. *Ictalurus nebulosus*, cross section of portion of the upper pharynx of right side. 2. *Neoceratodus forsteri*, gill arches, ventral parts, dorsal view



1-5. *Amia calva*, cross sections through different levels of the pharynx



Acanthodes bronni, latex cast of a specimen in Naturhistoriska Riksmuseet, Stockholm



1. *Atherina pinguis*, gill arches, ventral parts, dorsal view. 2. *Aphredoderus sayanus*, gill arches, posteroventral parts, dorsal view. 3. *Chlamydoselachus anguineum*, posteroventral parts, dorsal view. 4. *Lepisosteus spatula*, upper pharyngeal tooth plates, ventral view of left side. 5. *Chlamydoselachus anguineum*, enlarged detail of 3