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The Hyobranchial Apparatus of Teleostean Fishes of the Families Engraulidae and Chirocentridae

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In a previous study of the gill arches of teleostean fishes of the family Clupeidae, the writer defined certain phyletic trends, and on this basis erected an hypothesis of the phyletic interrelationships of the currently recognized subfamilies (Nelson, 1967a, fig. 9). To check these results, study of the gill arches is extended, in the present paper, to the families Engraulidae and Chirocentridae, which probably include the nearest Recent relatives of the Clupeidae. In addition, the structure of the branchiostegal apparatus is reviewed for all three families. On the basis of the new data, it is possible to arrive at a more precise conception of the phyletic interrelationships of the main groups of clupeiform fishes, and to propose a revised higher classification:

ORDER CLUPEIFORMES

SUBORDER DENTICIPITOIDEI

SUBORDER CLUPEOIDEI

SUPERFAMILY CHIROCENTROIDAE

SUPERFAMILY ENGRAULOIDAE

SUPERFAMILY PRISTIGASTEROIDAE

SUPERFAMILY CLUPEOIDAE

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MATERIAL AND METHODS

Specimens available included representatives of virtually all genera commonly recognized (e.g., by Norman, 1957; Hildebrand, 1943, 1963a, 1963b; Svetovidov, 1963; Whitehead, 1968a). They were generally small-to-medium adults. The hyobranchial apparatus was dissected as a unit from a given specimen, stained with alizarin (in aqueous 2% potassium hydroxide), and cleaned and examined under a binocular microscope. Drawings were prepared either freehand, with the aid of an ocular micrometer, or by tracing from photographs. Terminology follows that of Nelson (1969).

Gill-arch dentition was noted for at least one young adult per species (table 1). Teeth were recorded as being present when one or more could be observed. Branchiostegal rays were counted on both sides of the same specimens, with the highest number recorded (table 2). Some

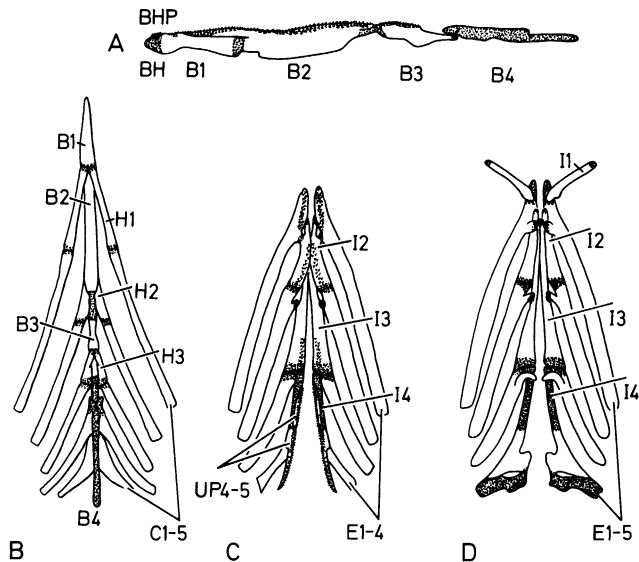


FIG. 1. *Engraulis mordax*, gill arches. A. Basibranchial series, lateral view of left side. B. Ventral parts, ventral view. C. Dorsal parts, ventral view. D. Dorsal parts, dorsal view. Cartilage stippled, bone clear. Cartilaginous articular areas at tips of ceratobranchials and epibranchials not shown. Basihyal omitted in B. E4-5 tilted backwards in D.

Abbreviations: B1-4, basibranchials 1-4; BH, basihyal; BHP, tooth plate overlying basihyal; C1-5, ceratobranchials 1-5; E1-5, epibranchials 1-5; H1-3, hypobranchials 1-3; I1-4, infrapharyngobranchials 1-4; UP4-5, upper pharyngeal tooth plates 4-5.

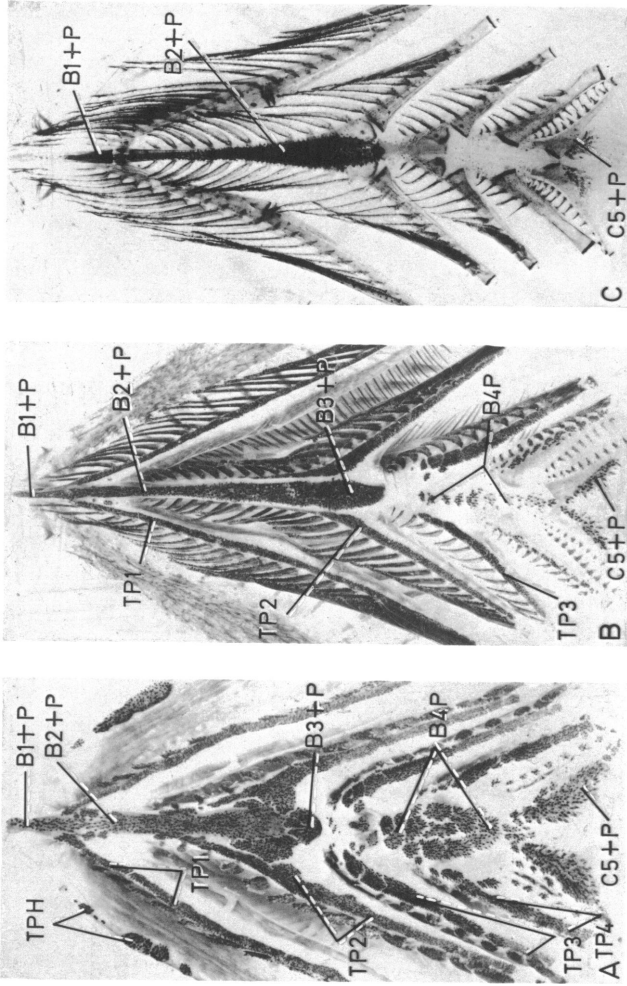


FIG. 2. Gill arches, ventral parts, dorsal view, showing alizarin-stained dermal bones. A. *Pterengraulis atherinoides*. B. *Thryssa malabarica*. C. *Anchoa mitchilli*.

Abbreviations: B1 + P, B2 + P, B3 + P, B4P, tooth plates fused with basibranchials 1, 2 or 3; B4P, tooth plate overlying basibranchial 4; C5 + P, tooth plate fused with ceratobranchial 5; TP1-4, tooth-plate series associated with arches 1-4; TPH, tooth-plate series associated with the hyoid arch.

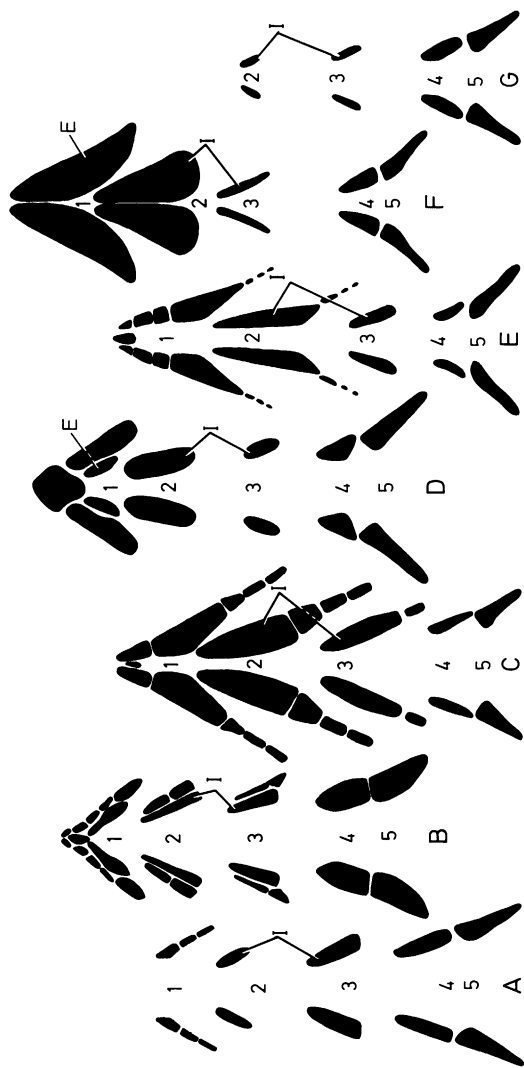


FIG. 3. Upper pharyngeal tooth patches. A. *Coilia mystus*. B. *Setipinna melanocheir*. C. *Thrissina baelama*. D. *Thryssa dussumieri*. E. *Thryssa kammalensis*. F. *Thryssa buccaneeri*. G. *Stolephorus indicus*.

Abbreviations: E, tooth plate fused with first epibranchial; I, tooth plates fused with infrapharyngeobranchials 2-3.

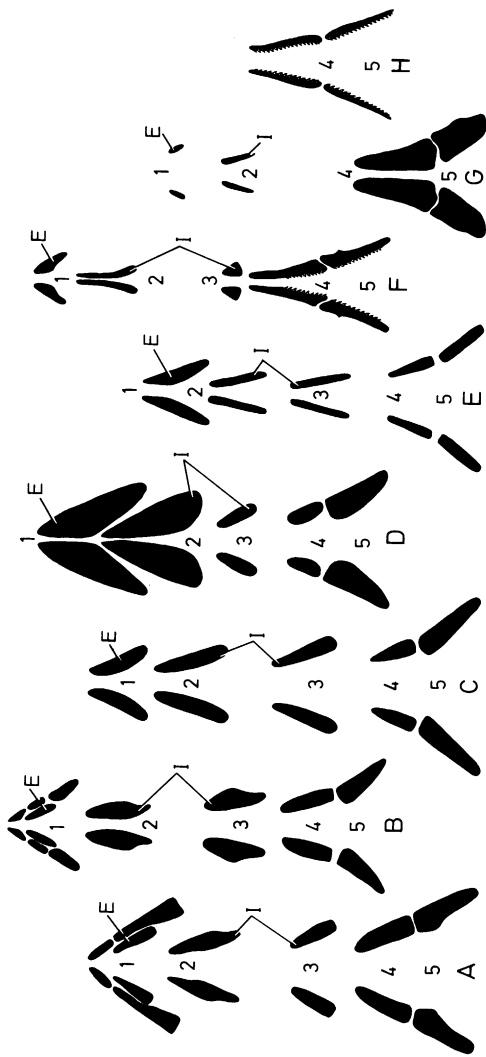


FIG. 4. Upper pharyngeal tooth patches. A. *Lycengraulis barboursi*. B. *Anchoa spumifer*. C. *Anchoviella elongata*. D. *Anchoa panamensis*. E. *Engraulis japonicus*. F. *Engraulis ringens*. G. *Cetengraulis edentulus*. H. *Anchovia clupeioides*. In F-H, 4-5 are the upper pharyngeal plates, with their entire dentition as shown.

specimens had different counts on each side, the left side usually having one ray more than the right. The counts are given as posterohyal ("epihyal") rays + anterohyal ("ceratohyal") rays. For cases in which the anterohyal had a distinct posteroventral process supporting a single ray, the count is given as posterohyal rays + this single ray + the remaining anterohyal rays.

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RESULTS

ENGRAULIDAE: Gill-arch structure is relatively uniform throughout the family, therefore only the gill arches of *Engraulis* are figured (fig. 1). Like those of clupeids (Nelson, 1967a, p. 394) the dorsal parts of the arches tend to be in contact along the dorsal midline, except in the examined species of *Coilia* (fig. 3A; see also Joshi and Bal, 1953, fig. 8). Whether or not in contact, the second and especially the third infrapharyngobranchials of each side have an elongate, anteriorly directed medial process, a feature by which gill arches of clupeoid fishes may be recognized at a glance. Unlike clupeids, the engraulids have the basihyal cartilaginous and rudimentary; the second basibranchial is the longest endoskeletal ossification of the basibranchial series; and dermal tooth plates generally occur in abundance over most of the gill-arch surfaces (figs. 2-4). The tooth plates include a basihyal tooth plate (BHP), which if present at all is severely reduced, and tooth plates fused with basibranchials 1-3 (in some species, however, one or more basibranchials are secondarily toothless). Tooth plates of irregular size and shape sometimes occur over the fourth basibranchial. "Lower pharyngeals" are almost always present, composed of tooth plates fused with the fifth ceratobranchials. Dorsally, the dermal skeleton is well represented by paired series of tooth plates, some free and others fused with their endoskeletal supports. Five pairs usually occur (figs. 3-4; Nelson, 1969,

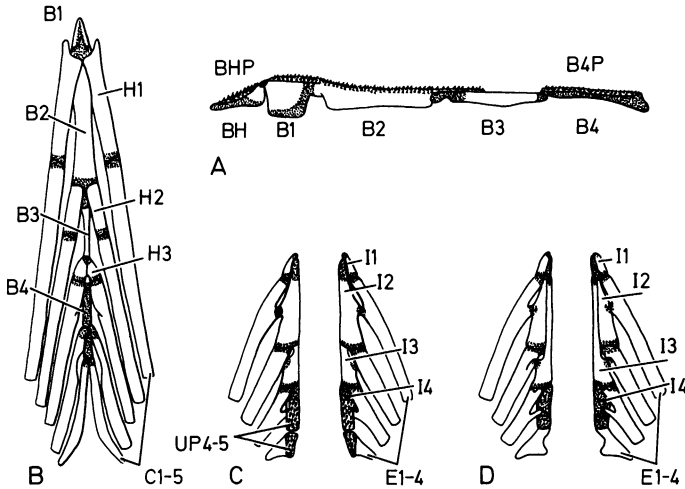


FIG. 5. *Chirocentrus dorab*, gill arches. A. Basibranchial series, lateral view of left side. B. Ventral parts, ventral view. C. Dorsal parts, ventral view. D. Dorsal parts, dorsal view.

Abbreviations: B1-4, basibranchials 1-4; B4P, tooth plate overlying basibranchial 4; BH, basihyal; BHP, tooth plate overlying basihyal; C1-5, ceratobranchials 1-5; E1-4, epibranchials 1-4; H1-3, hypobranchials 1-3; I1-4, infrapharyngobranchials 1-4; UP4-5, upper pharyngeal tooth plates 4-5.

pl. 82, figs. 4, 5). The anterior pair is supported by the anterior ends of the first epibranchials. In most Indo-Pacific genera these tooth plates are free, but in *Engraulis*, some species of *Stolephorus*, and in virtually all examined American engraulids, they are fused with the epibranchials, a feature which so far as is known does not characterize any other group of Recent teleostean fishes. Posteriorly, tooth plates are almost always fused with the second and third infrapharyngobranchials. Invariably present, more posteriorly, are paired tooth plates, one pair (UP4) underlying the cartilaginous fourth infrapharyngobranchials, and one pair (UP5) partially underlying the fourth epibranchials.

CHIROCENTRIDAE: Gill arches of *Chirocentrus* (fig. 5) have the dorsal parts well separated in the midline. The second and especially the third infrapharyngobranchials have long medial processes. The basihyal is small, but ossified and tilted downwards. Dermal tooth plates are well developed: one (BHP) over the basihyal, one fused with the second basibranchial, one (B4P) over the cartilaginous fourth basibranchial, and paired plates fused with the fifth ceratobranchial; dorsally, how-

TABLE 1
SUMMARY OF DERMAL GILL-ARCH ELEMENTS^a FOR RECENT CLUPEIFORM FISHES

	H	BP			4	LP	1	2	UP			
		1	2	3					3	4	5	
Chirocentridae												
<i>Chirocentrus dorab</i>	T	—	x	—	T	x	—	—	—	T	T	
Engraulidae												
Coilinae												
<i>Coilia mystus</i>	—	x	x	x	F	x	F	x	x	T	T	
<i>Coilia macrognaathus</i>	—	x	x	x	—	x	F	x	x	T	T	
Engraulinae												
Stolephorini												
<i>Thryssa spinidens</i>	0	x	x	x	F	x	F	x	x	T	T	
<i>Thryssa grayi</i>	—	x	x	x	F	x	F	x	x	T	T	
<i>T. malabarica</i>	—	x	x	x	F	x	F	x	x	T	T	
<i>T. purava</i>	—	x	x	x	—	x	x ^e	x	x	T	T	
<i>T. dussumieri</i>	—	x	x	x	—	x	F	x	x	T	T	
<i>T. mystax</i>	—	x	x	x	—	x	T	x	x	T	T	
<i>T. kammalensis</i>	—	x	x	x	—	x	T	x	x	T	T	
<i>Thrissina baelama</i>	0	x	x	x	—	x	T	x	x	T	T	
<i>Lycothrissa crocodilus</i>	—	x	x	x	F	x	F	x	x	T	T	
<i>Stolephorus baccaneeri</i>	T	x	x	—	—	x	x ^e	x	x	T	T	
<i>S. heterolobus</i>	T	x	x	—	—	x	x ^e	x	x	T	T	
<i>S. purpureus</i>	T	x	x	—	—	x	x ^e	x	x	T	T	
<i>S. conamersonii</i>	T	x	x	x	—	x	—	x	x	T	T	
<i>S. indicus</i>	T	x	x	x	—	x	—	x	x	T	T	
<i>S. tri</i>	—	x	x	x	—	x	—	x	x	T	T	

TABLE 1—(Continued)

	H				BP				UP				
	1	2	3	4	1	2	3	4	1	2	3	4	5
<i>Setipinna breviceps</i>	—	x	x	x	x	x	x	F	x	x	x	T	T
<i>S. melanocheir</i>	—	—	x	x	F	F	x	F	x	x	x	T	T
<i>Engraulini</i>													
<i>Pterengraulis atherinoides</i>	—	x	x	x	F	x	x	x ^e	x	x	x	T	T
<i>Lycengraulis barbouri</i>	T	x	x	x	—	—	x	x ^e	x	x	x	T	T
<i>L. batesi</i>	T	x	x	x	—	—	x	x ^e	x	x	x	T	T
<i>L. grossidens</i>	T	x	x	x	—	—	x	x ^e	x	x	x	T	T
<i>L. olidus</i>	—	x	x	x	—	—	x	x ^e	x	x	x	T	T
<i>Anchoa arenicola</i>	T	x	x	x	—	—	x	x ^e	x	x	x	T	T
<i>A. compressa</i>	0	x	x	x	—	—	x	x ^e	x	x	x	T	T
<i>A. delicatissima</i>	0	x	x	x	—	—	x	x ^e	x	x	x	T	T
<i>A. eigenmannia</i>	0	x	x	x	—	—	x	x ^e	x	x	x	T	T
<i>A. panamensis</i>	0	x	x	x	—	—	x	x ^e	x	x	x	T	T
<i>A. spinifer</i>	0	x	x	x	—	—	x	x ^e	x	x	x	T	T
<i>A. cubana</i>	T	x	x	x	—	—	x	x ^e	x	x	x	T	T
<i>A. hepsetus</i>	T	x	x	x	—	—	x	x ^e	x	x	x	T	T
<i>A. lamprotaenia</i>	T	x	x	x	—	—	x	x ^e	x	x	x	T	T
<i>A. mitchilli</i>	0	x	x	x	—	—	x	x ^e	x	x	x	T	T
<i>Anchoiella elongata</i>	0	x	x	x	—	—	x	x ^e	x	x	x	T	T
<i>A. pallida</i>	0	x	x	x	—	—	x	x ^e	x	x	x	T	T
<i>A. balboae</i>	—	x	x	x	—	—	x	x ^e	x	x	x	T	T
<i>A. eurystole</i>	T	x	x	x	—	—	x	x ^e	x	x	x	T	T
<i>A. estanquae</i>	T	x	x	x	—	—	x	x ^e	x	x	x	T	T
<i>A. hubbsi</i>	T	x	x	x	—	—	x	x ^e	x	x	x	T	T

TABLE 1—(Continued)

	H	BP				LP	1	2	3	4	5	UP							
		1	2	3	4							1	2	3	4	5			
<i>Anchoa clupeioides</i>	—	x	x	x	—	x	—	—	—	—	—	—	—	—	—	—	—	—	T
<i>Engraulis japonicus</i>	T	x	x	x	—	x	x ^c	x	—	—	—	x	x	x	x	x	x	x	T
<i>E. mordax</i>	T	x	x	x	—	x	x ^c	x	—	—	—	x	x	x	x	x	x	x	T
<i>E. ringens</i>	0	x	x	x	—	x	x ^c	x	—	—	—	x	x	x	x	x	x	x	T
<i>E. encrasicolus</i>	—	x	x	—	—	x	x ^c	—	—	—	—	x	x	x	x	x	x	x	T
<i>Cetengraulis edentulus</i>	—	x	x	—	—	—	—	—	—	—	—	x	x	x	x	x	x	x	0
<i>C. mysticetus</i>	—	x	x	—	—	—	—	—	—	—	—	x	x	—	—	—	—	—	0
Pristigasteridae																			
<i>Pellona flavipinnis</i>	T	—	x	—	T	x	—	—	—	—	—	x	x	x	x	x	x	x	T
<i>Raconda russeliana</i>	T	—	x	—	—	x	—	—	—	—	—	x	x	x	x	x	x	x	T
<i>Ilisha elongata</i>	T	—	x	—	—	x	—	—	—	—	—	x	x	x	x	x	x	x	T
<i>Opisthopterus doyii</i>	T	—	x	—	—	x	—	—	—	—	—	x	x	x	x	x	x	x	T
<i>Pristigaster cayana</i>	T	—	x	—	—	x	—	—	—	—	—	x	x	x	x	x	x	x	T
<i>Pliosteostoma lutipinnis</i>	F	—	x	—	—	x	—	—	—	—	—	x	x	x	x	x	x	x	T
<i>Odontognathus panamensis</i>	T	—	x	—	—	x	—	—	—	—	—	x	x	x	x	x	x	x	T
<i>Chirocentrodon bleekeriaianus</i>	T	—	x	—	—	x	—	—	—	—	—	x	—	—	—	—	—	—	T
Clupeidae																			
Alosinae																			
<i>Caspialosa maeotica</i>	T	x	x	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	T
<i>Alosa chrysochloris</i>	T	—	x	x	—	x	—	—	—	—	—	—	—	—	—	—	—	—	T
<i>Ethmidium maculata</i>	T	—	—	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	T
<i>Brevoortia tyrannus</i>	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Clupeinae																			
<i>Clupea harengus</i>	T	—	x	—	—	x	—	—	—	—	—	x	x	x	x	x	x	x	T
<i>Sprattus fuegensis</i>	T	—	x	—	—	x	—	—	—	—	—	x	x	x	x	x	x	x	T

TABLE 1—(Continued)

	H					BP					LP					UP				
	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
<i>Ramogaster melanostoma</i>	T	—	—	—	—	—	x	—	—	—	x	—	—	—	—	—	x	x	—	—
<i>Herklotsichthys punctata</i>	T	—	—	—	—	—	x	—	—	—	x	—	—	—	—	—	—	x	R	T
<i>Spratrus sprattus</i>	0	0	—	—	—	—	—	—	—	—	x	—	—	—	—	—	—	—	R	T
<i>Clupeonella delicatula</i>	0	—	—	—	—	—	—	—	—	—	x	—	—	—	—	—	—	x	T	T
<i>Harengula pensacolae</i>	T	—	—	—	—	—	x	—	—	—	x	—	—	—	—	—	—	—	0	T
<i>Lile stotifera</i>	T	—	—	—	—	—	x	—	—	—	x	—	—	—	—	—	—	—	R	R
<i>Sardinella anchovia</i>	T	—	—	—	—	—	x	—	—	—	x	—	—	—	—	—	—	—	0	T
<i>Opisthonema libertate</i>	T	—	—	—	—	—	x	—	—	—	x	—	—	—	—	—	—	—	0	T
<i>Sardinops sagax</i>	0	—	—	—	—	—	—	—	—	—	x	—	—	—	—	—	—	—	0	T
<i>Sardina pilchardus</i>	T	—	—	—	—	—	—	—	—	—	x	—	—	—	—	—	—	—	0	T
<i>Rhinocardium serrata</i>	0	—	—	—	—	—	x	—	—	—	x	—	—	—	—	—	—	—	—	T
Dussumierinae																				
<i>Etrumeus teres</i>	T	T	—	—	—	—	—	T	—	—	x	—	—	—	—	—	x	x	T	T
<i>Dussumieria acuta</i>	T	x	—	—	—	—	x	T	—	—	x	—	—	—	—	—	x	x	T	T
<i>Jenkinsia lamprotaenia</i>	0	—	—	—	—	—	—	—	—	—	x	—	—	—	—	—	x	x	—	T
<i>Spratelloides delicatulus</i>	0	—	—	—	—	—	—	—	—	—	x	—	—	—	—	—	—	—	R	T
Pellonulinae																				
<i>Potamalosa richmondia</i>	T	—	—	—	—	—	x	—	—	—	x	—	—	—	—	—	x	x	T	T
<i>Corica soborna</i>	0	—	—	—	—	—	—	—	—	—	x	—	—	—	—	—	x	x	R	T
<i>Hyperlophus vittata</i>	T	—	—	—	—	—	x	—	—	—	x	—	—	—	—	—	—	—	R	T
<i>Escualosa thoracata</i>	T	—	—	—	—	—	x	—	—	—	x	—	—	—	—	—	—	—	—	T
<i>Ehirava madagascarenensis</i>	T	—	—	—	—	—	x	—	—	—	x	—	—	—	—	—	—	—	—	T
<i>Spratellomorpha bicanalis</i>	T	—	—	—	—	—	x	—	—	—	x	—	—	—	—	—	—	—	—	T
<i>Clupeoides borneensis</i>	T	—	—	—	—	—	x	—	—	—	x	—	—	—	—	—	—	—	—	T
<i>Gilchristella aestuarius</i>	T	—	—	—	—	—	—	—	—	—	x	—	—	—	—	—	—	—	R	T

TABLE 1—(Continued)

	H	BP				LP	UP						
		1	2	3	4		1	2	3	4	5		
<i>Odaxothrissa losera</i>	T	—	—	—	—	x	—	—	—	—	—	—	T
<i>Limnothrissa miodon</i>	T	—	—	—	—	x	—	—	—	—	—	—	T
<i>Pellonula vorax</i>	T	—	—	—	—	x	—	—	—	—	—	—	T
<i>Potamothrissa acutirostris</i>	0	—	—	—	—	x	—	—	—	—	—	—	T
<i>Stoilothrissa tanganicae</i>	0	—	—	—	—	x	—	—	—	—	—	—	T
<i>Poecilothrissa congica</i>	0	—	—	—	—	x	—	—	—	—	—	—	T
<i>Microthrissa royauxi</i>	0	—	—	—	—	x	—	—	—	—	—	—	T
Dorosomatinae													
<i>Hilsa kelee</i>	0	—	—	—	—	x	—	—	—	—	—	—	T
<i>Hilsa ilisha</i>	0	—	—	—	—	—	—	—	—	—	—	—	0
<i>Ethmalosa fimbriata</i>	0	—	—	—	—	—	—	—	—	—	—	—	0
<i>Gudusia chapra</i>	0	—	—	—	—	—	—	—	—	—	—	—	0
<i>Dorosoma cepedianum</i>	0	—	—	—	—	—	—	—	—	—	—	—	0
<i>Konosius punctatus</i>	0	—	—	—	—	—	—	—	—	—	—	—	0
<i>Clupanodon thrissa</i>	0	—	—	—	—	—	—	—	—	—	—	—	0
<i>Nematalosa nasus</i>	0	—	—	—	—	—	—	—	—	—	—	—	0
<i>Anodontostoma chacunda</i>	0	—	—	—	—	—	—	—	—	—	—	—	0
<i>Goniatalosa mammina</i>	0	—	—	—	—	—	—	—	—	—	—	—	0

^aBPH, tooth plate overlying basihyal; BP1-4, tooth plates overlying basibranchials 1-4; LP, tooth plates overlying fifth ceratobranchials; UP1-5, toothplates primitively supported by infrapharyngobranchials; F, tooth plate in several pieces; 0, toothless dermal plate; R, tooth plate represented by a few isolated teeth; T, independent tooth plate; T-T, tooth plate overlying basibranchials 1-2; x, tooth plate fused with supporting endoskeletal element; x^c, tooth plate fused with first epibranchial; —, tooth plate or teeth absent.

ever, the only dermal elements represented are the upper pharyngeal plates (UP4-5).

A summary of the dermal gill-arch elements of clupeoid fishes is given in table 1, and a summary of counts of their branchiostegal rays in table 2.

DISCUSSION

GILL-ARCH STRUCTURE

There is ample evidence that for the Gnathostomata as a whole the primitive condition consisted of a well-developed dermal skeleton associated with the visceral arches. Present evidence indicates unequivocally that this primitive skeleton was in the form of numerous, independent, toothed bones capable of growth. During the evolution of the gnathostomes there were at least two types of phyletic trends involving this dermal skeleton: (1) the consolidation of small, primitive elements to form large tooth plates in certain areas on the surface of some visceral arches, often with apparent fusion between primitively separate dermal elements, and between dermal elements and their endoskeletal supports; and (2) the reduction and eventual loss of teeth and toothed bones, either in certain areas or on the surface of the visceral arches generally.

The phyletic trends that characterized the early differentiation of the gnathostomes into their main groups apparently did not involve any notable reduction of the dermal gill-arch skeleton. At least a well-developed dermal skeleton, present in a near-primitive completeness, occurs on the gill arches of Recent Elasmobranchiomorpha such as *Chlamydoselachus*, of Sarcopterygii such as *Latimeria*, and of Actinopterygii such as *Elops*. During the origin or early differentiation of the teleostomes, consolidation apparently first resulted in paired tooth plates supported by the anterior part of the basibranchial series (i.e., by the "tongue"). Within the lineage leading to and including the teleosts these paired plates apparently fused together to form median ones, and the condition presumably present in the earliest teleosts included a median basihyal tooth plate, and behind it a larger, median tooth plate over basibranchials 1-3. In the earliest teleosts there probably was some consolidation of the dermal elements supported by the fifth ceratobranchials, and probably also those supported by some of the dorsal elements, particularly the infrapharyngobranchials and the anterior ends of the epibranchials. Such a condition, or one close to it, occurs in many Recent teleostean groups, including the Engraulidae, Chirocentridae, Pristigasteridae, and Clupeidae. At present there is no reasonable alternative to the conclusion that a well-developed dermal skeleton of such a form is a primitive feature of the Recent teleostean

TABLE 2
SUMMARY OF BRANCHIOSTEGAL RAYS FOR RECENT CLUPEIFORM FISHES

Ray Number	Species
Chirocentridae	
3 + 1 + 4	<i>Chirocentrus dorab</i>
Engraulidae	
Coilinae	
2 + 10	<i>Coilia mystus</i>
2 + 8	<i>Coilia macrognathus</i>
Engraulinae	
Stolephorini	
3 + 17	<i>Setipinna breviceps</i>
3 + 11	<i>Stolephorus indicus</i>
3 + 10	<i>Stolephorus commersonii</i>
2 + 12	<i>Setipinna melanochir</i>
2 + 11	<i>Stolephorus buccaneeri</i> , <i>S. heterolobus</i> , <i>Thryssa dussumieri</i> , <i>T. mystax</i> , <i>T. purava</i> , <i>T. spinidens</i> , <i>Lycotrissa crocodilus</i>
2 + 10	<i>Thrissina baelama</i> , <i>Thryssa grayi</i> , <i>T. malabarica</i>
2 + 9	<i>Thryssa kammalensis</i>
2 + 8	<i>Stolephorus tri</i>
Engraulini	
2 + 13	<i>Lycengraulis barbouri</i> , <i>L. grossidens</i>
2 + 12	<i>Anchoa arenicola</i> , <i>A. spinifer</i> , <i>Anchoviella estanquae</i> , <i>Engraulis encrasicolus</i> , <i>Lycengraulis batesi</i> , <i>L. olidus</i>
2 + 11	<i>Anchoa compressa</i> , <i>A. eigenmannia</i> , <i>A. hepsetus</i> , <i>A. lamprotaenia</i> , <i>A. panamensis</i> , <i>Anchovia clupeoides</i> , <i>Anchoviella elongata</i> , <i>A. eury- stole</i> , <i>A. hubbsi</i> , <i>Engraulis japonicus</i> , <i>E. mordax</i> , <i>E. ringens</i> , <i>Pterengraulis atherinoides</i>
2 + 10	<i>Anchoa cubana</i> , <i>A. delicatissima</i> , <i>A. mitchilli</i> , <i>Anchoviella pallida</i>
2 + 7	<i>Anchoviella balboae</i>
2 + 6	<i>Cetengraulis edentulus</i> , <i>C. mysticetus</i>
Pristigasteridae	
2 + 1 + 3	<i>Chirocentron bleekermanus</i> , <i>Ilisha indica</i> , <i>I. elongata</i> , <i>Odontognathus panamensis</i> , <i>Ophisthopterus dovii</i> , <i>Pellona flavipinnis</i> , <i>Pliosteostoma lutipinnis</i> , <i>Pristigaster cayana</i> , <i>Raconda russeliana</i>
Clupeidae	
Alosinae	
2 + 1 + 6	<i>Caspialosa maeotica</i>
2 + 1 + 5	<i>Alosa chrysochloris</i> , <i>A. fallax</i>
2 + 1 + 4	<i>Alosa aestivalis</i> , <i>A. pseudoharengus</i> , <i>A. sapidissima</i>
3 + 1 + 5	<i>Ethmidium maculata</i>
2 + 1 + 4	<i>Brevoortia guntheri</i> , <i>B. patronus</i> , <i>B. tyrannus</i>
Clupeinae	
3 + 1 + 3	<i>Ramnogaster melanostoma</i>
2 + 1 + 6	<i>Clupea harengus</i>
2 + 1 + 5	<i>Sprattus fuegensis</i>
2 + 1 + 4	<i>Sprattus sprattus</i> , <i>Sardina pilchardus</i> , <i>Sardinops sagax melanosticta</i>

TABLE 2 — (Continued)

Ray Number	Species
2 + 1 + 3	<i>Clupeonella delicatula</i> , <i>Harengula pensacolatae</i> , <i>Herklotsichthys punctata</i> , <i>Lile stotifera</i> , <i>Sardinella anchovia</i> , <i>S. aurita</i> , <i>S. brachysoma</i> , <i>Opis-</i> <i>thonema libertate</i>
2 + 1 + 2	<i>Lile platana</i>
1 + 2 + 2	<i>Rhinosardinia serrata</i>
Dussumieriinae	
5 + 11	<i>Dussumieria acuta</i>
4 + 11	<i>Etrumeus teres</i>
3 + 4	<i>Spratelloides delicatulus</i>
3 + 3	<i>Jenkinsia lamprotaenia</i>
Pellonulinae	
3 + 1 + 4	<i>Potamalosa richmondia</i>
2 + 1 + 4	<i>Ehivara madagascarensis</i> , <i>Gilchristella aestuarius</i> , <i>Limnothrissa miodon</i> , <i>Stolothrissa tanganicae</i>
2 + 1 + 3	<i>Laeviscutella decimpei</i> , <i>Odaxothrissa losera</i> , <i>Pellonula vorax</i> , <i>Pota-</i> <i>mothrissa acutirostris</i> , <i>Spratellomorpha bianalis</i>
2 + 1 + 2	<i>Clupeoides borneensis</i> , <i>Corica soborna</i> , <i>Escualosa thoracata</i> , <i>Micro-</i> <i>thrissa royauxi</i> , <i>Poecilothrissa congica</i>
1 + 1 + 2	<i>Hyperlophus vittata</i>
Dorosomatinae	
2 + 1 + 3	<i>Ethmalosa fimbriata</i> , <i>Hilsa ilisha</i> , <i>H. kelee</i> , <i>H. macrura</i> , <i>H. toli</i> , <i>Gudusia chapra</i> , <i>Dorosoma cepedianum</i> , <i>D. petenense</i> , <i>Konosirus punc-</i> <i>tatus</i>
1 + 2 + 3	<i>Clupanodon thrissa</i> , <i>Nematalosa nasus</i> , <i>N. horn</i>
1 + 2 + 2	<i>Anodontostoma chacunda</i> , <i>Gonialosa manminna</i>

fishes in which it occurs (Nelson, 1969, and references cited therein).

From this perspective it is possible to recognize, in various teleostean groups, trends of specialization involving the dermal skeleton of the gill arches (Nelson, 1966, 1967b, 1967c, 1968, 1969). This is possible also for the family Clupeidae (Nelson, 1967a), in which is apparent a repeated evolutionary tendency toward reduction of the dermal skeleton. Among clupeids this tendency is correlated with the adoption of microphagous habits and the elaboration of epibranchial organs (Nelson, 1967c; see also Hubbs, 1944, p. 301; R. V. Miller, 1969, pp. 308–309 and Bertmar and Strömberg, 1969, pp. 108–109, however, assume otherwise for reasons which the writer finds completely spurious [for a discussion of epibranchial organs from another standpoint, see Svetovidov and Skvorzowa, 1968]). Thus, the main advanced features of the gill arches of clupeiform fishes, and the groups characterized by these advanced features, can be summarized as follows (the structure and re-

relationships of *Denticeps* have been dealt with at length by Greenwood, 1968a, 1968b, and will not be reconsidered here):

Clupeoidei: (1) Development of a long medial process on the second and especially the third infrapharyngobranchials, with their juxtaposition in the dorsal midline. (2) Fusion of tooth plates with the second basibranchial. Chirocentroidea: ? Separation of the dorsal, paired elements of the gill arches.

Engrauloidea: (1) Reduction of the basihyal and loss of its ossification center. (2) Reduction and loss of the basihyal tooth plate. (3) Elongation of the second basibranchial. (4) Elongation of the dorsal parts of the gill arches. (5) Fusion of tooth plates with the first and third basibranchials.

Engraulidae

Coilinae: ? Separation of the dorsal, paired elements of the gill arches.

Engraulinae: A tendency toward fusion of tooth plates with the first epibranchials.

Pristigasteroidea: Fusion of tooth plates with the second hypobranchials, and sometimes with the first, third, or both first and third hypobranchials.

Clupeoidea: Tendencies toward loss of teeth, proliferation of gillrakers, and development of a mediopharyngobranchial cartilage and epibranchial organs.

Clupeidae

? Clupeinae (including the Dussumieriinae, Pellonulinae, and perhaps also the Alosinae, in part): A tendency, admittedly rare, toward development in the fourth epibranchial of a foramen accommodating the fourth efferent artery.

? Dorosomatinae (including the Alosinae, at least in part, and perhaps also the Clupeinae, in part): (1) Development of non-overlapping gillrakers. (2) Elongation of the dorsal parts of the gill arches. (3) Development of large epibranchial organs. (4) Expansion of the fifth ceratobranchials. (5) A tendency toward perforation of the fourth epibranchials.

CHIROCENTROIDEA: The gill arches of *Chirocentrus* have long medial processes on the second and third infrapharyngobranchials, and in this respect are very similar to those of clupeoids. The dorsal gill-arch elements of either side are separated from each other across the midline, a condition perhaps primitive, perhaps advanced, relative to that of other clupeoids. The gill arches of *Chirocentrus* in most respects are primitively organized with few if any advanced features of use in assessing the relationships between *Chirocentrus* and other clupeoids.

ENGRAULINAE: The trend toward consolidation of tooth plates supported by the first epibranchial is apparently shown in various species of the genus *Thryssa*. Thus, a relatively primitive condition is apparent in

Thryssa malabarica (Nelson, 1969, pl. 82, fig. 4; this figure erroneously is labeled *Pterengraulis atherinoides*), in which the tooth plates are small and numerous. A relatively advanced condition is apparent in *Thrissina baelama* (fig. 3C) and *Thryssa kammalensis* (fig. 3E), in which the tooth plates are large and few. *Thryssa dussumieri* (fig. 3D) appears even more advanced in having paired plates fused with the epibranchials, but the epibranchial tooth patches are rather small.

The condition of the epibranchial tooth plates of *Thrissina* is not very different from that in some species of *Stolephorus* (fig. 3F), except that the plates of *Stolephorus* are fused to the epibranchials. It is interesting that *Thrissina* in other respects, too, is "intermediate between *Stolephorus* and *Thryssa*" (Whitehead, 1965, p. 271). Indeed, the apparent tendency toward consolidation of epibranchial tooth plates might indicate that the closest relatives of *Stolephorus* are to be found within the *Thryssa-Thrissina* complex. But it is a curious fact that the species currently assigned to the genus *Stolephorus* either have very well-developed epibranchial tooth patches, or none at all (fig. 3G), as in *S. bataviensis*, *S. commersonii*, *S. indicus*, *S. macrops*, *S. tri* and possibly all other species of division II of Ronquillo's key to the species of the genus (in Whitehead, 1968a, pp. 16-17). Thus there is a possibility that the genus, as currently defined, is polyphyletic. If so, the relationships of the species of division II might have to be reassessed. But in this connection, the only other anchovies which show a similar reduction of the upper pharyngeal dentition are those of the genus *Cetengraulis* (fig. 4G), and in this genus tooth reduction is associated with the development of epibranchial organs, and for this reason is probably not comparable with that of *Stolephorus*, from which epibranchial organs are absent.

One genus of American engraulids (*Anchoa*, fig. 4D) characteristically has very well-developed epibranchial tooth patches, as impressive as those of some species of *Stolephorus*. But there is evidence of parallel development, for the tooth patches of *Anchoa spinifer* (fig. 4B) are smaller and probably more primitively organized than those of any other examined species of *Anchoa*. The tooth patches of *A. spinifer* are very similar to those of *Lycengraulis* and *Pterengraulis*. Indeed, all examined American engraulids, with the exception of *Cetengraulis*, have tooth plates fused with the first epibranchials (in *Cetengraulis* there is evidence of secondary reduction and loss of teeth). The possibility that all American engraulids, including the genus *Engraulis*, are interrelated among themselves is suggested by this character (see also Whitehead, Boeseman and Wheeler, 1966, p. 108; Whitehead, 1967, p. 136).

The much reduced dentition of *Cetengraulis* is very near that of some

species of *Engraulis* (figs. 4E, 4F) and *Achovia* (fig. 4H), in which there is also some tendency toward development of epibranchial organs (Nelson, 1967c). Thus, there is some gill-arch evidence to support a relationship between the species currently placed in these three genera. On the basis of other characters (e.g., the distinctive, and probably advanced, condition of the frontal fontanelles, Whitehead, 1967, p. 132) the closest relatives of *Cetengraulis* are probably to be found within the genus *Engraulis* rather than *Anchovia*. But clarification of the interrelationships of other American anchovies, particularly those currently placed in the genera *Anchovia* and *Anchoviella* (see e.g., Whitehead, 1964) is needed before a reasonably phyletic classification of these fishes can be attempted.

PRISTIGASTEROIDAE: The gill-arch characters of this group are perhaps as distinctive and as constant as any to be found among clupeiform fishes. The principal advanced character is the fusion of tooth plates with one or more pairs of hypobranchials, particularly the second hypobranchials (Nelson, 1967a, fig. 8). Gill arches of pristigasterids lack the advanced characters peculiar to the engraulids and clupeids, and in many ways are as primitively organized as those of *Chirocentrus*.¹ From this standpoint, therefore, the relationships of the pristigasterids within the Clupeoidei are relatively obscure. This fact is reason enough to give the pristigasterids the rank of a superfamily equivalent to the Chirocentroideae, Engrauloideae, and Clupeoideae, for the nearest relatives of the pristigasterids might be any one or a combination of any of these groups.

Pristigasterids traditionally have been classified with the clupeids, usually given the rank of a subfamily but sometimes that of a family (Greenwood, Rosen, Weitzman and Myers, 1966, p. 394). But no evidence has ever been presented that pristigasterids are not, for example, more closely related either to engraulids (see e.g., Jordan and Seale, 1926, p. 418) or to *Chirocentrus* (see e.g., Breder, 1942; cf. Bardack, 1965, p. 78) than to clupeids. How to classify the pristigasterids, of course,

¹ Both Svetovidov and Skvorzowa (1968) and Bertmar and Strömberg (1969) intimated that epibranchial organs occur in pristigasterids. Svetovidov and Skvorzowa (p. 186) referred to them as "weakly developed" and Bertmar and Strömberg (p. 108) as "vestigial." According to Nelson (1967c, table 1), they are absent from pristigasterids, but he stated (p. 84) that "it often is difficult, except in an arbitrary way, to decide whether epibranchial organs, when not well developed, are absent or present in a given fish." This conflict is due in part to arbitrarily different definitions of epibranchial organs, and in part to different interpretations of their phyletic development. Thus, this conflict is mainly subjective. Nevertheless, the writer would still maintain that well-developed epibranchial organs are primitively absent from pristigasterids, on the basis of what is known of the phyletic trends of the gill-arch dermal skeleton (see above).

will remain a matter of taste until their relatives can be ascertained and classified with them. At present, however, it is useful to exclude the pristigasterids from the family Clupeidae, for there is some evidence that the "remaining clupeids" themselves form a monophyletic group.

CLUPEOIDAE: The family Clupeidae heretofore has been treated generally as a "horizontal" grade-group defined on the basis of primitive characters (i.e., the lack of specializations peculiar to whatever other clupeoid families might be recognized, e.g., Chirocentridae, Engraulidae, and Dorosomatidae). To split off one or more of the usually recognized subfamilies might not in itself make the group remaining any more or less monophyletic. If the Pristigasteridae are split off from the Clupeidae, five clupeid subfamilies would remain: Alosinae, Clupeinae, Dorosomatinae, Dussumieriinae, and Pellonulinae. The splitting off of the Pristigasteridae would be justified only to the extent that the remaining five subfamilies can be shown to be more closely related to one another than to the Pristigasteridae. The evidence pertaining to these interrelationships admittedly is not overwhelming, but the following points can be added to those already mentioned: (1) the difficulty in separating the Pellonulinae from either the Clupeinae or the Dussumieriinae (Poll, Whitehead and Hopson, 1965; Whitehead, 1968b); (2) the probable interrelationship of all five subfamilies, as shown by the peculiar type of connection between the swimbladder and gut (Harder, 1957, 1958, 1960).

It is true that gut structure among clupeids is not well understood, but within the five subfamilies most species with feeding habits that can be considered generalized for the group have the ductus pneumaticus opening into the gut at the posterior end of a well-formed stomachic diverticulum, a condition that so far as known is unique among teleostean fishes. In other teleostean fishes, when the ductus pneumaticus persists into the adult stage, it usually joins the gut, at a relatively anterior position in the esophagus, close behind the pharyngeal-esophageal boundary (personal observ.). This anterior position of the ductus doubtless is primitive relative to its posterior position in clupeids.

Among clupeoids, a relatively primitive condition is retained in the Chirocentridae (personal observ.), Engraulidae and Pristigasteridae (Harder, 1958, 1960; personal observ.). A few clupeids (*Herklotsichthys*, *Dussumieria*) have what Harder (1960, fig. 31) shows as an intermediate condition, and those species (e.g., *Opisthonema*, *Dorosoma*) with microphagous habits have lost, presumably secondarily, the stomachic diverticulum. Considerable parallelism is likely if microphagous forms, such as *Opisthonema* and *Centengraulis* (fig. 6; Harder, 1960, fig. 31), are as

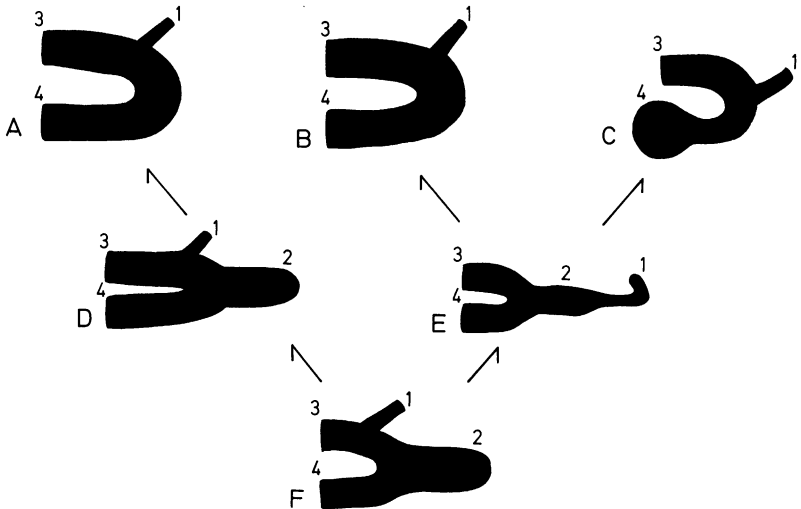


FIG. 6. Gut types and their possible phyletic trends (modified from Harder, 1960). A-C. Advanced types found in microphagous fishes such as *Cetengraulis* (A), *Opisthonema* (B), and *Dorosoma* (C). D, F. Primitive types found in carnivorous fishes such as most engraulids and pristigasterids. E. A possibly intermediate type characteristic of *Clupea* and its relatives.

Abbreviations: 1, ductus pneumaticus; 2, stomachic diverticulum (*Magenblindsack*); 3, esophagus; 4, pylorus.

similar in gut structure as Harder's diagrams would indicate. It is particularly interesting that the genus *Etrumeus* has the typical clupeid condition (Suyehiro, 1942, fig. 12; Harder, 1958, fig. 5D, pers. obs.), in view of the previous, and apparently erroneous, belief that in most respects this genus is a very primitive clupeid (Chapman, 1948; Whitehead, 1963; Nelson, 1967a).

If the condition of the ductus really is indicative of such interrelationships, the Pristigasteridae would emerge as an evolutionary lineage at least as old as the youngest of the other main groups of clupeoids: the Chirocentridae, Engraulidae, and Clupeidae. If the pristigasterids really represent one of four main lineages of clupeoids, particular phyletic trends within the group can be better evaluated. In particular, the absence of abdominal scutes in certain Recent clupeoids (e.g., *Etrumeus*, *Engraulis*) would more probably be a secondary rather than a primary condition.

The scute story is doubly complicated by the occurrence in some fossil and Recent clupeoids of dorsal as well as abdominal scutes. Tra-

ditionally, these fossil and Recent "double-armed herrings" have been thought by paleontologists to be somehow related (Woodward, 1901, p. 139; Schaeffer, 1947, p. 24). But both Regan (1917) and Nelson (1967a) considered the Recent forms to belong to two different, major groups of Recent clupeids (Pellonulinae and Alosinae). The fossil species concerned are those of the genera *Diplomystus*, *Knightia*, and *Gasteroclupea*, which in general body shape parallel very closely the Recent species of the Pristigasteridae. On this basis one might suppose that if the fossil diplomystids are related to one major group of Recent clupeoids, that group might be the Pristigasteridae. However, the fossil diplomystids that have recently been studied are so primitive in organization that their relationships within the Clupeioidi are very obscure. Thus the Cretaceous *D. brevissimus* is equipped with a basiptyergoid process, parasphenoid teeth, a well-developed dermosphenotic, and apparently no recessus lateralis (Patterson, 1967; Greenwood, personal commun.). But, interestingly, in the same material could be observed a basibranchial dentition very similar to that of the Recent pristigasterids (personal observ.), and a recessus lateralis has been observed in material of *Knightia* from the Eocene of the Green River (Greenwood, personal commun.). Certainly the evidence pertaining to the relationships of the fossil diplomystids is equivocal, but their possible relationship to the Pristigasteridae cannot be rejected.

With the Pristigasteridae excluded from the Clupeidae, the problem of subdividing this family is somewhat simplified. It must be admitted, however, that hyobranchial structure offers very little to the solution of this problem. At best, there are only two characters of possible value, both previously discussed elsewhere (Nelson, 1967a). One, seemingly trivial, is the foramen in the fourth epibranchial of *Etrumeus*, *Jenkinsia*, *Spratelloides*, *Clupea*, *Sprattus*, and *Potamalosa* (see also Nelson, 1967c, figs. 2(a), 2(b); Miller, 1969, fig. 4), genera usually classified in three different subfamilies (Dussumieriinae, Clupeinae, and Pellonulinae; it perhaps is no coincidence that some members of each subfamily have a reduced complement of abdominal scutes). The other character is the non-overlap of the gillrakers, first noted by Regan (1917), in fishes such as *Sardinella*, *Opisthonema*, *Hilsa*, *Dorosoma* and several other genera probably related to them. Both of these characters probably are advanced, as is now evident after examination of gill arches in engraulid and chirocentrid fishes. The gillraker character perhaps is the more significant because it occurs in all species commonly called "gizzard shads" as well as the "shads" (e.g., *Hilsa*) probably related to them.

To classify in different subfamilies fishes such as *Hilsa* and *Doro-*

soma cannot be maintained, as was evident long ago to Regan (1917). Accordingly, the genera *Hilsa*, *Gudusia*, and *Ethmalosa*, often placed in the Alosinae, are here transferred to the subfamily Dorosomatinae. The remaining alosines (*Alosa*, *Pomolobus*, *Brevoortia*, *Ethmidium*) might provisionally be kept in a separate subfamily Alosinae, but there is little

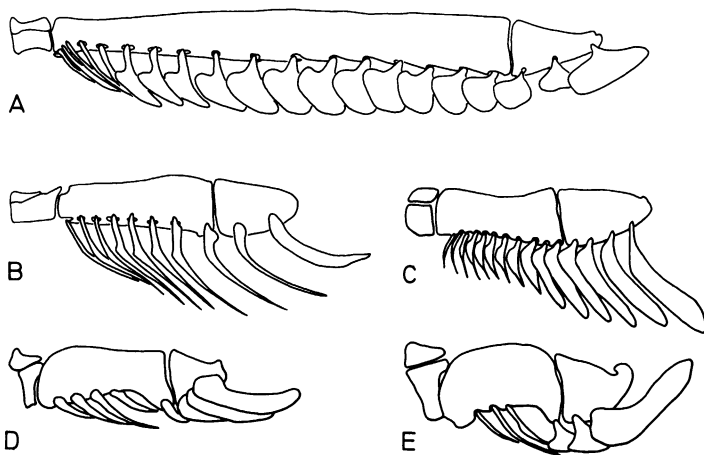


FIG. 7. Branchiostegal apparatus, lateral view of left side. A. *Setipinna breviceps*. B. *Coilia mystus*. C. *Etrumeus teres*. D. *Chirocentrus dorab*. E. *Ilisha indica*.

evidence that they themselves form a monophyletic group, and little indication of what the relationships of such a group might be, either with the Dorosomatinae as here conceived, or with one or more of the remaining subfamilies usually recognized: Clupeinae, Dussumieriinae, and Pellonulinae.

To the writer it seems a very real possibility that some genera currently classified with *Clupea* (e.g., *Sardinella*, *Opisthonema*, and possibly *Harengula* and *Herklotsichthys*) will eventually be shown to be related to the Dorosomatinae and classified with them. It seems possible also that other "clupeine" genera (e.g., *Sardina* and *Sardinops*) really are close relatives of *Alosa* and should be classified with that genus, and the entire group so formed allied either with the Dorosomatinae or with one or more of the other subfamilies. If so, there would be some reason to favor a basic subdivision of the Clupeidae into two groups, Clupeinae and Dorosomatinae, which might themselves be given the rank of families. But present evidence is not strong enough to warrant its thorough discussion, or to justify such a reclassification, which is stated here only

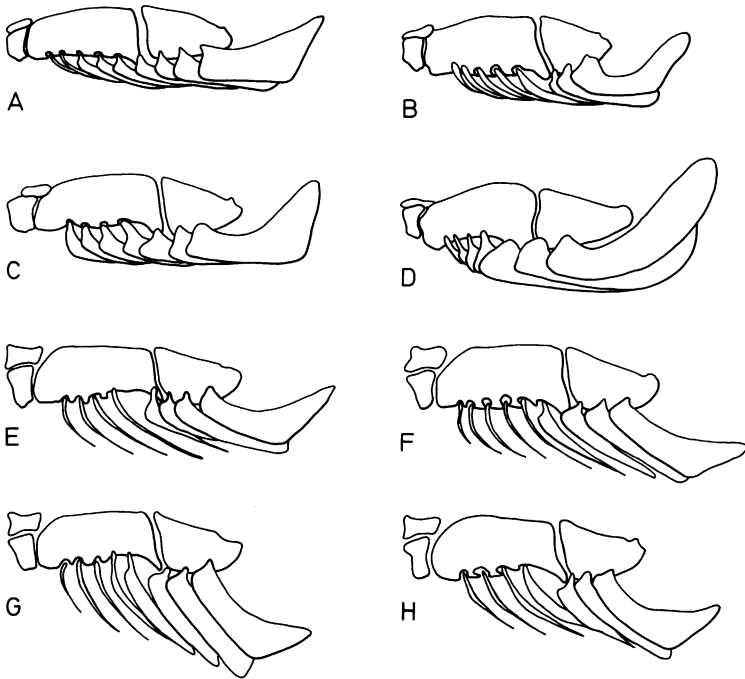


FIG. 8. Branchiostegal apparatus, lateral view of left side. A. *Ethmidium maculata*. B. *Alosa chrysochloris*. C. *Sardina pilchardus*. D. *Brevoortia tyrannus*. E-H. *Clupea harengus*.

as a working hypothesis (fig. 11).

BRANCHIOSTEGAL RAYS

The number of branchiostegal rays in clupeoids is variable: among engraulids the number usually is 11-15, but in the material at hand *Cetengraulis* has eight, and *Setipinna* (fig. 7A) as many as 20; among chirocentrids (fig. 7D), pristigasterids (fig. 7E) and clupeoids (figs. 7-9) the number usually is six to nine, but *Etrumeus* (fig. 7C) and *Dussumieria* have 15-16, and *Hyperlophus* has four.

On the basis of the distribution of ray counts and the probable relationships of Recent clupeoids, the number of rays in the earliest clupeoids probably was 10-15. If so, ray numbers have been both increased and decreased during the evolution of clupeoid fishes. Secondary increase in ray number is relatively rare, the only apparent example being the engraulid species *Setipinna breviceps*. Secondary decrease, in contrast,

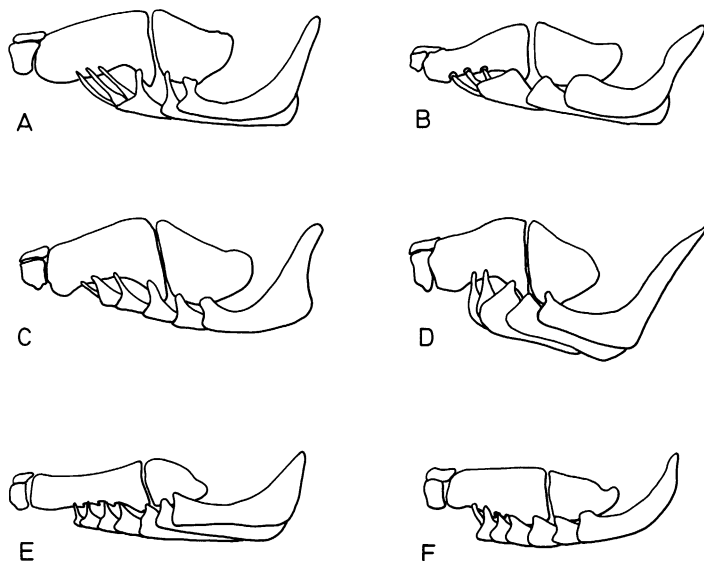


FIG. 9. Branchiostegal apparatus, lateral view of left side. A. *Dorosoma cepedianum*. B. *Hilsa ilisha*. C. *Konosirus punctatus*. D. *Anodontostoma chacunda*. E. *Limnothrissa miodon*. F. *Gilchristella aestuarius*.

is relatively common, apparently having occurred in all major lineages of clupeoids.

According to McAllister (personal commun.) loss of branchiostegal rays in teleostean fishes has generally taken place at the anterior end of the series, with the posterior rays shifting forward. From this standpoint, the most primitive condition in clupeoids would be that with the greatest total number of rays, or that with the greatest number of posterohyal rays. Most clupeoids have only two posterohyal rays, but some have three, and some (*Etrumeus*, *Dussumieria*) have four or five. Most clupeoids with two posterohyal rays have these two rays enlarged, and a third enlarged ray supported by a ventrally directed process of the anterohyal (figs. 7-9). Most engraulids have two posterohyal rays, with only the posterior ray enlarged (figs. 7B, 10; this enlarged ray has sometimes been identified as the subopercle, e.g., by Ridewood, 1905, fig. 135; perhaps, for this reason, this ray has been overlooked by other authors, e.g., Chapman, 1944, fig. 6, McAllister, 1968; Moona, 1968, fig. 6). Thus it is possible to suppose that the condition of the branchiostegals of early clupeoids was approximately that shown in *Etrumeus* (see also Whitehead, 1963), and that there has been a repeated tendency

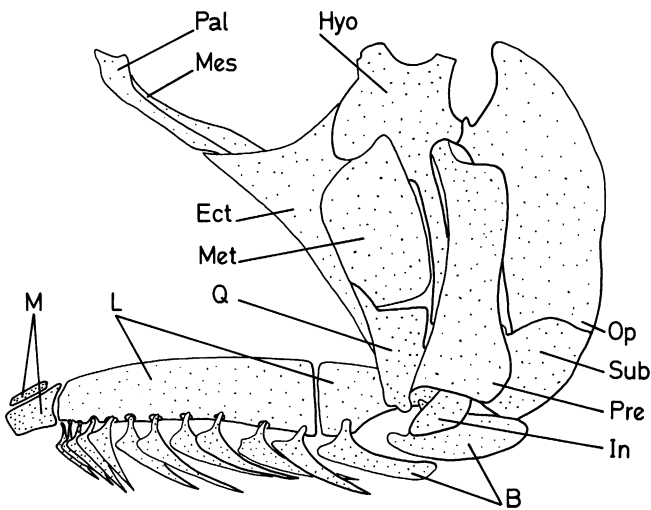
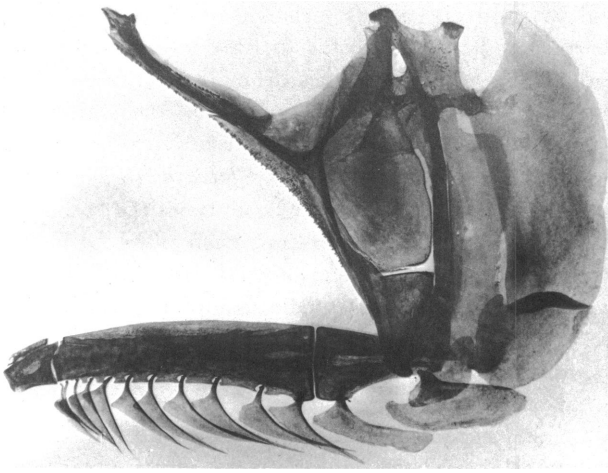


FIG. 10. Photograph and diagram of *Anchoa hepsetus*, some bones of the cheek, lateral view of left side.

Abbreviations: B, branchiostegal rays; Ect, Ectopterygoid; Hyo, hyomandibula; In, interopercle; L, lateral ossifications of the hyoid arch; M, medial ossifications of the hyoid arch; Mes, mesopterygoid; Met, metapterygoid; Op, opercle; Pal, palatine; Pre, preopercle; Q, quadrate; Sub, subopercle.

toward loss of rays, with anterior shifting of those remaining, a tendency toward development of a ventral process of the anterohyal, and a tendency toward enlargement and differentiation of one or more of the

posterohyal rays. In engraulids, pristigasterids, and many clupeids the number of posterohyal rays seems to have stabilized at two, but in a few clupeids the number sometimes drops to one.

In species with a relatively high number of branchiostegal rays, considerable variation in ray number and relative position might be expected. A sample of 106 specimens of *Clupea harengus* (Baltic Sea specimens) could be subdivided into four basic types (fig. 8E-H), with about 94 per cent of type G, and 2 per cent each of types E, F, and H. In all of these types, the four posterior rays are noticeably enlarged, regardless of their position, and can be assumed to be homologous on a one-to-one basis. If so, variation in ray number involves only the anterior rays, and among these, probably the addition or deletion of one or more small rays at the anterior end of the series.

Branchiostegal characters would seem to have little value in assessing the interrelationships of the major groups of clupeoids. Considerable parallelism involving reduction of rays and differentiation of the posterior rays is apparent. Only at lower taxonomic levels, has the branchiostegal apparatus been modified enough to be of much help in assessing relationships. Thus, e.g., the Indo-Pacific genera *Clupanodon*, *Nematalosa*, *Gonialosa*, and *Anodontostoma* are distinctive in having one of the large rays normally supported by the posterohyal shifted to the anterohyal, a condition unusual but not unique among clupeoids (for *Rhinosardinia*, see table 2). Such an anterior shift apparently led to the loss of an anterior ray in *Anodontostoma* (fig. 9D) and *Gonialosa*, which on this basis appear to be closely related to each other. It is interesting to note also that the genera *Hilsa* (fig. 9B), *Gudusia*, and *Ethmalosa* (as well as *Sardinella*, *Opisthonema*, *Harengula*, and *Herklotsichthys*) have the same, moderately advanced pattern of rays as *Dorosoma* (fig. 9A) and *Konosirus* (fig. 9C).

Counts of branchiostegals in fossil specimens are difficult to make accurately and little reliable information has so far been accumulated (McAllister, 1968). Here may be added counts for *Allothissops mesogaster* (7 + 12), *Leptolepis sprattiformis* (6 + 12), *Scombroclupea macrophthalmia* (? + 11), and *Diplomystus brevissimus* (3 + 1 + 5) from specimens P3367 (Jurassic, Solnhofen), P1897 (Jurassic, Solnhofen), P1979 (Cretaceous, Syria), and P1987 (Cretaceous, Syria) of the Swedish Museum of Natural History. A common character of all these genera is the presence in the anterohyal of a large foramen (the so-called "beryciform foramen" of McAllister, 1968, p. 6), which appears to be a feature primitive for many teleostean groups (Rosen and Patterson, 1969, pp. 408-409), but which apparently is absent from all Recent clupeoids.

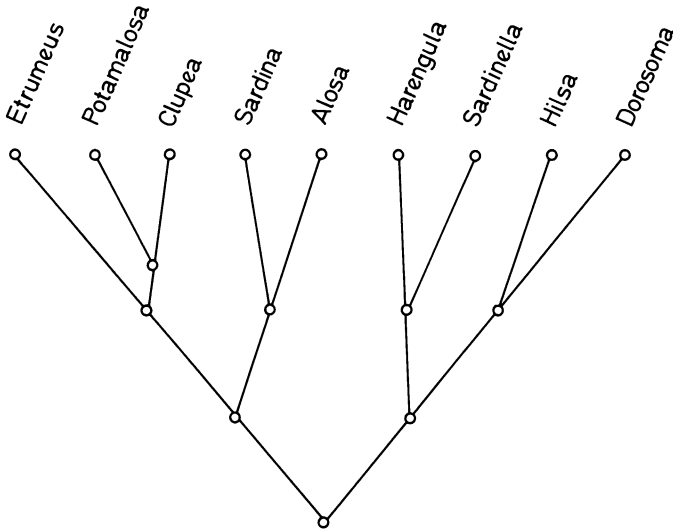


FIG. 11. One possible interpretation of the phyletic relationships of representative genera of clupeid fishes.

The high ray counts of the fossils, whatever their relationships, support the idea that early clupeoids also had high ray counts, and that a similar condition in *Etrumeus*, *Dussumieria*, and most engraulids might be primitive. It is interesting also that the Cretaceous *Diplomystus*, identifiable as a clupeomorph on the basis of its caudal skeleton (Patterson, 1967), has a pattern of branchiostegals not particularly primitive and very similar to that of many Recent clupeoids.

SUMMARY

This study completes a review of hyobranchial structure for Recent fishes of the order Clupeiformes. Its results support previously suggested phyletic trends involving reduction in number of branchiostegal rays, reduction and loss of gill-arch dentition, and elaboration of epibranchial organs within clupeiform fishes.

Certain advanced characters of the gill arches characterize some of the major groups of Clupeiformes. On this basis it has been possible to arrive at a more precise conception of the interrelationships of these major groups. One result has been the splitting off of the Pristigasteridae from the Clupeidae.

The problem of subdividing the families Engraulidae and Clupeidae is discussed from the standpoint of gill-arch structure.

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