

Gill Arches of Teleostean Fishes of the Order Anguilliformes^{1,2}

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THE GILL ARCHES of eels have required a broad, comparative study since Cope (1871) erected a separate order for the morays chiefly on the basis of their highly specialized gill arch skeleton. The work reported herein was undertaken to provide such a study, with the hope that it might contribute to the solution of some of the problems in eel systematics.

SOURCES OF MATERIAL AND ACKNOWLEDGMENTS

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METHODS AND MATERIALS

In general, the gill arches were removed as a unit from a given specimen, stained with alizarin in an aqueous solution of 2% potassium hydroxide, cleaned, and examined under a dissecting microscope. Drawings of the bones were executed freehand or, in some cases, with the aid of retouched photographs.

Specimens, usually young adults, of the following species were available for study:

Congridae: *Anago anago*, *Ariosoma bowersi*, *Conger marginatus*, *Congrina aequorea*, *Japanoconger sivicolus*

Heterocongridae: *Gorgasia punctata*, *Gorgasia* sp.

Derichthyidae: *Derichthys serpentinus*

Nettastomidae: *Metapomycter denticulatus*

Muraenesocidae: *Muraenesox cinereus*, *Oxyconger leptognathus*

Ophichthidae: *Ablia egmontis*, *Echelus myrus*, *Leptenchelys labialis*, *Muraenichthys cookei*, *M. gymnotus*, *M. laicaudata*, *M. macrop-terus*, *M. schultzei*, *Myrophis punctatus*, *M. uropterus*, *Neenchelys buitendijki*, *Schultzidia johnstonensis*, *Bascanichthys teres*, *Brachysomopsis henshawi*, *Caecula platyrhyncha*, *Callechelys melanotaenia*, *Cirrhimuraena macgregori*, *Leiuranus semicinctus*, *Letharchus velifer*, *Machaerenchelys phoenixensis*, *Myrichthys maculosus*, *Mystriophis intertinctus*, *Ophichthus polyophthalmus*, *Phyllophichthus xenodontus*

Synaphobranchidae: *Synaphobranchus affinis*

Simenchelidae: *Simenchelys parasiticus*

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- Dysommidae: *Dysomma anguillare*
 Anguillidae: *Anguilla rostrata*
 Heterenchelidae: *Heterenchelys biaggii*
 Moringuidae: *Moringua javanica*, *M. macrochir*
 Xencongridae: *Chilorhinus platyrhynchus*,
Chlopsis bicolor, *Kaupichthys brachyichirus*,
K. diodontus
 Dysomminidae: *Dysommina rugosa*
 Muraenidae: *Anarchias cantonensis*, *A. leucurus*,
Channomuraena vittata, *Uropterygius fuscoguttatus*,
U. knighti, *U. marmoratus*, *U. supraforatus*,
U. tigrinus, *U. xanthopterus*, *Echidna nebulosa*,
E. polyzona, *E. unicolor*, *Enchelycore nigricans*,
Enchelymassa canina, *Evenchelys macrurus*,
Gymnomuraena zebra, *Gymnothorax eurostus*,
G. javanicus, *G. meleagris*, *G. petelli*,
Muraena helena, *M. pardalis*,
Rabula fuscomaculata, *Strophidon brummeri*
 Serrivomeridae: *Serrivomer sector*
 Nemichthyidae: *Avocettina bowersi*, *Cyema atrum*,
Nemichthys scolopaceus

RESULTS

In all of the eels examined, with only one exception, the following bones of the gill arch skeleton are present: ceratobranchials and epi-branchials 1, 2, 3, 4 and the upper and lower pharyngeal tooth-bearing dermal bones. Pharyngobranchial 1 is absent without known exception. Other bones of the gill arch skeleton, either present or absent, are summarized in Table 1, for the species examined and others reported in the literature. Information on eel gill arches is present in the following papers: Asano (1962); Beebe (1935*a*, 1935*b*); Beebe and Crane (1936, 1937*a*, 1937*b*); Böhlke (1957); Castle (1961); Cope (1871, 1884); Gill (1890*a-e*); Gosline (1950, 1951*a*); Jang (1957); Jaquet (1920); Popta (1904); Regan (1912*b*); Takai (1959); Trewavas (1932).

DISCUSSION

Eel Lineages

Cope (1871, 1884) split the eels into two orders: one, the Colocephali, included only the morays; the other, the Enchelycephali, included the other eels. Cope apparently did not regard

these two orders as separate lineages. The morays he regarded simply as a specialized offshoot of a more generalized stock, of which the Anguillidae were examples (Cope, 1884: 584).

Cope's two groups were sometimes considered by later authors as orders (e.g., Herre, 1953), as suborders (e.g., Gill, 1890*a*; Jordan and Davis, 1892; Jordan and Evermann, 1896; Jordan and Snyder, 1901), or sometimes as groups without specific rank (e.g., Fowler, 1936).

Regan (1912*b*) did not discuss the matter of eel lineages as such, but in his key to the families he divided the eels into two groups, each including several families, depending on whether the frontal bones are fused or, alternatively, are separated by a suture. Subsequent authors have generally followed Regan, but further suggested that his two groups represent two primary evolutionary lineages within a single order (Gosline, 1951*a*:304-5; Asano, 1962:62).

It is not possible to divide the eels into two such groups on the basis of gill arch characters. Yet Regan's groups seem to this author to be natural ones and his division of the order is used here. It is possible, however, to subdivide one of Regan's groups, that characterized by fused frontal bones, on the basis of gill arch characters discussed below. Thus, in the material comprising this study three lineages are apparent:

1. Anguilloid: Anguillidae, Heterenchelidae, Serrivomeridae, Nemichthyidae(?), Moringuidae, Xencongridae, Dysomminidae, and Muraenidae.
2. Synaphobranchoid: Synaphobranchidae, Ilyophidae, Simenchelidae, and Dysommidae.
3. Congroid: Congridae, Heterocongridae, Nessorhamphidae, Nettastomidae, Derichthyidae, Ophichthidae, and Muraenesocidae.

During the history of each of these three lineages the gill arch skeleton seems to have been similarly modified. The modifications have involved: (1) progressive enlargement or progressive reduction with eventual loss of certain skeletal parts, (2) simplification in the form of the skeletal parts (loss of grooves and processes), (3) an anterior shift in position of the lower pharyngeal tooth plates, which gradu-

TABLE 1
SUMMARY OF THE GILL ARCHES IN 18 EEL FAMILIES¹

FAMILY AND GENUS	B1	B2	B3	B4	H1	H2	H3	C5	I2	I3	UP3	UP4
Congridae												
<i>Conger</i>	O	O	O	C	O	O	C	O	O	O	O	O
<i>Japanoconger</i>	O	O	O	C	O	O	C	O	O	O	O	O
<i>Anago</i>	O	O	O	C	O	O	C	O	O	O	-O-	O
<i>Ariosoma</i>	O	O	O	C	O	O	C	O	O	O	-O-	O
<i>Congrina</i>	O	O	O	C	O	O	C	O	O	O	-O-	O
Heterocongridae												
<i>Gorgasia</i>	O	O	O	C	O	O	C	O	O	O	-O-	O
* <i>Nystaticthys</i>	O	O	O	X	O	O	X	O	O	O	-O-	O
Derichthyidae												
<i>Derichthys</i>	O	O	O	C	O	O	C	O	O	O	O	O
Nettastomidae												
<i>Metapomycter</i>	O	O	-	C	O	O	C	O	O	O	O	O
Nessorhamphidae												
* <i>Nessorhamphus</i>	O	O	O	X	O	O	X	?	X	O	O	O
Muraenesocidae												
<i>Oxyconger</i>	O	O	O	C	O	O	C	O	O	O	O	O
<i>Muraenesox</i>	O	O	O	C	O	O	C	O	O	O	-O-	O
Synphobranchidae												
<i>Synphobranchus</i>	O	O	O	C	O	O	C	O	R	O	O	O
Simenchelidae												
<i>Simenchelys</i>	O	O	O	C	O	O	C	O	O	O	O	O
Dysommidae												
<i>Dysomma</i>	O	-	-	-	O	O	C	O	-	O	O	O
Ophichthidae												
<i>Echelus</i>	O	C	C	C	O	O	C	O	O	O	O	O
<i>M. punctatus</i>	O	R	-	-	O	O	C	-	O	O	O	O
<i>M. uropterus</i>	O	-	-	-	O	O	C*	-	O	O	O	O
<i>Ablia</i>	O	-	-	-	O	O	-	-	-	O	O	O
<i>Neenchelys</i>	R	-	-	-	O	O	C	-	O	O	O	O
<i>M. laticaudata</i>	-	-	-	-	O	O	C*	-	O	O	O	O
<i>M. cookei</i>	-	-	-	-	O	O	C*	-	C*	O	O	O
<i>M. gymnotus</i>	-	-	-	-	O	O	C*	-	-	O	O	O
<i>M. macropterus</i>	-	-	-	-	O	O	C	-	C*	O	-O-	O
<i>M. schultzei</i>	-	-	-	-	O	O	C*	-	-	O	-O-	O
<i>Schultzidia</i>	-	-	-	-	O	O	C	-	-	O	-O-	O
<i>Lepienchelys</i>	-	-	-	-	O	O	-	-	-	O*	-O-	O
<i>Ophichthus</i>	O	C	R	R	O	O	C	O*	O	O	O	O
<i>Mystriophis</i>	O	R	R	C	O	O	C	O	O	O	O	O
<i>Brachysomophis</i>	O	C	-	C	O	O	C	O	O	O	O	O
<i>Myrichthys</i>	O	C	R	C	O	O	C	O	O	O	O	O
<i>Bascanichthys</i>	O	C	-	C	O	O	C	O	O	O	O	O
<i>Letharchus</i>	O	C	-	R	O	O	C	-	O	O	O	O
<i>Cirrhimuraena</i>	O	C	R	R	O	O	C*	C	O	O	O	O
<i>Caecula</i>	O	-	-	C	O	O	C*	O	O	O	O	O
<i>Phyllophichthus</i>	O	R	R	-	O	O	C*	-	O	O	O	O
<i>Callechelys</i>	O	C	-	-	O	O	C	-	O	O	O	O
<i>Leiuranus</i>	O	C	-	C	O	O	C*	-	O	O	-O-	O
<i>Machaerenchelys</i>	O	C	-	-	O	O	C*	-	O	O	-O-	O

¹ Symbols used: O, ossified; O*, probably ossified and fused with dermal bone; -O-, UP3 and UP4 probably fused together; C, cartilaginous element; C*, cartilaginous process of cerato- or epibranchial; X, cartilaginous or absent; R, rudimentary; -, absent; ?, status unknown. Other symbols as in Figures 1 and 2.

* Not examined in the present study.

TABLE 1 (Continued)

FAMILY AND GENUS	B1	B2	B3	B4	H1	H2	H3	C5	I2	I3	UP3	UP4
Heterenchelidae												
<i>Heterenchelys</i>	O	O	C	C	O	O	C	O	O	O	O	O
Anguillidae												
<i>Anguilla</i>	O	O	-	C	O	O	C	O	O	O	O	O
Serrivomeridae												
<i>Serrivomer</i>	O	C	-	C	O	O	C	O	O	O	O	O
* <i>Platuronides</i>	O	X	X	X	O	O	X	?	O	O	-O-	
Nemichthyidae												
<i>Nemichthys</i>	O	-	-	-	O	O	C*	O	O	O	O	O
<i>Avocettina</i>	C	-	-	-	O	O	C*	O	C*	O	O	O
* <i>Labichthys</i>	X	X	X	X	O	O	X	?	X	O	O	O
* <i>Nematoprora</i>	X	X	X	X	X	X	X	?	?	?	O	O
<i>Cyema</i>	-	-	-	-	C*	C*	C*	-	-	-	-O-	
(<i>Cyema</i> lacks E1, E2, and E3. E4 is ossified.)												
Moringuidae												
<i>M. javanica</i>	C	R	-	-	O	O	C	O	O	O	O	O
<i>M. macrochir</i>	O	-	-	-	O	O	C	O	O	O	O	O
Xenocoelidae												
<i>Chlopsis</i> , etc.	-	-	-	-	O	O	-	O	O	O	O	O
<i>K. diodontus</i>	-	-	-	-	O	O	-	O	R	O	O	O
Dysommidae												
<i>Dysommia</i>	-	-	-	-	O	O	-	O	-	O	-O-	
Muraenidae												
<i>Anarchias</i> , etc.	-	-	-	-	O	O	-	-	-	O*	-O-	
<i>Echidna</i> , etc.	-	-	-	-	-	-	-	-	-	O*	-O-	

ally become supported by the fourth rather than the fifth ceratobranchials.

The tendency toward loss of elements has been so pronounced that it is possible within each lineage to separate primitive from advanced forms simply on the basis of the relative completeness of the gill arch skeleton, the primitive forms having more, the advanced, fewer skeletal elements (Table 1).

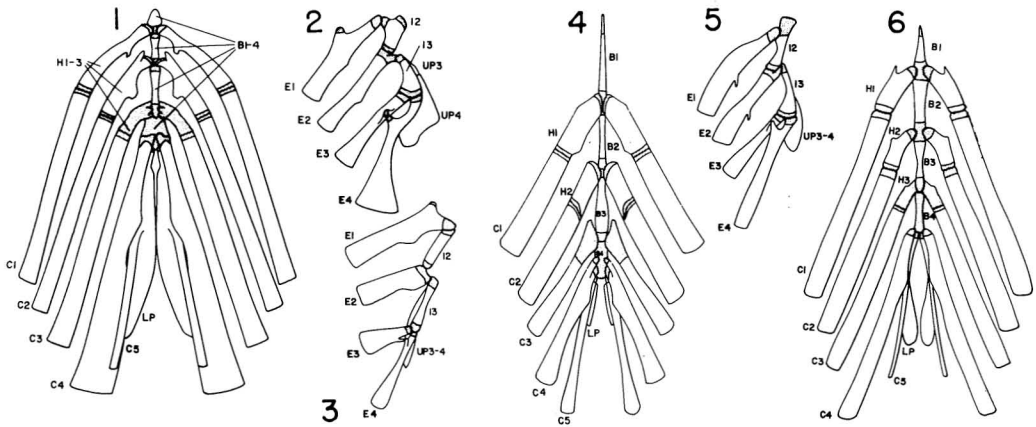
Congroid Lineage

A rather complete set of gill arches is present in most members of this lineage, except for the ophichthids. The arches of *Conger* (Figs. 1, 2) are perhaps the most generalized. Dorsally, epibranchial one (E1) bears an anterior, cartilage-capped process, presumably an articular surface for, or perhaps a rudiment of, pharyngobranchial one, which is not present as an independent skeletal element among eels. Pharyngobranchial two (I2) bears a cartilage-capped medial process, another primitive feature not generally present in eels.

The arches of *Muraenesox* are very similar to those of *Conger*. Those of *Gorgasia* (Figs. 3, 4), *Ariosoma* (Figs. 5, 6), *Japanoconger*, and *Anago* are hardly more specialized.

Most ophichthids are distinguished in having the proximal ends of the dorsal parts of the first and second arches connected through a continuous cartilage, a peculiarity not present in any other of the eel families studied. Among generalized ophichthines might be placed those eels with a reasonably developed series of basibranchials and an ossified fifth ceratobranchial (C5), namely *Bascanichthys*, *Mystriophis*, *Brachysomophis*, *Ophichthus*, and *Myrichthys*. Even in these forms, however, the basibranchials are somewhat reduced (Table 1), and C5 is in various stages of reduction.

Bascanichthys (Fig. 7) retains one primitive feature not found in the other genera examined, the double articulation of C4 with basibranchial four (B4). In this genus C5 seems reduced to a minute ossicle on the posterior edge of the lower pharyngeal tooth plates.



FIGS. 1-6. 1, *Conger marginatus*, gill arch skeleton, ventral view. B1-4, basibranchials; H1-3, hypobranchials; C1-5, ceratobranchials; LP, lower pharyngeal dermal tooth plates. Cartilage stippled. Articular cartilages at distal tips of ceratobranchials not shown. 2, *Conger marginatus*, dorsal view. E1-4, epibranchials; I,2-3, (infra)pharygobranchials; UP3-4, upper pharyngeal dermal tooth plates. Articular cartilages at distal tips of epibranchials not shown. 3 and 4, *Gorgasia* sp. 5 and 6, *Ariosoma bowersi*.

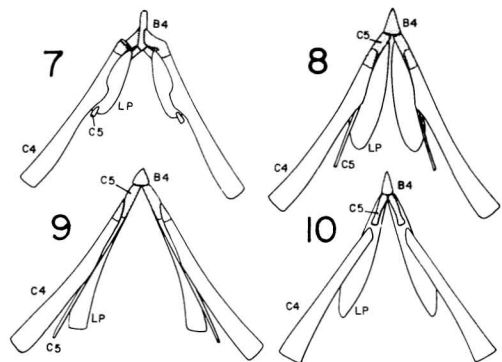
In *Mystriophis* and *Brachysomophis* (Fig. 9) C4 has lost its double articulation with B4, but C5 is prominent. C4, however, is without any direct articulation with B4, being supported entirely by C5, which retains a firm articulation with B4. From this condition may have been derived that of *Myrichthys* (Fig. 8) and *Ophichthus* (Fig. 10). *Cirrhimuraena* and *Myrichthys* are alike in having the proximal portion of C5 cartilaginous, situated between C4 and B4, the distal portion extending posteriorly as a thin filament of cartilage (*Cirrhimuraena*) or bone (*Myrichthys*). In *Letharcus*, C5 is present proximally as a small cartilage between C4 and B4, but seems entirely absent distally. Reduction of C5 has proceeded somewhat differently in *Ophichthus* (Fig. 10). C4 is without a proximal articular cartilage, being supported entirely by the lower pharyngeal tooth plates, which it seems have surrounded and fused with C5, leaving only the intermediate cartilaginous portion of C5 as evidence of the fact.

The only other ophichthine examined having an ossified C5 is *Caecula* (Figs. 11, 20). In this form C4 has retained its primitive connection with B4, but not a double articulation as in *Bascanichthys*.

Gill arch structure in *Phyllophichthus*, *Callichelys*, and *Machaerenchelys* is about that shown

for *Leiuranus* (Figs. 17, 18). C5 is lost altogether, perhaps fused with the tooth plate or with C4.

Relationships between the genera examined here have never been established. Gill arch structures, however, suggest certain relationships. One lineage may perhaps be represented by those forms having C4 not articulating with B4, but being supported by C5, including *Mystriophis*-*Brachysomophis*-*Ophichthus*, with *Myrichthys*, *Cirrhimuraena*-*Letharcus* branch-



FIGS. 7-10. 7, *Bascanichthys teres*, posterior portion of gill arch skeleton, ventral view. Ventral articulation of C4 with B4 not shown on right side, where a portion of cartilage is omitted to show dorsal articulation. 8, *Myrichthys maculosus*. 9, *Brachysomophis henshawi*. 10, *Ophichthus polyophthalmus*.

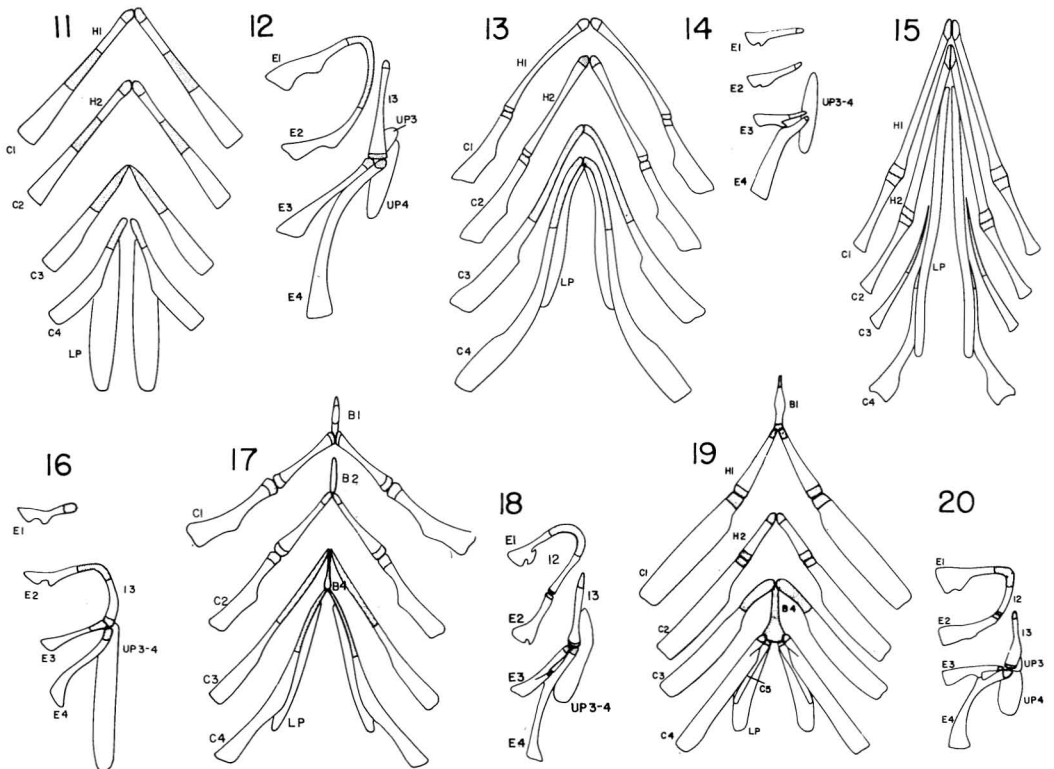
ing off early in its history. Another lineage may be represented by those forms having C4 contacting B4, including *Caecula* and *Bascanichthys*. The remaining genera, *Leiuranus* *Phyllophichthys*, *Machaerembelys*, and *Callechelys* are generally similar and have no trace of C5. Whether they might be more closely related to one or the other of the groups suggested above cannot therefore be commented on.

Among most members of the subfamily Echelinae the gill arch skeleton is severely reduced and approaches the form characterizing the muraenids. *Echelus*, however, is a notable exception, for its gill arch skeleton is perhaps the most generalized of any of the ophichthids examined (Table 1).

Among echeline eels there is a tendency for the lower pharyngeal tooth plates to be somewhat anteriorly displaced in the more specialized forms. In *Echelus* they occupy a position similar to that of the tooth plates of *Conger*

and are supported by C5. *Schultzidia* (Figs. 11, 16) has the tooth plates posterior in position, supported by C4. *Muraenichthys cookei* (Figs. 12, 13) has them more forward and *M. laticaudata* still more so. In *Ablia* and *Leptenchelys* (Figs. 14, 15) the tooth plates are very elongate, far forward in position, separating the ventral parts of the third arch on either side. In their high degree of specialization *Ablia* and *Leptenchelys* bear some resemblance to the group characterized by *Uropterygius* of the Muraenidae (Table 1, Fig. 41).

There has been continuing discussion of intergeneric relationships between echeline eels, much of which has concerned the limits of the genera *Myrophis* and *Muraenichthys* (Parr, 1930; Myers and Storey, 1939; Myers and Wade, 1941; Wade, 1946; Schultz and Woods, 1949; Gosline, 1950, 1951a, 1951b; Schultz, 1953; Böhlke, 1956, 1960; Nelson, 1966). On the basis of gill arch characters the relationships



FIGS. 11-20. 11, 16, *Schultzidia johnstonensis*. 12 and 13, *Muraenichthys cookei*. 14 and 15, *Leptenchelys labialis*. 17 and 18, *Leiuranus semicinctus*. 19 and 20, *Caecula platyrhyncha*.

between the species examined may be depicted by the rather linear reduction in gill arch elements (Table 1), with *Echelus* being the most primitive form and *Leptenchelys* the most advanced. In view of the variability exhibited in gill arch structure, a supplementary study was made on the sensory canal pores of the following material, mainly from the University of Hawaii collections:

Ablia egmontis, 2 specimens, 103, 235 mm, Puerto Rico; *Myrophis punctatus*, 3, 127–139 mm, Texas Coast; *M. uropterus*, 1, 82 mm, Palmyra; *Muraenichthys cookei*, 1 Oahu, 4 Johnston, 128–225 mm; *M. macropterus*, 1 Hull, 3 Makatea, 102–200 mm; *M. gymnotus*, 1 Aitutaki, 1 Eniwetok, 1 Johnston, 1 Rarotonga, 4 Tahiti, 84–136 mm; *M. laticaudata*, 1 Aitutaki, 1 Bikini, 1 Eniwetok, 2 Onotoa, 1 Rongelap, 2 Tonga, 92–139 mm; *M. schultzei*, 1 Arno, 1 Guadalcanal, 3 Johnston, 1 Papeete, 53–120 mm; *Leptenchelys labialis*, 1 Eniwetok, 5 Johnston, 122–136 mm; *Schultzidia johnstonensis*, 2 Johnston, 1 Midway, 2 Oahu, 84–163 mm.

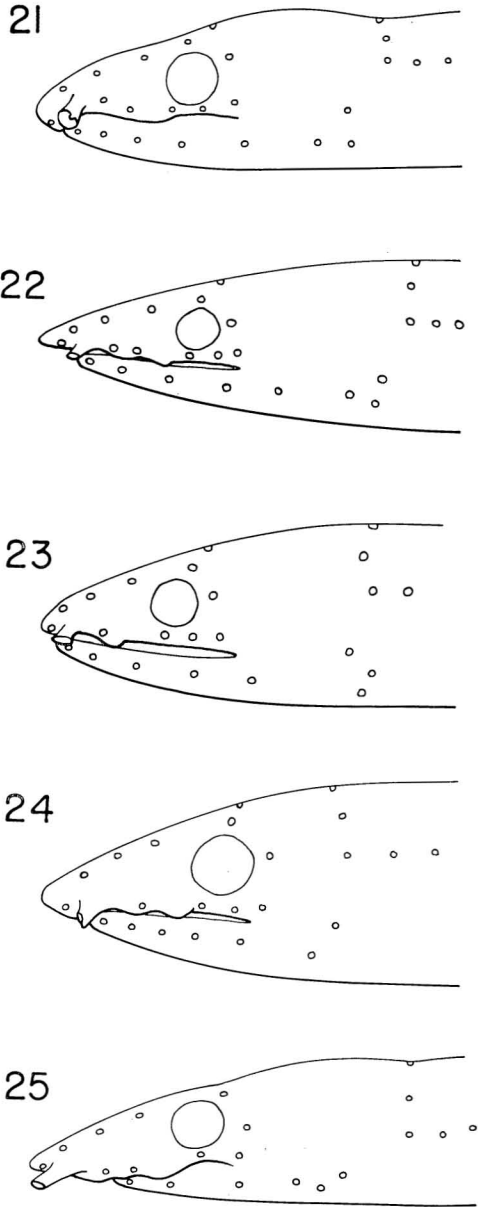
The number and pattern of sensory pores of the head exhibited great stability in specimens of the some species, sometimes being distinctive enough to permit identification on this basis alone.

The pattern of cephalic pores basic to the group is probably that shown in *Myrophis punctatus*, *M. uropterus*, *Ablia egmontis*, *Muraenichthys cookei*, *M. laticaudata*, *M. macropterus* (Fig. 21), and *Pseudomyrophis nimius* (Böhlke, 1960:2–4, fig. 1). The pattern in *Echelus* apparently is secondarily simplified (Allis, 1903; Gosline, 1952), as seems to be that also of *Hesperomyrus* (Myers and Storey, 1939).

The pores of the head are easily divided into groups (paired unless otherwise indicated): a supraorbital group of five pores, beginning with the one on the underside of the snout; a median interorbital pore; a postorbital pore; three pores below the eye; two between the nostrils; five in a row along the lower jaw; three over the preopercle, forming an angle of about 90 degrees; a series of five across the

nape, including the anteriormost pore of the lateral line on either side.

The supraorbital pores, including probably those on the underside of the snout (Allis,



FIGS. 21–25. 21, *Muraenichthys cookei*, sensory pores of the head and anterior trunk. 22, *M. gymnotus*. 23, *M. schultzei*. 24, *Schultzidia johnstonensis*. 25, *Leptenchelys labialis*.

1903), mark the course of the supraorbital canal. The interorbital pore arises from an interorbital commissure by way of a median dorsal opening in the frontal bones. The postorbital pore, those pores below the eye, and those between the nostrils mark the course of the infraorbital canal. Those on the lower jaw and over the preopercle mark the course of the preoperculo-mandibular canal.

M. gymnotus (Fig. 22) is close to the basic pattern, differing only slightly in the position of a few pores. The three below the eye are somewhat posteriorly displaced. The three over the preopercle form an angle perhaps a little less than 90 degrees.

M. schultzei (Fig. 23) diverges more significantly, having the nostrils close together and only a single pore between them. The three pores over the preopercle form an angle considerably greater than 90 degrees.

Schultzidia johnstonensis (Fig. 24) likewise has a single pore between the nostrils. There are but two pores over the preopercle.

Leptenchelys labialis (Fig. 25) has the pore system the most reduced, lacking the median interorbital pore, one of the three below the eye, two of the usual five along the lower jaw. The three over the preopercle form an angle greater than 90 degrees. The pattern of *L. labialis* seems similar to that of *L. pinnaceps* (Schultz, 1953: Fig. 16), but both of these differ markedly from that of *L. vermiformis* (Myers and Wade, 1941: Pl. 10), which has a greater number of pores behind the eye and along the lower jaw. In this regard, it has recently been discovered that the Central Pacific eels described in the genus *Leptenchelys* by Schultz (1953) are probably not congeneric with *Leptenchelys vermiformis* Myers and Wade, the type of the genus (Rosenblatt, personal communication).

Neenchelys buitendijki (Nelson, 1966: Fig. 1A) has only two of the usual three pores over the preopercle. The series along the lower jaw number seven–eight, instead of five. The other pores have the same basic arrangement as in *M. cookei*.

In all the specimens examined the only variability in pore number and position occurred in the pores of the lower jaw. The specimen of *S.*

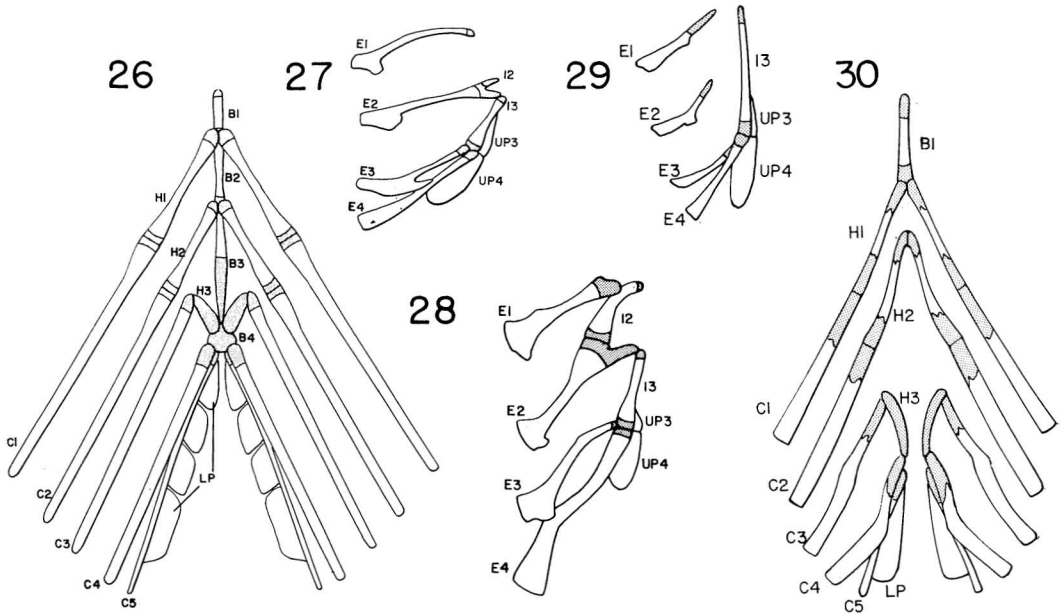
johnstonensis from Johnston Island has six pores on each side. The specimen of *M. laticaudata* from Aitutaki has six on the right side and five on the left.

Abliia, *M. schultzei*, and *Schultzidia* have lateral line pores generally restricted to the trunk, numbering about 40–70. In all other species examined lateral line pores number nearly or over 100 and extend well onto the tail.

The present author agrees with Schultz (1953:61) "that recognition of echelid genera must be done on a world-wide basis and not on the study of local fauna." However, on the basis of this study, *Echelus*, *Myrophis*, *Abliia*, *Muraenichthys*, *Neenchelys*, *Leptenchelys*, and *Schultzidia* might be considered valid genera. *Abliia* seems distinct from *Myrophis* on the basis of gill arch characters. It differs in gill arch structure also from *M. schultzei* and *Schultzidia*, although in all three the dorsal origin is posterior to the anus and lateral line pores are generally absent from the tail. Within the genus *Muraenichthys*, *M. cookei*, *M. laticaudata*, and *M. macropterus* seem quite similar and may be representatives of a generalized stock having given rise to separate offshoots in *M. schultzei* and *M. gymnotus*. *M. schultzei* and *Schultzidia* share some characters as noted above. The specialized jaws and teeth (Gosline, 1951a) and distinctive pharyngeal tooth plates (Figs. 11, 16) of *Schultzidia* would seem to rule out any close relationship with *M. schultzei*. *Leptenchelys* shows no great similarity with any of the other species examined. Its gill arches are perhaps most similar to those of *Abliia*, but the tendency toward forward displacement of the lower pharyngeal tooth plates is also quite pronounced in *M. laticaudata*.

Synphobranchoid Lineage

It is possible to separate *Synphobranchus* (Figs. 26, 27), *Diastobranchus* (Castle, personal communication), *Simenchelys* (Fig. 28; see Jaquet (1920) for ventral view), and *Dysomma* (Figs. 29, 30) from other eels on the basis of the posteriorly directed third hypobranchials. This is in contrast to the condition observed in other eels and bony fishes generally,



FIGS. 26-30. 26 and 27, *Synaphobranchus affinis*. 28, *Simenchelys parasiticus*. 29 and 30, *Dysomma anguillare*.

in which the hypobranchials are characteristically anteriorly directed. The gill skeleton of *Simenchelys* is the most generalized in terms of the number of elements (Table 1), yet that of *Synaphobranchus* has the lower tooth plates in four pairs. Other such multiple tooth plates occur in such lower teleosts as *Osteoglossum*, *Hiodon*, *Elops*, and *Albula*, but not generally in other teleosts nor in the other eels examined. In *Conger*, however, the lower tooth plates are initially in two pairs which later fuse together and with C5 during ontogeny to form a single pair (personal observations). The multiple tooth plates of *Synaphobranchus*, therefore, seem to be primitive features and are evidence against the derivation of *Synaphobranchus* from such a form as *Conger*. For this reason it seems appropriate to consider the synaphobranchoid lineage as possibly equivalent to the other two, the congroid and the anguilloid.

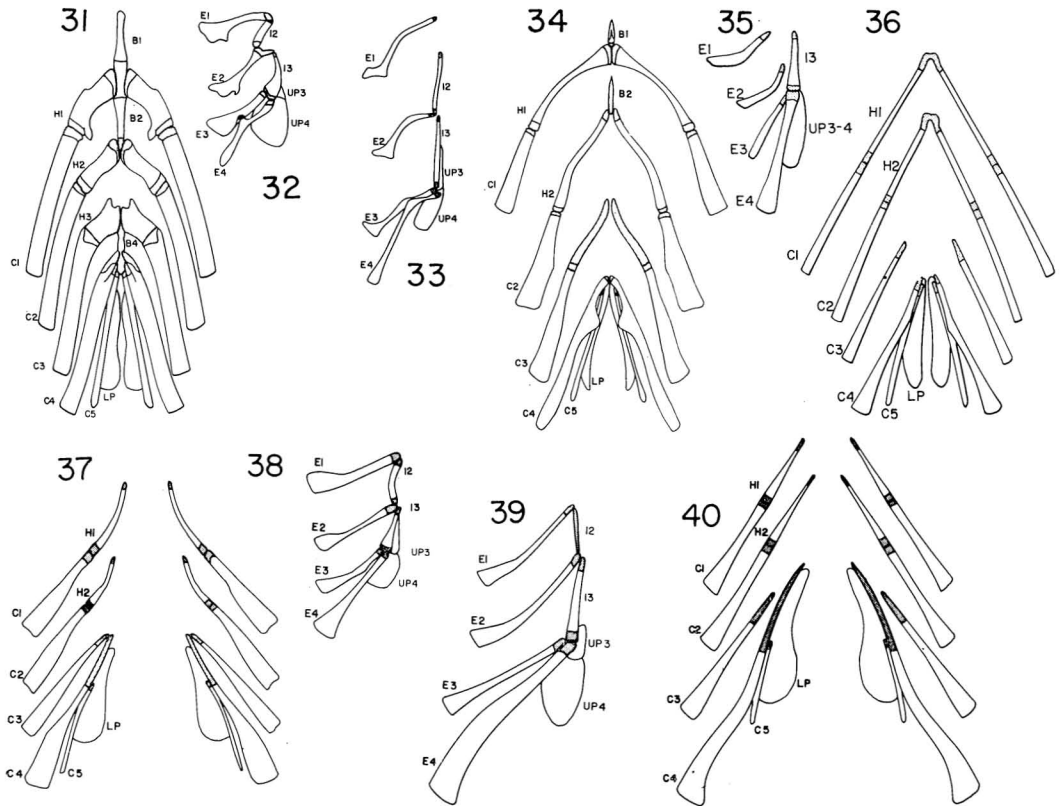
Specimens of *Ilyophis* have not been available for study. The genus is included in this lineage primarily on the evidence of Castle (1964), who included *Ilyophis* in the family Synaphobranchidae.

Anguilloid Lineage

The arches of *Heterenchelys* and *Anguilla* (Figs. 31, 32) are quite similar and are the most generalized. All of the skeletal elements found in eels are present in *Heterenchelys*, while *Anguilla* lacks only B3 (Table 1). According to Norman (1926) even this element occurs in cartilaginous form in the embryo.

The arches of *Heterenchelys* are much nearer those of *Anguilla* than those of *Moringua* (Figs 33, 34), which has them noticeably reduced, basibranchials being either rudimentary or absent. Dorsally, I2 has lost its usual connection with the proximal end of E1. Gill arch characters, therefore, suggest that *Heterenchelys* is more closely related to *Anguilla* than to *Moringua* (cf, Regan, 1912a:32).

The xenocongrids, *Dysommima*, and the muraenids are alike in having lost the entire basibranchial series. While the hypobranchials of either side retain midventral connections in *Dysommima* (Fig. 36), they are without such connections in the xenocongrids (Figs. 37-40) and muraenids (Figs. 41, 42). Among xenocongrids and *Dysommima*, C5 is present and ossi-



FIGS. 31-40. 31 and 32, *Anguilla rostrata*. 33 and 34, *Moringua javanica*. 35 and 36, *Dysommima rugosa*. 37 and 38, *Chilorbinus platyrhynchus*. 39 and 40, *Kaupichthys diodontus*.

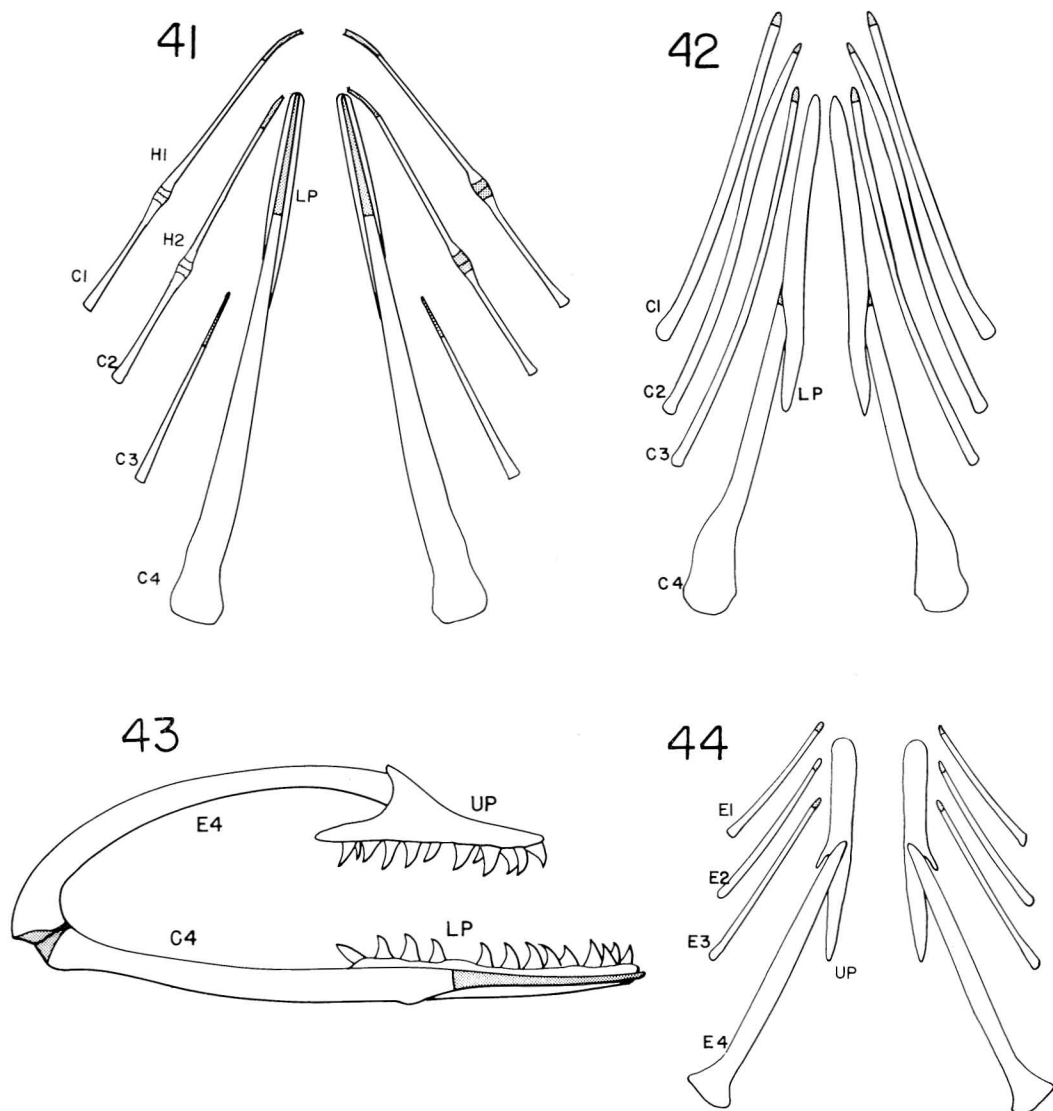
fied, although reduced in *Kaupichthys*. Among muraenids it is lost as an independent element.

Dorsally, the skeleton is complete in terms of number of elements in *Heterenchelys*, *Anguilla*, *Moringua*, *Chilorbinus*, *Chlopsis*, and *Kaupichthys brachybirus*. I2 is rudimentary in *K. diodontus* (Fig. 39) and absent altogether in *Dysommima* (Fig. 35) and the muraenids (Fig. 44). In *Dysommima* there is but a single upper tooth plate, probably representing a fusion of the two present in more generalized forms. In the muraenids the tooth plate is likewise single and apparently has fused with I3.

On the basis of gill arch characters, the xenocongrids, *Dysommima*, and the muraenids resemble one another more than they do other members of the lineage to which they presumably belong. *Dysommima* in this regard resembles the xenocongrids in having C5 well

developed and the lower pharyngeal tooth plates rather small and posterior in position, with small conical teeth in numerous rows. It is more generalized in having the hypobranchials interconnected, but more specialized in having lost I2 altogether and having the upper pharyngeal tooth plates in a single pair, as in the muraenids. For these reasons the arches of *Dysommima* seem intermediate in structure between those of the xenocongrids and muraenids (cf. Ginsburg, 1951; Böhlke and Hubbs, 1951).

Within the Muraenidae two structural types are apparent: one (Fig. 41), including only *Uropterygius*, *Anarchias*, and *Channomuraena*, has independent hypobranchials in the first and second arches. The lower pharyngeal tooth plates lie generally on the dorsal surface of the proximal end of C4. The other type (Fig. 42),



FIGS. 41-44. 41, *Uropterygius knightii*. 42, *Gymnothorax petelli*. 43, *G. petelli*, pharyngeal jaws of right side, lateral view. 44, *G. petelli*, dorsal view.

including *Muraena*, *Echidna*, *Gymnothorax*, and the remaining genera examined, are somewhat more specialized in gill arch structure, having lost all hypobranchials. The lower tooth plates tend to lie on the medial surface of the proximal end of C4, which fits into a prominent groove in the plate. These two groups may be considered as distinct subfamilies within the family Muraenidae.

UROPTERYGIINAE new subfamily

Ossified hypobranchials in first and second arches; lower pharyngeal tooth plates without a lateral groove; retractor ossium pharyngealium muscles without an attachment to the vertebral column; anterior portion of dorsal aorta usually enclosed in a canal formed by vertebral processes; vertical fins reduced, with rays confined to the posterior part of the tail.

Genera examined: *Uropterygius*, *Anarchias*, *Channomuraena*.

Subfamily MURAENINAE

No ossified hypobranchials in branchial skeleton; lower pharyngeal tooth plates with a prominent lateral groove; retractor ossium pharyngealium muscles with an attachment to the vertebral column; anterior portion of dorsal aorta not enclosed in a canal formed by vertebral processes; vertical fins not reduced, with rays confined to the posterior part of the tail.

Genera examined: *Echidna*, *Enchelycore*, *Enchelynassa*, *Evenchelys*, *Gymnomuraena*, *Gymnotborax*, *Muraena*, *Rabula*, *Strophidon*.

The outstanding feature of the gill arch skeleton of the muraenids is the enlargement of the fourth arch and with the loss of C5 the tooth-bearing bones it comes to support. Teeth on these bones are enlarged, recurved, and generally in two rows (Popta, 1904). These elements form the so-called pharyngeal jaws (Fig. 43).

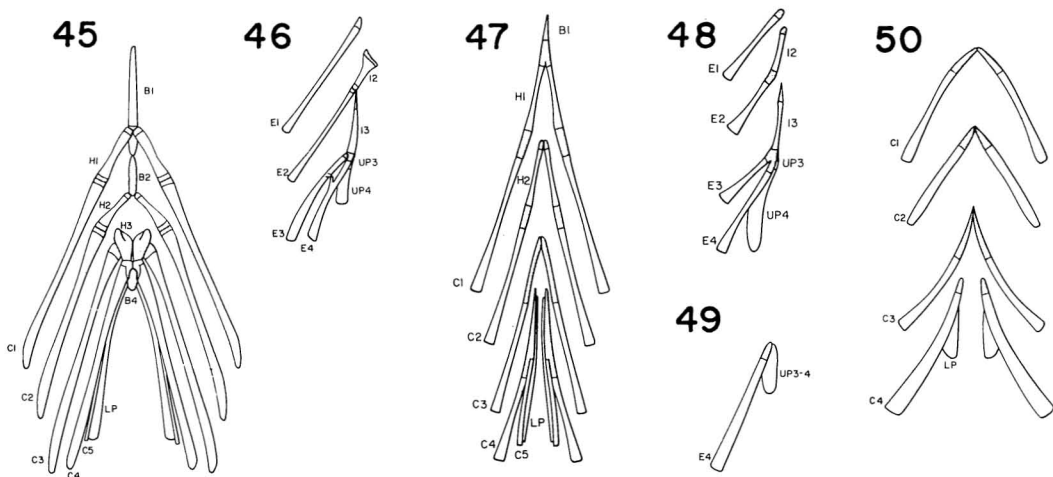
In view of the above, the structure of the gill arch skeleton of the muraenids, although specialized, is not sufficient to warrant the separation of this group at the ordinal or even subordinal level from the other eels. Rather, stages in the derivation of the gill arches of the muraenids are suggested in the more generalized eels

of the same lineage. These exhibit the progressive loss of some bones, the fusion of others, the gradual enlargement of the fourth arch and the dermal tooth-bearing bones it comes to support.

Serrivomeridae and Nemichthyidae

The arches of *Serrivomer* (Figs. 45, 46), although somewhat specialized, are rather like those of *Anguilla*, especially as regards the loss of B3, and the form of H3. They are rather complete in terms of the number of elements, and generalized in retaining the double articulation of C4 with B4. The arches of *Avocettina* and *Nemichthys* (Figs. 47, 48) are somewhat more reduced but still relatively complete. They differ markedly from those of *Cyema* (Figs. 49, 50), which has the branchial skeleton severely reduced, more so than that of any other eel examined.

The systematic position of the eels of the families *Serrivomeridae* and *Nemichthyidae* (as interpreted by Böhlke and Cliff, 1956) has not yet been satisfactorily determined. Whether they are closely related families is open to some doubt (Trewavas, 1932:652; Berlin, 1942:108). The separate frontals and generalized gill arch characters of *Serrivomer*, however, suggest that this form may represent an early offshoot from the anguilloid lineage. The condition of the frontals in the *Nemichthyidae* is variable, some members having them fused,



FIGS. 45-50. 45 and 46, *Serrivomer sector*. 47 and 48, *Nemichthys scolopaceus*. 49 and 50, *Cyema atrum*.

others separate. The consensus seems to favor the view that the group is a natural one. The dorsal parts of the gill arches in *Nemichthys* bear some resemblance to those of *Serrivomer*, whereas the ventral parts in *Nemichthys* are somewhat more reduced, paralleling perhaps the trend toward reduction in other eel groups. Thus, gill arch structure may be consistent with the opinion that these two families are closely related, but can neither confirm nor refute this opinion. In any event, the Nemichthyidae is here included in the anguilloid lineage for want of clear evidence to the contrary.

Functional Significance of Gill Arch Modifications in Eels

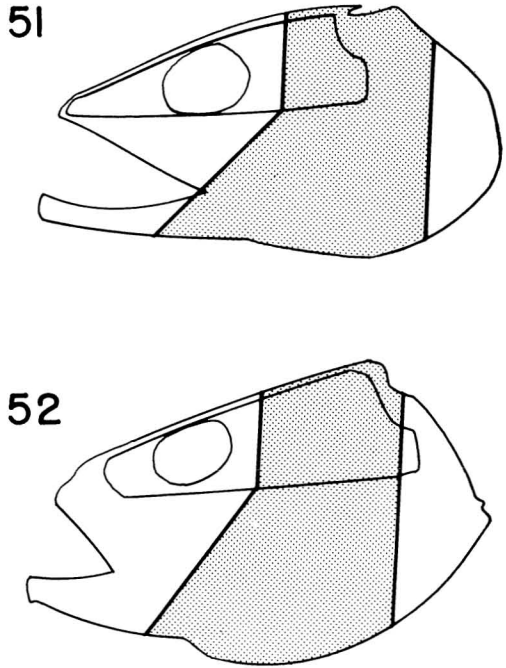
Much could be said concerning the functional significance of the various types of gill apparatus found among the eels. The following remarks concern one possible interpretation of some of those of the anguilloid lineage.

In generalized teleosts, the cranium, jaws, and gill arches form closely integrated parts of a mechanical system functioning to seize prey organisms. The functional roles of the parts of this system have been analyzed by several authors (Höller, 1935; Hofer, 1945; Tchernavin, 1947, 1953; Kirchhoff, 1958; Kampf, 1961; and others). The functional interdependence of these parts is dependent on their near relative positions. In such generalized teleosts as *Elops* and *Epinephelus*, the gill arches are located close behind the jaws, more or less beneath the posterior part of the cranium (Figs. 51, 52).

In the eels, however, the arches are posteriorly displaced from a position beneath the cranium to a position behind it. This displacement is slight in *Conger*, moderate in *Anguilla* and *Chilorhinus*, and extreme in *Gymnothorax* and *Moringua* (Figs. 53–57).

Probably as a result of this displacement, both the pectoral girdle and the gill arches lost the attachments to the cranium characteristically present in other teleosts. In the case of the gill arches, this attachment occurs through the first pharyngobranchial. In the case of the pectoral girdle, it is through the posttemporal. Both of these bones are absent without known exceptions among the eels.

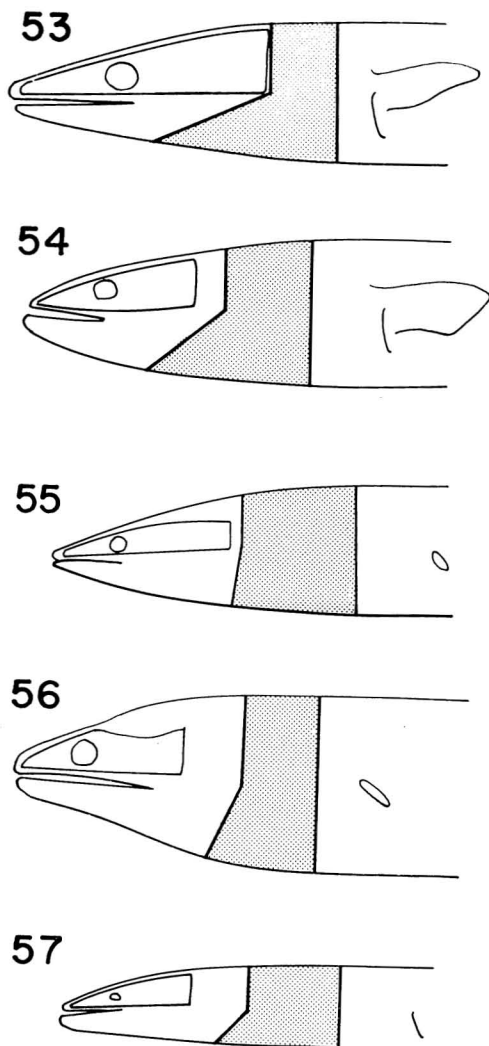
It seems likely that the position of the gills



FIGS. 51 and 52. 51, Position of branchial region in relation to cranium and jaws of *Elops hawaiiensis*. "Branchial region" denotes that space bounded anteriorly by the dorsal and ventral proximal ends of the first arch, posteriorly by the rear border of the dermal tooth plates. 52, *Epinephelus fuscoguttatus*.

is not without some functional significance. The habits of eels, of wedging themselves through crevices or burrowing in the sand, seemingly require an eel-like body, long and narrow, especially in front. Reduction in head diameter seems to have been achieved in part by the movement posteriorly of the gill arches from a position beneath the cranium to one behind it. In this connection, the degree of elongation—the relation between body length and diameter—seems to be correlated with the posterior displacement of the gill region (Fig. 58).

With the arches posteriorly displaced, they tend to lose their role in seizing prey, which then is left to the jaws and cranium alone. This loss in function perhaps may account for the obvious trend toward the loss of certain gill arch elements among eels. This entails the loss of firm interconnections between the gill skeleton and the cranium, between successive arches of the gill skeleton, and between the paired elements of either side. Each of these losses tends



FIGS. 53-57. 53, *Conger marginatus*. 54, *Anguilla rostrata*. 55, *Chilorbinus platyrhynchus*. 56, *Gymnothorax eurostus*. 57, *Moringua javanica*.

to augment the expansibility of the pharynx, which is of obvious significance to an eel-like fish. Interestingly, many of these same modifications have occurred independently among syngnathiform fishes (Jungerson, 1910; Rauther, 1925) and symbranchiform fishes (personal observation), possibly also as a result of spatial separation of jaws and gill arches.

The functional significance of the so-called pharyngeal jaws of the morays and other forms remains to be commented on. On the basis of the nature of the teeth and the branchial

musculature, which is to be discussed elsewhere (Nelson, MS), these prominent tooth-bearing bones apparently function in moving food from the jaws into the esophagus. They have developed, it seems, in relation to mechanical problems involved in moving relatively large food organisms through a secondarily elongate pharynx.

Remarks on Eel Origins

For several reasons, eels are customarily regarded as isospondylous derivatives, and, because of larval features, as being particularly close to the elopoids. Some gill arch characters of eels also suggest an isospondylous origin: (1) pharyngeal tooth plates are generally not fused with underlying endochondral bones, (2) the lower pharyngeal tooth plates are sometimes multiple, (3) retractor ossium pharyngealium muscles are without an attachment to the vertebral column except among some muraenids (Nelson, MS).

Among teleosts above the isospondylous level, pharyngeal tooth plates are generally fused with their endoskeletal supports, and the lower ones are in a single pair (Nelson, MS). Retractor muscles with an attachment to the vertebral column probably are present in all forms above the isospondylous level (Dietz, 1912, 1914, 1921; Holstvoogd, 1960, 1965).

One striking difference between the arches of isospondylous fishes and eels is that in most of the former prominent tooth plates overlie the basibranchials, while no such plates are present in any of the eels examined. These, however, may be presumed to have been lost in relation to the posterior displacement of the arches.

In view of this peculiarity of the gill arch skeleton in eels, no striking resemblance between it and that of any of the major groups of isospondylous fishes can be demonstrated. One feature, however, may deserve mention. This concerns the loss of medial processes on the pharyngobranchials of eels. These processes are important supports for the upper pharyngeal bones in most teleosts (Nelson, MS). They are absent, however, on the third pharyngobranchial of *Albula* among elopoids (but not of *Megalops*, *Elops*, or *Pterothrissus*), and in at least *Aldrovandia* among halosaurids (per-

sonal observations). Perhaps the tendency toward the reduction of these processes may be evidence of genetic relationship.

SUMMARY

1. On the basis of gill arch and other characters the eels may be divided into at least three evolutionary lineages: anguilloid (Anguillidae, Heterenchelidae, Serrivomeridae, Nemichthyidae(?), Moringuidae, Xencongridae, Dysommidae, Muraenidae), synphobranchoid (Synphobranchidae, Ilyophidae, Simenchelidae, Dysommidae), and congroid (Congridae, Heterocongridae, Nessorhamphidae, Nettastomidae, Derichthyidae, Ophichthidae, Muraenesocidae).

2. In each of these lineages the gill arches seem to have been similarly modified through (a) the progressive enlargement, or reduction with eventual loss, of skeletal parts, (b) simplification in form of the skeletal parts (loss of grooves and processes), (c) an anterior shift in position of the lower pharyngeal tooth plates, which gradually become supported by the fourth rather than fifth ceratobranchials.

3. Within the anguilloid lineage the Heterenchelidae and Anguillidae are the most generalized in gill arch structure. *Moringua* is somewhat more specialized. The Xencongridae, *Dysommia*, and Muraenidae resemble one another more than they do other members of this lineage. The Muraenidae have the gill arches most highly specialized, and on the basis

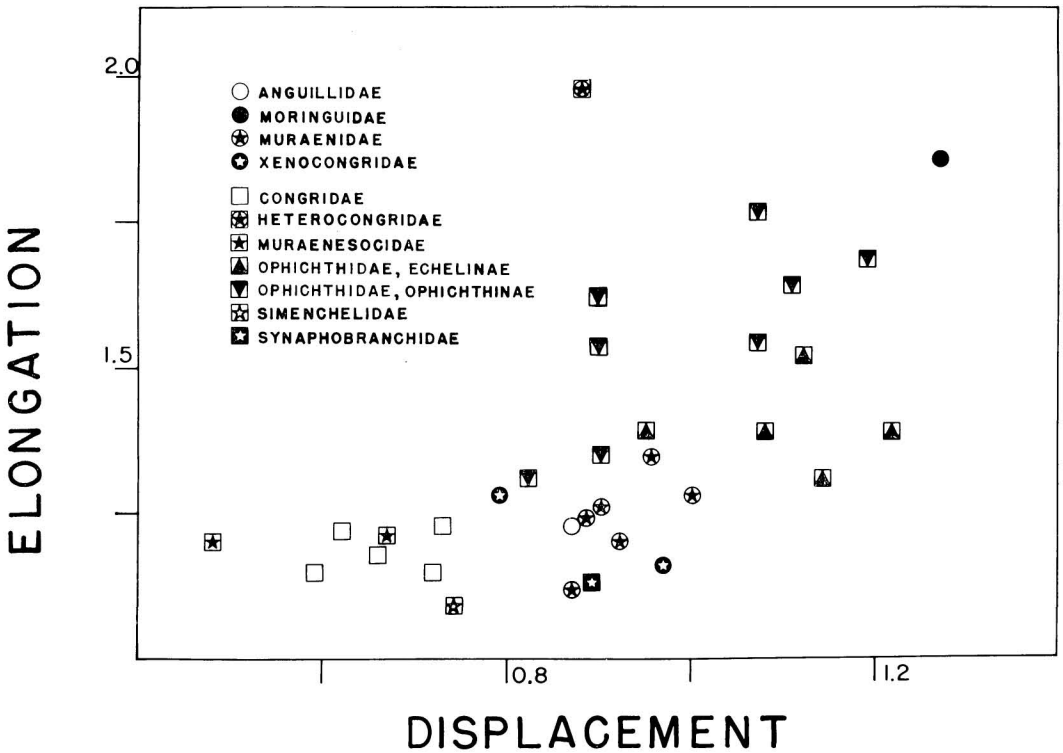


FIG. 58. Scatter diagram showing correlation between body elongation and posterior displacement of the branchial region in selected representatives of some eel families. Elongation = log body length/maximum body diameter. Displacement = log 10 × postcranial head length/cranial length. Example: for *Moringua javanica* the following measurements were taken: total length 805 mm, maximum body diameter 11 mm, head 49 mm, cranium (snout tip to posterior limit of cranium) 17 mm.

$$\text{Elongation} = \log 805/11 = 1.86$$

$$\text{Displacement} = \log 320/17 = 1.27$$

Measurement data on other species will be furnished by the author on request.

of gill arch and other structures may be divided into two subfamilies, one of which is proposed as new, Uropterygiinae and Muraeninae. The arches of *Serrivomer* are sufficiently similar to those of *Anguilla* to suggest a relationship between these forms. Those of nemichthyids are somewhat reduced (*Nemichthys*, *Avocettina*) or severely reduced (*Cyema*).

4. The members of the synphobranchoid lineage are alike in having the third hypobranchials posteriorly directed.

5. Within the congroid lineage most of the members have a well ossified and complete gill arch skeleton. The only major exceptions are found among the Ophichthidae, whose members show great variability in gill arch structure.

6. Gill arch modifications seem related to body form and habits of eels. The gills are posteriorly displaced in the more elongate forms. Loss of skeletal elements has resulted in many eels in a highly expandible pharynx, seemingly an adaptation for swallowing large prey. The development of "pharyngeal jaws" in the more highly specialized eels seems related to mechanical problems of moving relatively large prey through a secondarily elongate pharynx.

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