Branchial Muscles in Representatives of Five Eel Families[1, 2]

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DURING THE EVOLUTION of eels the gill arch skeleton of some forms was profoundly modified in gross structure. The modifications are adaptive and are associated with body form and feeding habits of eels (Nelson, 1966). The present paper deals with the musculature attached to the gill arch skeleton of eels representing five families, primarily of the suborder Anguilloidei. Six genera were chosen for study: *Conger* (Congridae), *Anguilla* (Anguillidae), *Moringua* (Moringuidae), *Kaupichthys* (Xenocongridae), *Uropterygius*, and *Gymnothorax* (Muraenidae). The gill arch skeleton of these forms shows a progressive reduction of elements, showing probable stages in the evolutionary development of the specialized "pharyngeal jaws" of the morays—eels of the family Muraenidae.

Gill arch musculature in eels has been studied previously only in *Anguilla* by Dietz (1912) and again by Kesteven (1943). Muscle terminology in the present work follows Vetter (1878) and Edgeworth (1935) as far as possible. Names of gill arch elements are abbreviated as follows: B, basibranchial; H, hypobranchial; C, ceratobranchial; E, epibranchial; I, infrapharyngobranchial; LP, lower pharyngeal tooth plate; UP, upper pharyngeal tooth plate. Gill arches in eels are discussed in detail elsewhere (Nelson, 1966).

MATERIAL AND METHODS

Muscles were dissected in preserved adult specimens and illustrated for *Conger marginatus, Anguilla rostrata, Moringua javanica, Kaupichthys diodontus, Uropterygius knighti,* and *Gymnothorax petelli.* Observations on related genera (those listed in Nelson, 1966) suggested that the six genera selected for study are representative of the families or subfamilies to which they belong. All material was obtained from the collections of the Department of Zoology, University of Hawaii. With the exception of specimens of *Anguilla,* study material originally was collected by means of shallow water rotenone poisoning around Oahu and Christmas Island.

The illustrations show the muscles in approximately their relative size and positions. Muscles attaching to structures other than gill arches are shown transected. Occasionally other muscles are shown with parts removed to reveal underlying structures. Roots of the branchial arteries are included in the illustrations, for they serve as convenient landmarks, separating adjacent muscles. Bertmar (1962) and Petukat (1965) have dealt with the ontogeny and comparative anatomy of these vessels in some other teleostean fishes.

RESULTS

Conger

Ventral muscles are shown in Figure 1 and listed in Table 1. Obliqui (01–3) occur on arches 1–3, extending between cerato- and hypobranchials. O3 has its insertion apparently transferred anteriorly to H2. A rectus (R4) is present only between arches 3–4, extending between the proximal ends of C4 and H3. It probably represents part of the oblique of arch 4 with the insertion anteriorly transferred to H3. A rectus communis (RC) extends from the proximal end of C4, with some of its fibers inserting on H3, others on H2 in common with O3. An anterior transversus (AT) extends between the proximal ends of C4 of either side. Extending posteriorly from C5, a single pharyngo-clavicularis (PC) attaches to the cleithrum. A posterior transversus (PT) extends between the distal ends of C5 of either side. An adductor (A5) joins the distal ends

[1] This paper is part of a thesis submitted to the Graduate Division of the University of Hawaii in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Zoology.

[2] Contribution No. 261, Hawaii Institute of Marine Biology. Manuscript received May 6, 1966.

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TABLE 1
MUSCLES ATTACHED TO THE VENTRAL PARTS OF THE GILL ARCHES IN SOME EELS*

GENUS	O1	O2	O3	R1	R2	R3	R4	RC	AT	PT	PC	S	VR	A5	SP
Conger	X	X	X	–	–	–	X	X	X	X	X	X	X	X	–
Anguilla	X	X	X	–	X	X	X	X	X	X	X	X	X	X	–
Moringua	X	X	X	–	–	–	X	X	X	X	X	X	X	X	X
Kaupichthys	–	–	–	–	–	–	X	X	X	X	X	X	X	X	X
Uropterygius	–	–	–	–	–	–	–	–	–	X	X	X	X	–	X
Gymnothorax	–	–	–	–	–	–	–	–	X	X	X	X	X	–	X

* A5, Adductor 5; AT, transversus anterior; O1–3, obliqui 1–3; PC, pharyngo-clavicularis; PT, transversus posterior; R1–4, recti 1–4; RC, rectus communis; S, sphincter oesophagi; SP, subpharyngealis; VR, retractor ventralis. X, Muscle present; –, muscle absent.

of C4–5. A sphincter (S) encircles the esophagus and also interconnects C5 of either side. Internal to the sphincter extend longitudinal fibers tending to separate anteriorly, forming a paired muscle, the ventral retractor (VR), attaching to LP and posteriorly extending some distance in the esophageal wall.

Dorsal muscles are shown in Figure 2 and listed in Table 2. External levators (EL1–4) occur on arches 1–4, extending between the cranium and the proximal ends of E1–4. Internal levators (IL1–2) occur on arches 1–2. IL1 extends between the fascia of the trunk and I2. Inferior obliques (IO2–3) interconnect E1–3. A small accessory oblique (AO) extends between E1 and I2. A superior oblique (SO) extends between E3 and I3. An adductor (A4) extends between E4 and C4. A posterior oblique (PO) extends between E4 and C5. The sphincter (S) encircles the esophagus and its anterior portion extends between the arches of either side. Internal to the sphincter occurs a longitudinal layer tending to separate anterior, forming a paired muscle, the dorsal retractor, attaching to UP4 and posteriorly extending some distance in the esophageal wall.

Anguilla

Muscles are shown in Figures 3 and 4 and listed in Tables 1 and 2. They are rather similar to those of *Conger* and have been studied by Dietz (1912) and Kesteven (1943), whose terminologies are compared with that used here in Tables 3 and 4. In the second arch, that portion of the oblique (02) inserting on H1 corresponds to a rectus (Table 1, R2). A posterior transversus (Table 1, PT) is represented by the anteroventral portion of the sphincter (S).

Moringua

Muscles are shown in Figures 5 and 6 and listed in Tables 1 and 2. A major feature of the musculature is the subpharyngealis (SP), a sheet of longitudinal fibers dorsal to the ventral arch elements. A transverse (Fig. 6, TD) is partly distinct from the anterodorsal part of the sphincter.

Kaupichthys

Muscles are shown in Figures 7 and 8 and listed in Tables 1 and 2. With some minor differences the muscles are most similar to those of *Moringua.*

TABLE 2
MUSCLES ATTACHED TO THE DORSAL PARTS OF THE GILL ARCHES IN SOME EELS*

GENUS	EL1	EL2	EL3	EL4	IO1	IO2	IO3	AO	IL1	IL2	SO	PO	A4	DR	S	MP	LP	PP
Conger	X	X	X	X	–	X	X	X	X	X	X	X	X	X	X	–	–	–
Anguilla	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	–	–	–
Moringua	X	X	–	X	X	X	X	–	X	X	X	X	X	X	X	–	–	–
Kaupichthys	X	X	X	–	X	X	X	–	X	X	X	X	X	X	X	–	–	–
Uropterygius	–	–	–	–	–	X	X	–	X	–	–	–	X	X	X	X	–	X
Gymnothorax	X	X	X	–	X	X	X	–	X	X	–	–	X	X	X	X	X	–

* A4, Adductor 4; AO, obliquus inferior accessorius; DR, retractor dorsalis; EL1–4, levatores externi 1–4; IL1–2, levatores interni 1–2; IO1–3, obliqui inferiores 1–3; LP, protractor lateralis; MP, protractor medialis; PO, obliquus posterior; PP, protractor posterior; S, sphincter oesophagi; SO, obliquus superior. X, Muscle present; –, muscle absent.

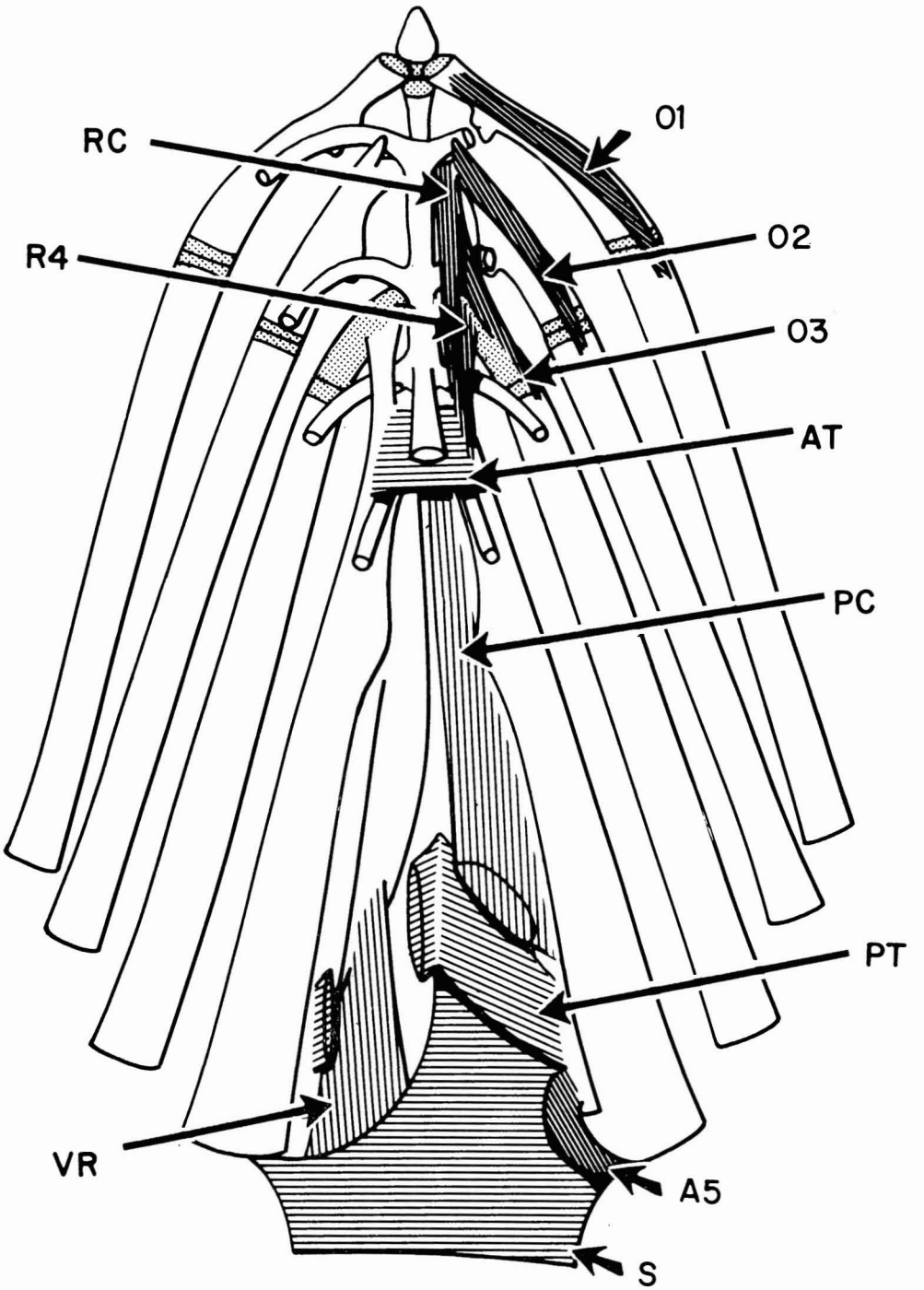

FIG. 1. *Conger marginatus,* ventral gill arch muscles of left side, ventral view, showing roots of afferent branchial arteries. *A5,* Adductor 5; *AT,* transversus anterior; *O1–3,* obliqui 1–3; *PC,* pharyngo-clavicularis; *PT,* transversus posterior; *R4,* rectus 4; *RC,* rectus communis; *S,* sphincter oesophagi; *VR,* retractor ventralis.

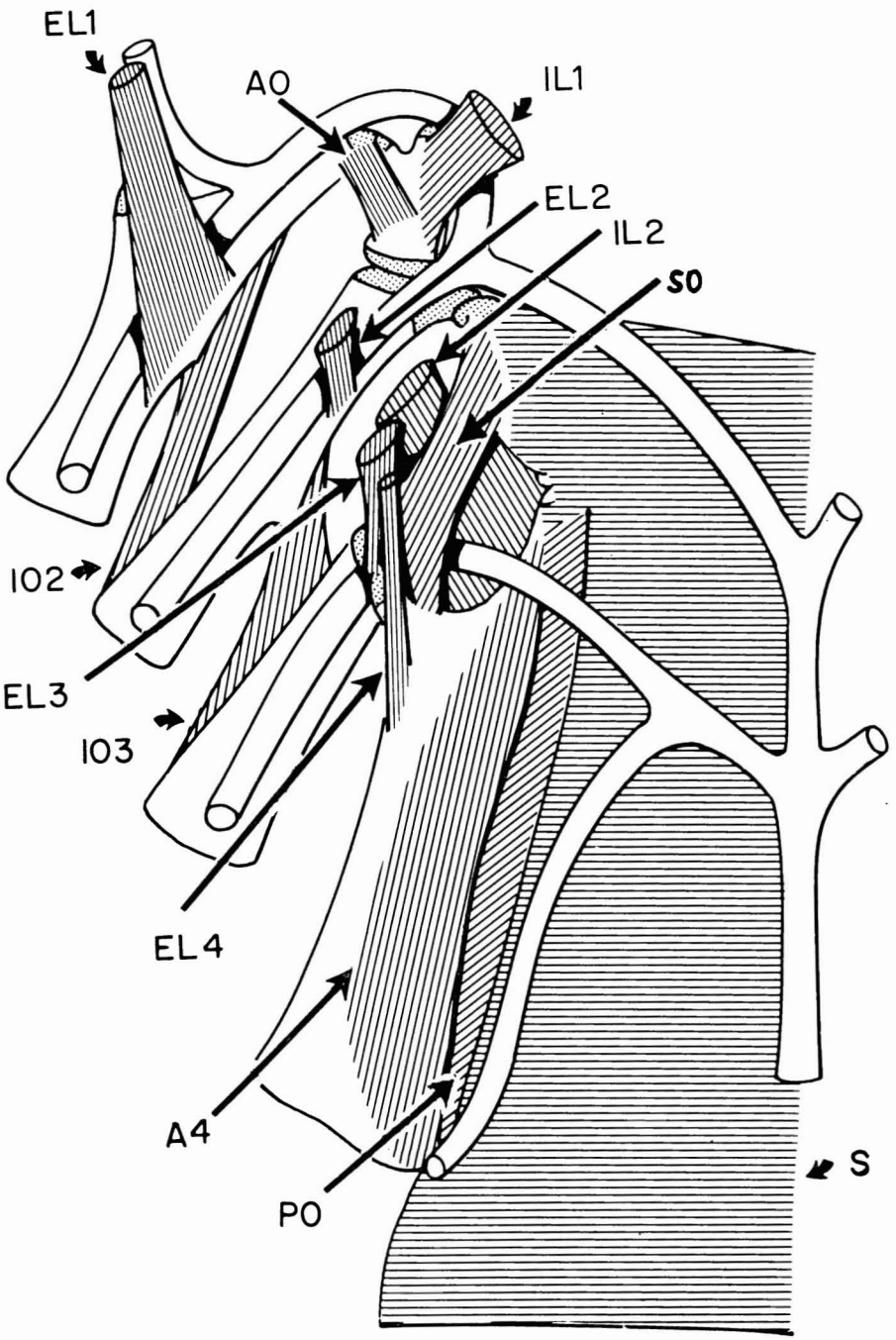

FIG. 2. *Conger marginatus,* dorsal gill arch muscles, dorsal view of left side, showing parts of efferent branchial arteries. *A4,* Adductor 4; *AO,* obliquus inferior accessorius; *EL1–4,* levatores externi 1–4; *IL1–2,* levatores interni 1–2; *IO2–3,* obliqui inferiores 2–3; *PO,* obliquus posterior; *S,* sphincter esophagi; *SO,* obliquus superior.

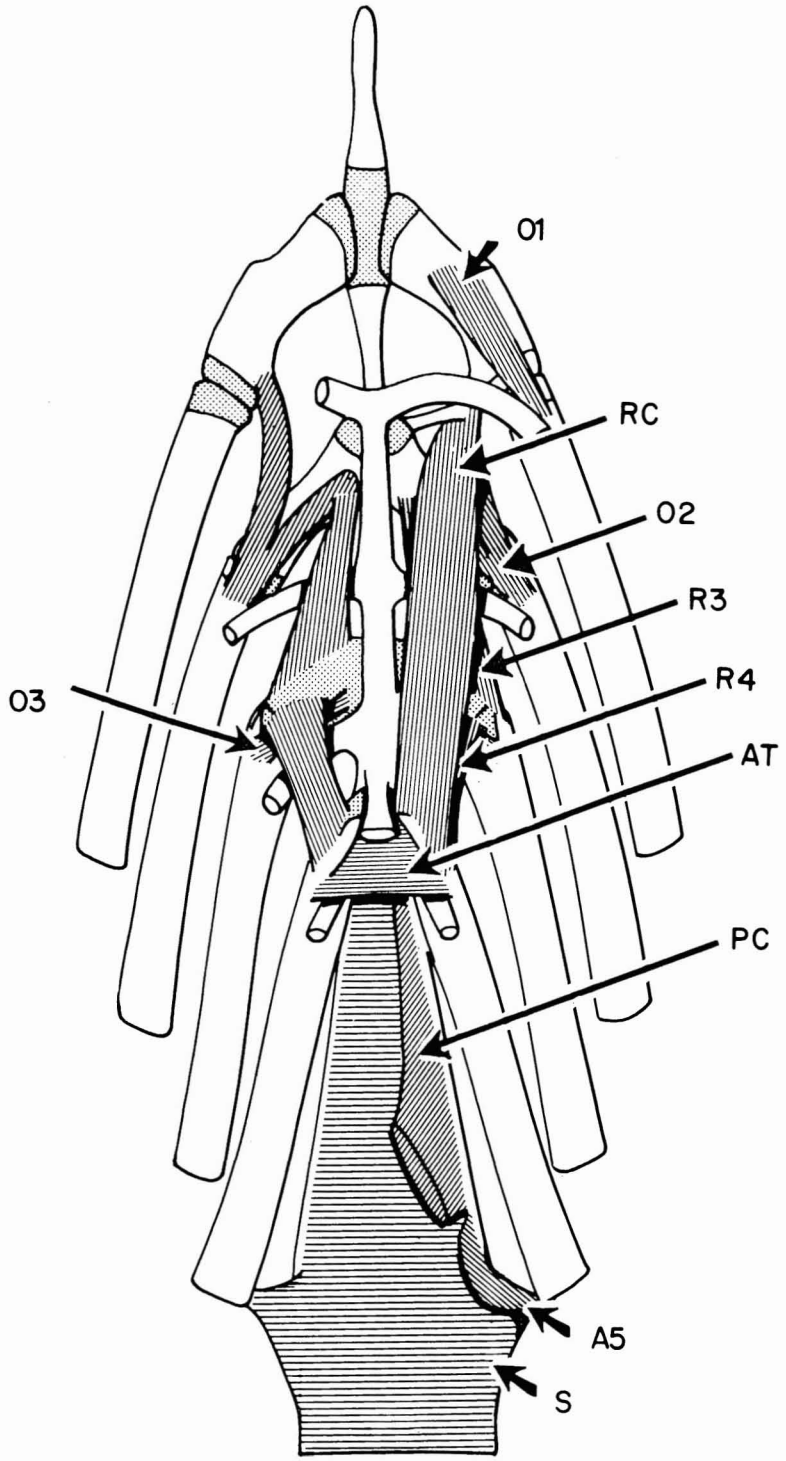

FIG. 3. *Anguilla rostrata,* ventral gill arch muscles, ventral view, with some of those of right side omitted, and showing roots of afferent branchial arteries. Muscles as in Figure 1.

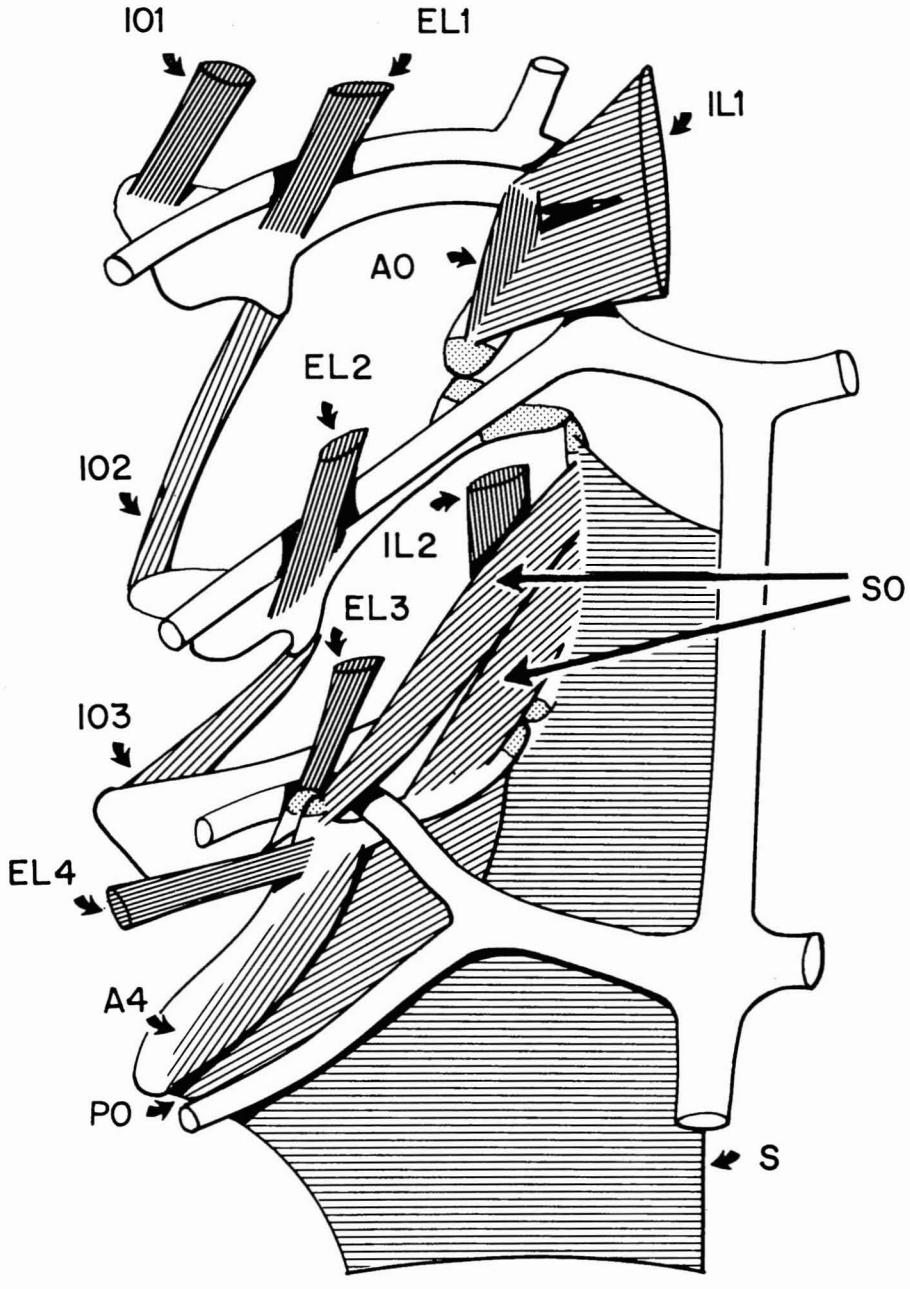

FIG. 4. *Anguilla rostrata,* dorsal gill arch muscles, dorsal view of left side, showing parts of efferent branchial arteries. Muscles as in Figure 2.

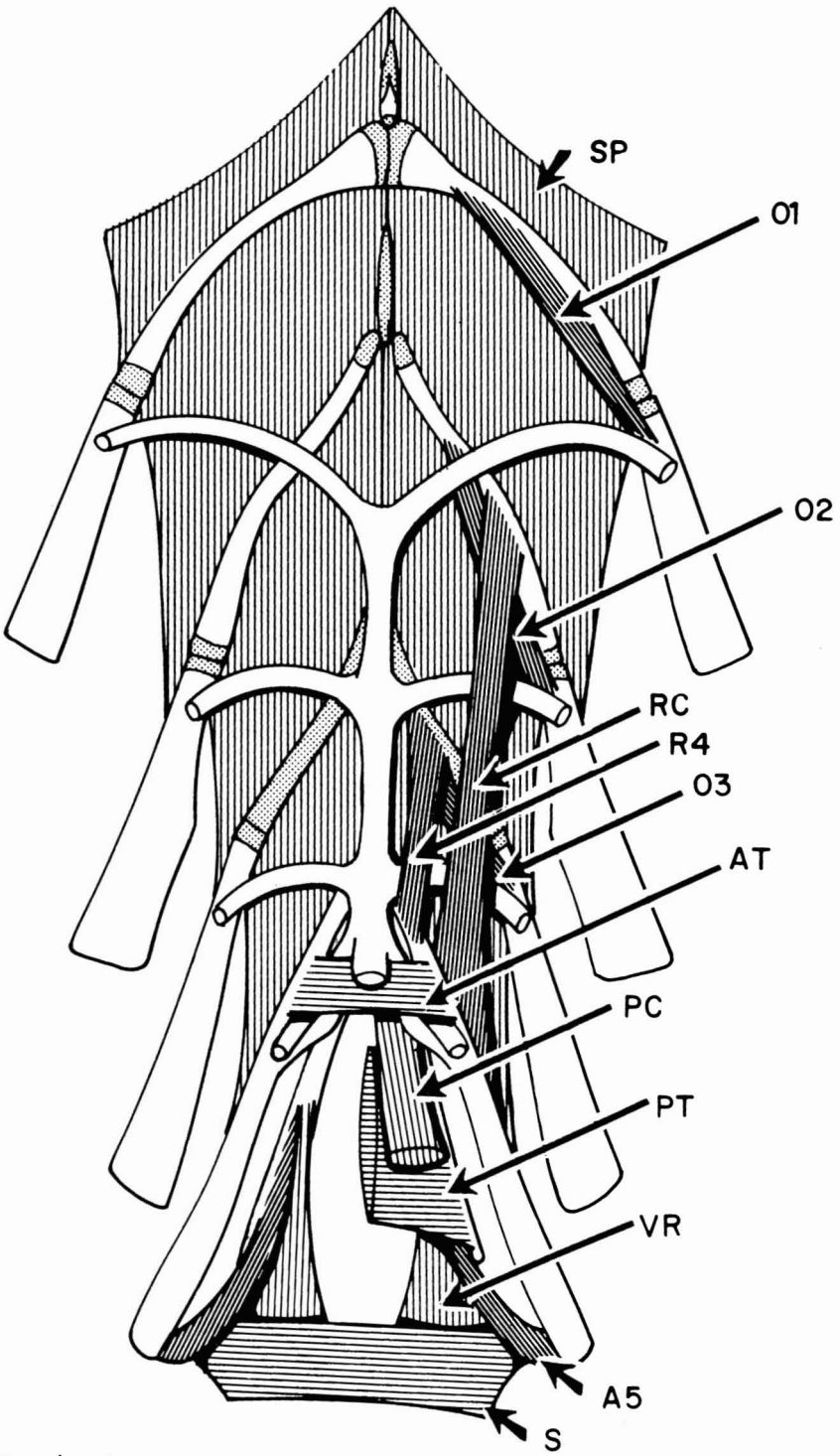

FIG. 5. *Moringua javanica,* ventral gill arch muscles, ventral view, with some of those of right side omitted, showing roots of afferent branchial arteries. *SP,* Subpharyngealis. Other muscles as in Figure 1.

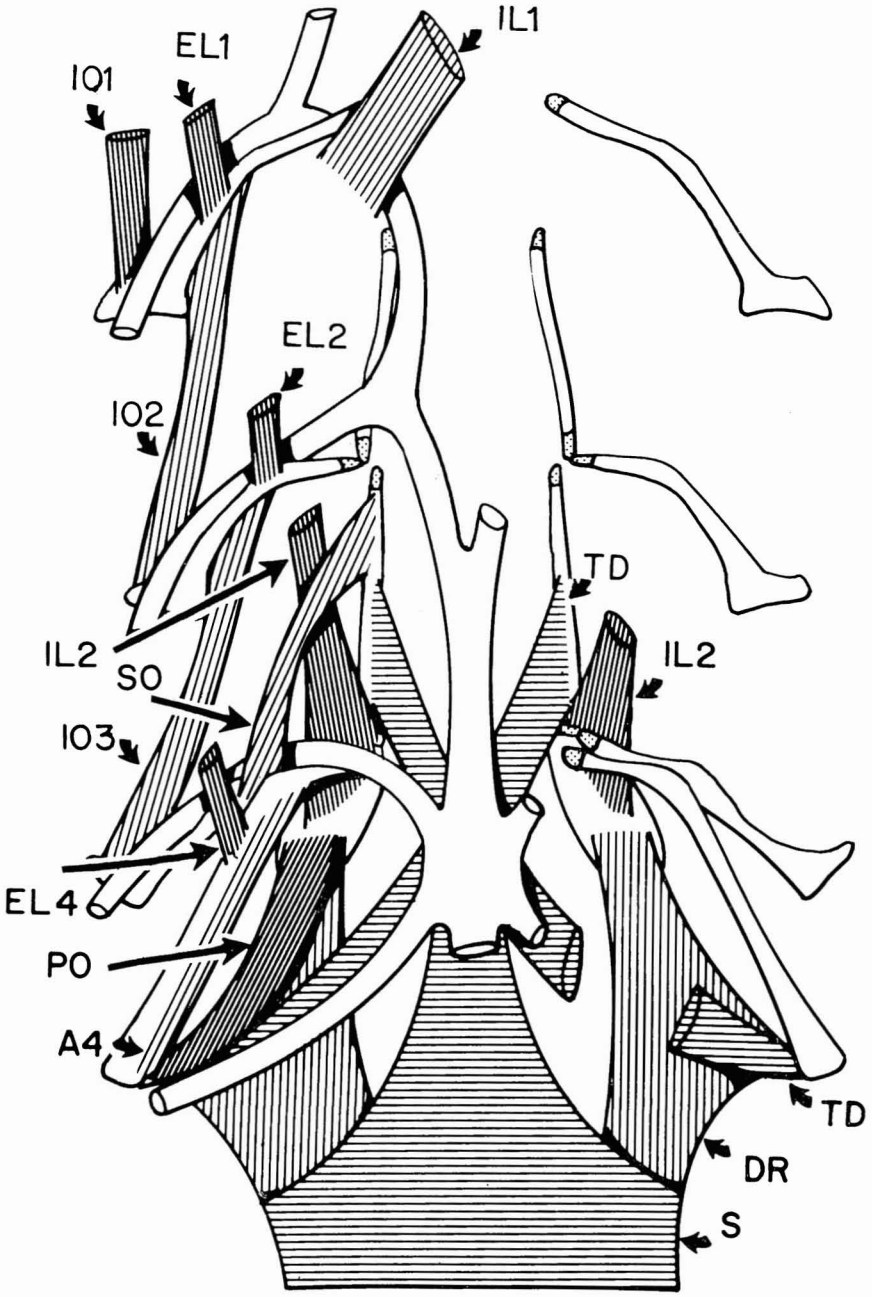

FIG. 6. *Moringua javanica,* dorsal gill arch muscles, dorsal view, with some of those of right side omitted, showing parts of the efferent branchial arteries. *DR,* Retractor dorsalis; *TD,* transversus dorsalis. Other muscles as in Figure 2.

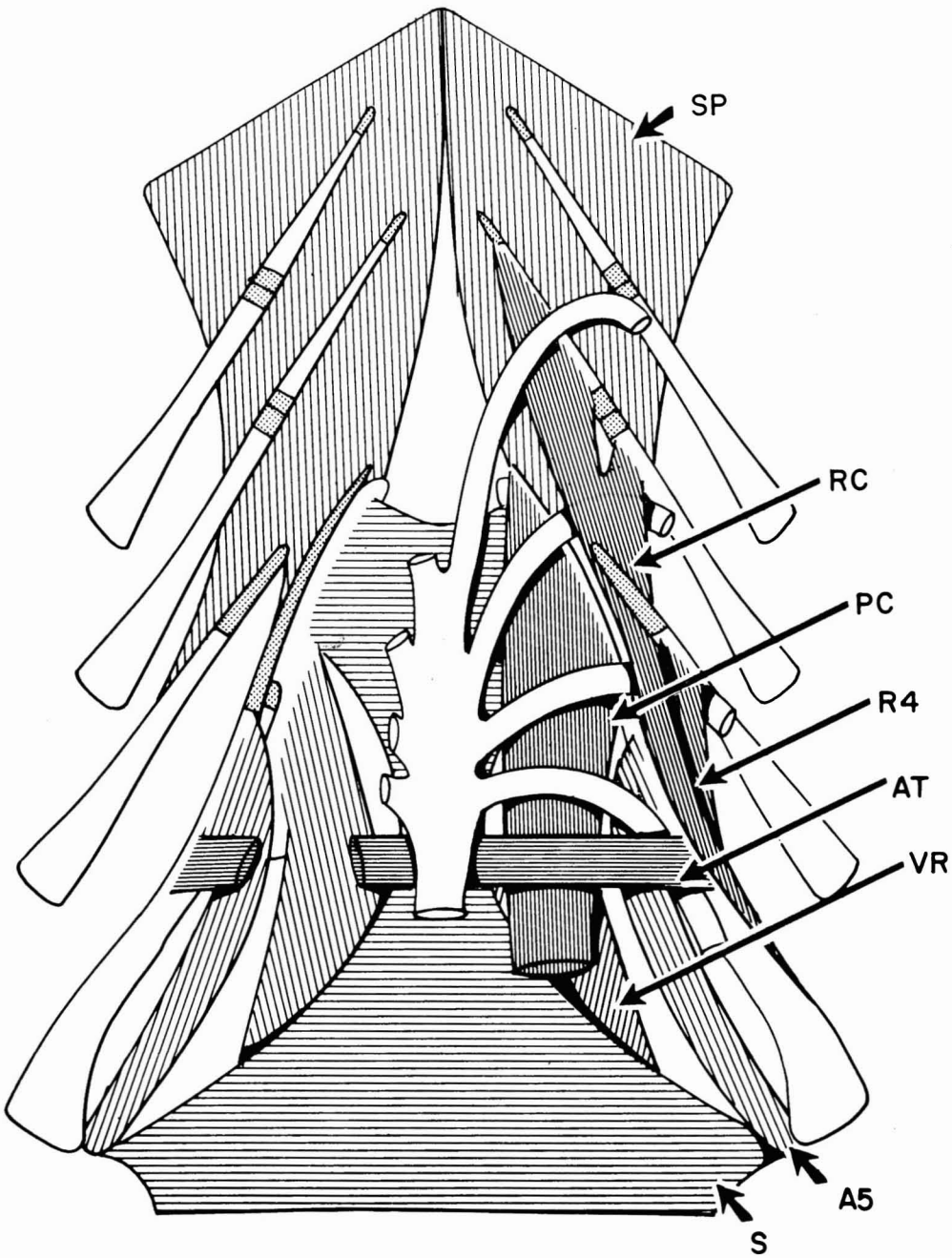

FIG. 7. *Kaupichthys diodontus,* ventral gill arch muscles, ventral view, with some of those of the right side omitted, and showing roots of afferent branchial arteries. Muscles as in Figures 1 and 5.

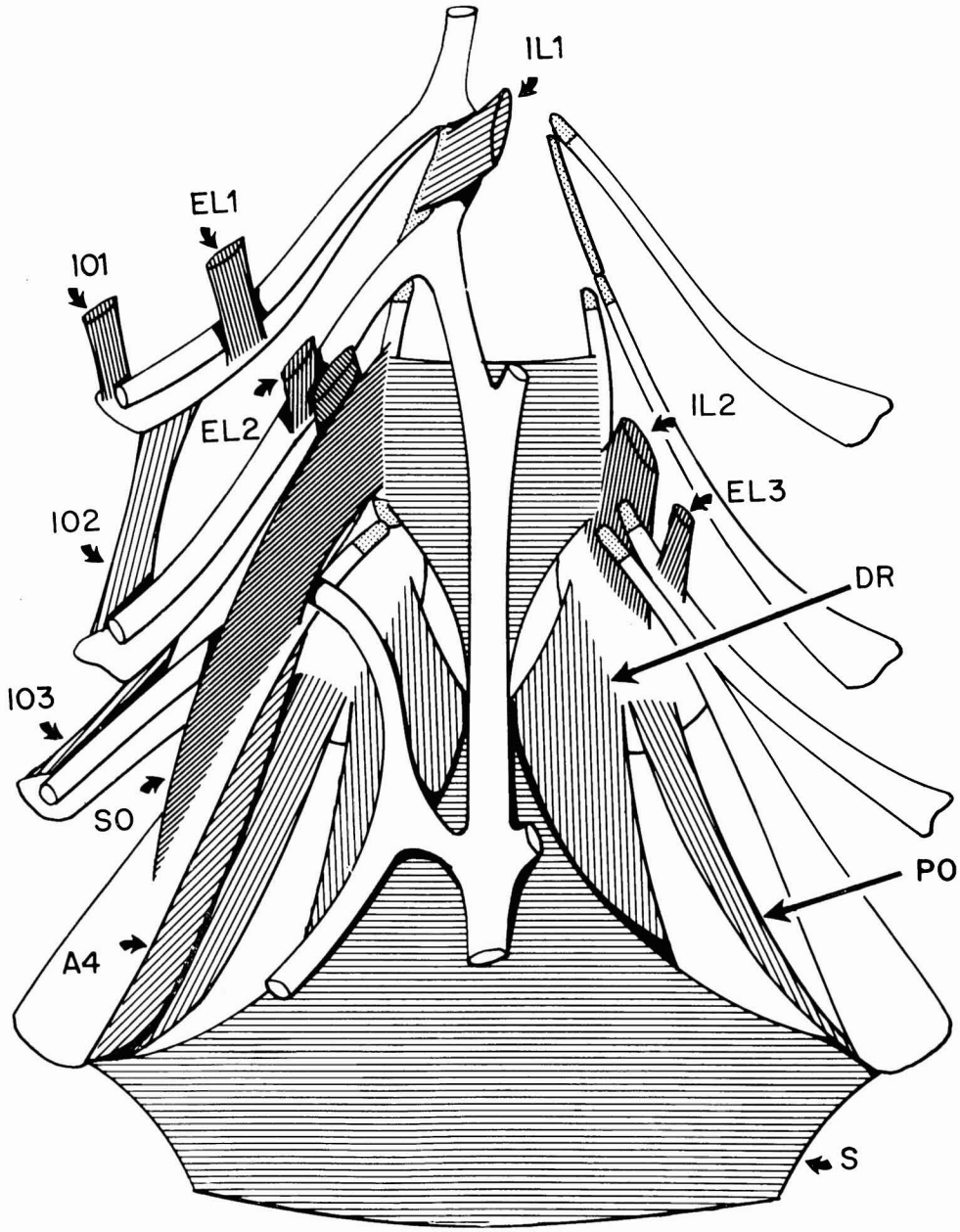

FIG. 8. *Kaupichthys diodontus,* dorsal gill arch muscles, dorsal view, with some of those of right side omitted, and showing parts of efferent branchial arteries. Muscles as in Figure 2.

TABLE 3
MUSCLE TERMINOLOGY FOR VENTRAL GILL ARCH MUSCLES IN *Anguilla*

PRESENT TERMINOLOGY	DIETZ (1912)	KESTEVEN (1943)
Obliquus 1 (01)	Obl. I	Subarc. obl. 1
Obliquus 2 (02)	Obl. II	Subarc. obl. 2
Obliquus 3 (03)	Obl. III	Subarc. obl. 3
Rectus 2 (R2)	Interarc. I/II	none
Rectus 3 (R3)	Interarc. II/III	none
Rectus 4 (R4)	Interarc. III/IV	none
Rectus communis (RC)	Interarc. I/IV	Rectus
Transversus anterior (AT)	Trans. IV	Transversus
Transversus posterior (PT)	Trans. V	Transversus
Pharyngo-clavicularis (PC)	Phar.-clav. ex. + int.	Clav.-pharyng. ext.
Adductor 5 (A5)	none	none
Retractor ventralis (VR)	none	none
Sphincter oesophagi (S)	Pharynxmuskulatur	Sphincter oesophagi

TABLE 4
MUSCLE TERMINOLOGY FOR DORSAL GILL ARCH MUSCLES IN *Anguilla*

PRESENT TERMINOLOGY	DIETZ (1912)	KESTEVEN (1943)
Levator externus 1 (EL1)	Lev. ext. I	none
Levator externus 2 (EL2)	Lev. ext. II	Lev. ext. 2
Levator externus 3 (EL3)	Lev. ext. III	Lev. ext. 3
Levator externus 4 (EL4)	Lev. ext. IV	Lev. ext. 4
Levator internus 1 (IL1)	Lev. int. I?	Retractor dorsalis
Levator internus 2 (IL2)	Lev. ext. IV	Lev. int.
Obliquus inferior 1 (IO1)	Obliq. inf. hy/I	none
Obliquus inferior 2 (IO2)	Obliq. inf. I/II	none
Obliquus inferior 3 (IO3)	Obliq. inf. II/III	none
Obliquus inferior accessorius (AO)	none	none
Obliquus superior (SO)	Obliq. sup. ant.	Epiarc. obl. 1
Obliquus posterior (PO)	Obliq. dors. post.	Epiarc. obl. 2
Adductor 4 (A4)	none	none
Retractor dorsalis (DR)	none	none

Uropterygius

The ventral muscles are similar to those of *Kaupichthys* but are reduced in number (Table 1). The dorsal muscles are shown in Figure 9. Levators are lacking, having been replaced it seems by two new muscles, one extending between the cranium and UP3–4, the medial protractor (MP), the other extending between the cranium and E4, the posterior protractor (PP).

Gymnothorax

The ventral muscles are similar to those of *Uropterygius* with the exception of the subpharyngealis, which appears subdivided into many parts (interbranchial attractors). These are shown in Figure 10. The dorsal muscles (Fig. 11) resemble those of *Kaupichthys* more than those of *Uropterygius*. However, they do include a medial protractor. They include in addition a lateral protractor extending between UP3–4 and the ventral part of the hyoid arch, attaching there in common with the ventral muscles LA1, OA1–2. The dorsal retractors attach in common with the ventral retractors to the ventral surfaces of the 13th–15th vertebrae.

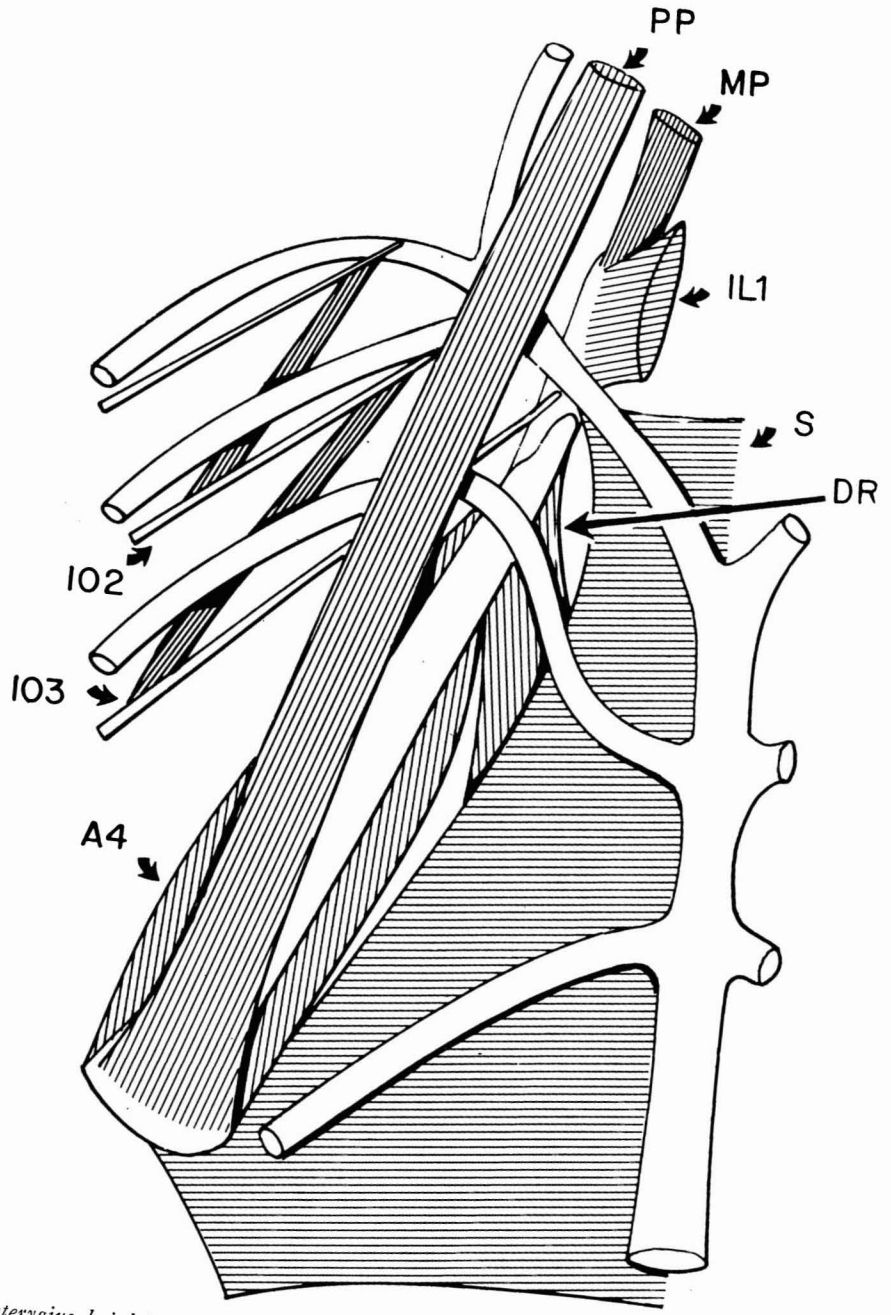

FIG. 9. *Uropterygius knighti*, dorsal gill arch muscles, dorsal view of left side, showing parts of efferent branchial arteries. *MP*, Protractor medialis; *PP*, protractor posterior. Other muscles as in Figure 2.

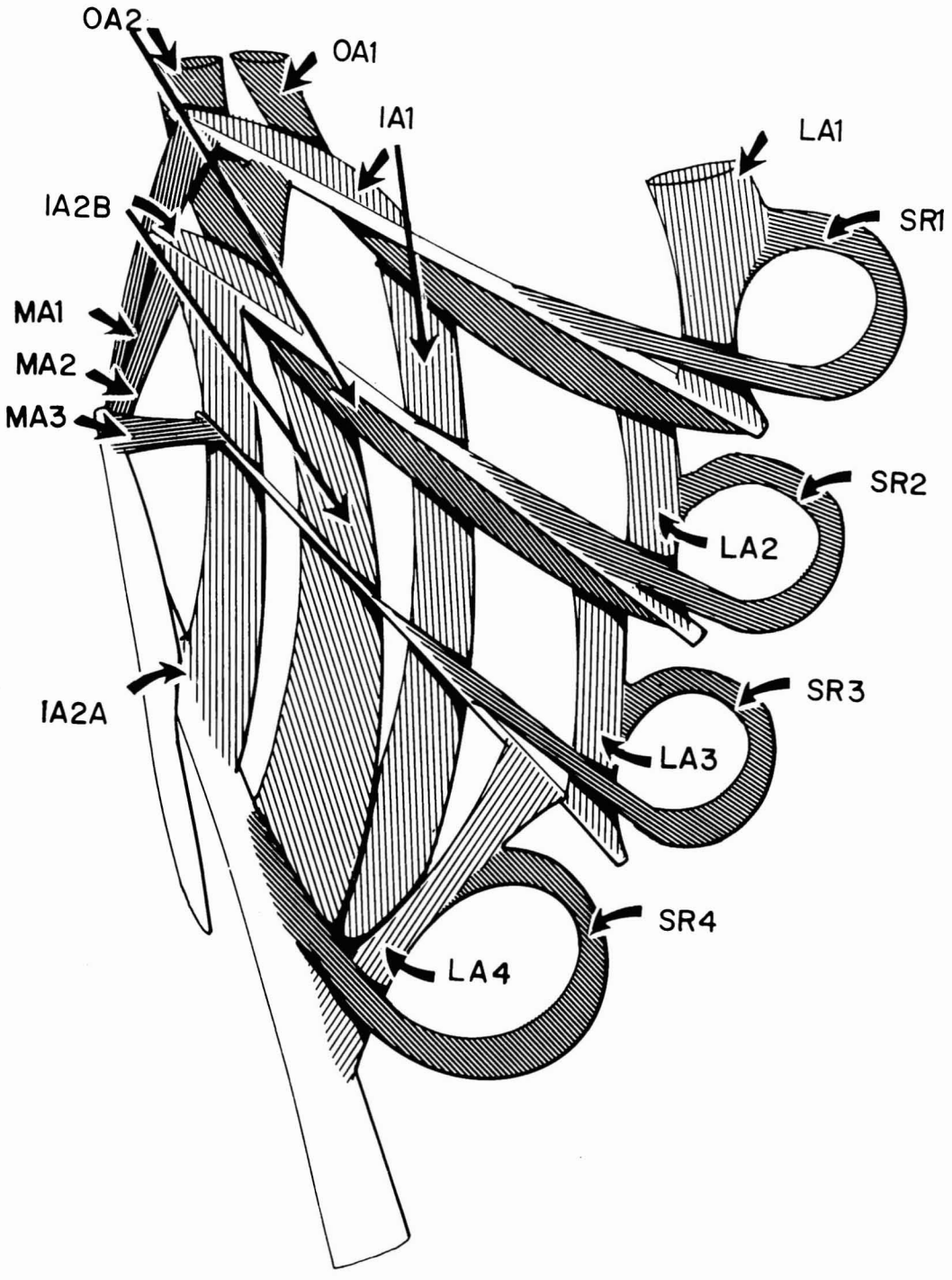

FIG. 10. *Gymnothorax petelli,* some of the gill arch muscles of the left side, ventral view, showing subdivisions (attractores interbranchiales and sphincteres branchiales) of the subpharyngealis. *IA1–2,* Attractores intermediales 1–3; *LA1–4,* attractores laterales 1–4; *MA1–3,* attractores mediales 1–3; *OA1–2,* attractores obliqui 1–2; *SR1–4,* sphincteres branchiales 1–4.

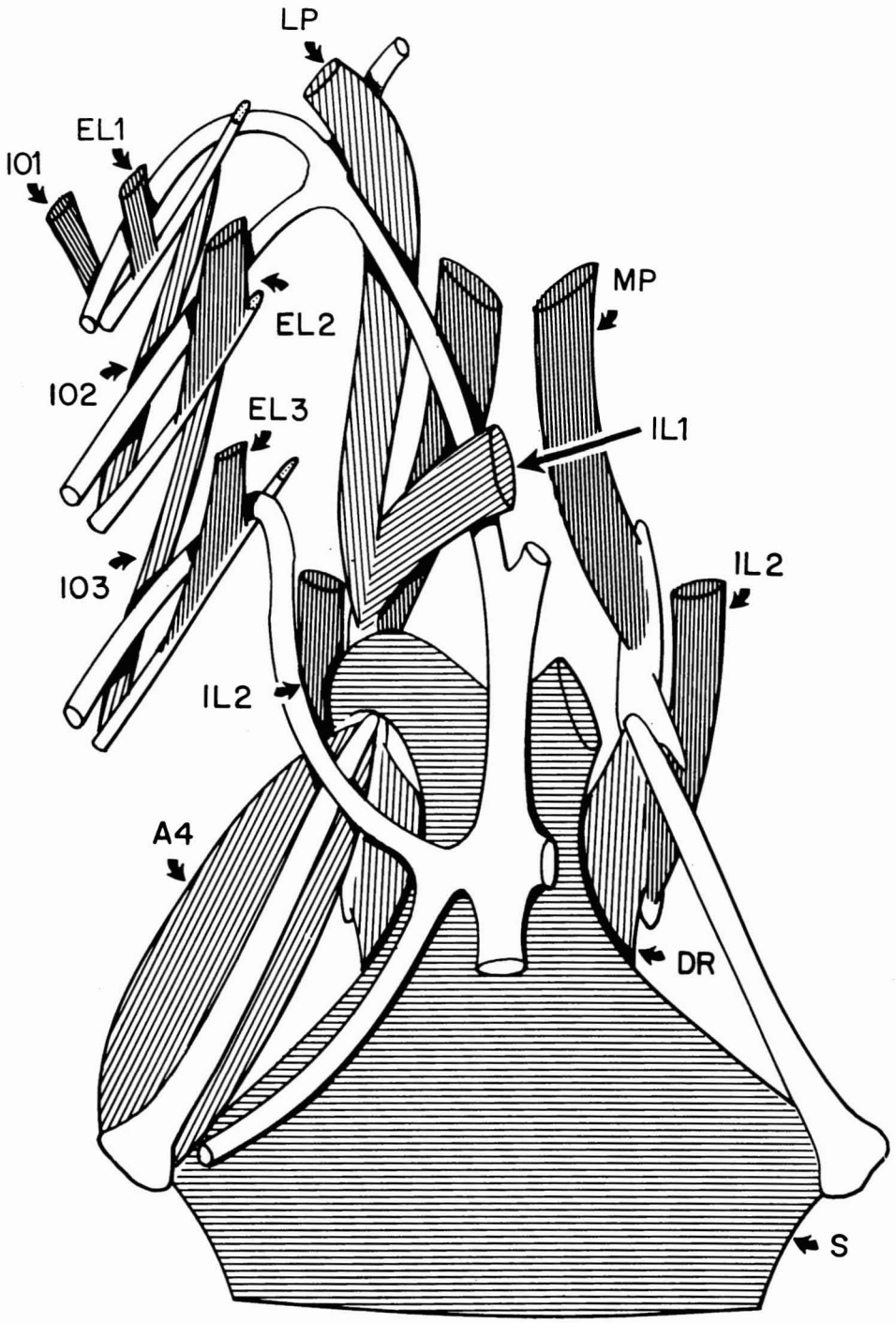

FIG. 11. *Gymnothorax petelli,* dorsal gill arch muscles, with some of those of the right side omitted, and showing parts of efferent branchial arteries. *LP,* Protractor lateralis; MP, protractor medialis. Other muscles as in Figure 2.

DISCUSSION

If they are represented by the rather linear reduction in gill arch elements, relationships among the examined genera may be as diagrammed in Figure 12. Thus, *Conger* would be the most primitive and *Gymnothorax* the most advanced. Gill arch muscles of *Conger* are not structurally far removed from those of *Elops* (Nelson, 1967) or those of other generalized lower teleostean fishes (Vetter, 1878; Dietz, 1912, 1914, 1921; Greene and Greene, 1913). On the other hand, the muscles of *Uropterygius* or *Gymnothorax* are far removed structurally from those of *Conger* and consequently appear to be advanced rather than primitive. The series of studied forms ranging from *Conger* to *Gymnothorax* shows a progressive series of muscle modifications, involving the loss of some muscles and the appearance of others (Tables 1 and 2). The series of muscle modifications in a general way parallels the linear reduction in gill arch elements of these forms.

Particular modifications of gill arch muscles in eels seem correlated with particular modifications of the gill arches themselves. Reduction of ventral musculature (obliqui and recti) parallels reduction in ventral arch elements (basi- and hypobranchials). Appearance of protractors and enlargement of the retractors and their attachment to the vertebral column in muraenines parallel the enlargement of the fourth arch and the tooth plates it supports.

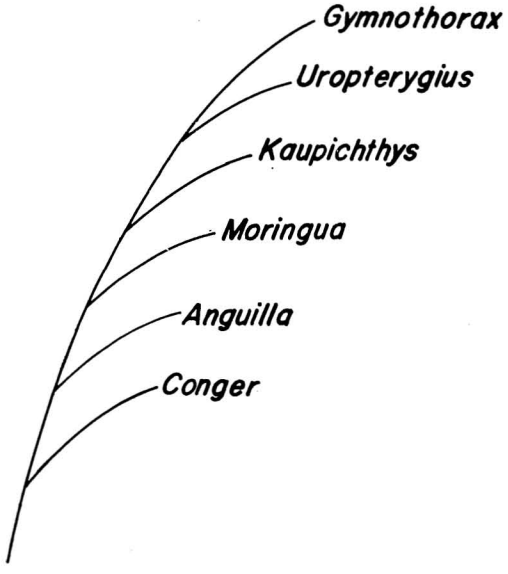

FIG. 12. Diagram of possible relationships among some eels.

The appearance of the subpharyngealis is not so easily correlated with any particular modification of the gill arch skeleton. It appears, seemingly, in place of the obliqui and recti. However, nothing is known of its embryonic development and it may or may not represent modified obliqui or recti. Its position is distinctive, being internal to the skeletal elements rather than external as are the obliqui and recti. Probably the ventral musculature shifted from a relatively external to a relatively internal position with the reduction and loss of basibranchials. In any event, it assumed a sheetlike form, gradually encroaching upon the gill slits, which in the more advanced eels (e.g., the muraenids) are reduced to small round openings.

Dorsal and ventral paired retractor muscles are present in all of the eels examined. In most forms they are only partly distinct subdivisions of the inner longitudinal muscle layer of the anterior esophagus. In eels of the subfamily Muraeninae, they acquire an attachment to the vertebral column.

The taxonomic significance of retractors in other groups of bony fishes has been dealt with by Dietz (1912, 1914, 1921) and Holstvoogd (1960, 1965). According to Nelson (1967), retractors probably have developed an attachment to the vertebral column independently in many evolutionary lineages of bony fishes. Probably in each lineage they are associated with and constitute part of an improvement or specialization in the feeding mechanism.

It is hardly to be doubted that the attachment to the vertebral column has been acquired independently among the eels. No other group having retractor muscles has both dorsal and ventral retractors attaching in common to the vertebral column. Indeed, except among eels, ventral retractors seem to be lacking. Thus, the attachment to the vertebral column of muraenines no doubt is another example of independent development. In this case they attach to the tooth plates of the pharyngeal

jaws and apparently constitute, with the pharyngeal jaws, an advancement or specialization in the feeding mechanism.

The common course and attachment of the retractors, both ventral and dorsal, to the vertebral column in morays are evidence that the muscles act together, simultaneously retracting both upper and lower tooth plates. Indeed, the construction of the plates and their supporting bones prohibits independent movement of the ventral and dorsal plates. Protraction probably occurs through the contraction of the subpharyngealis and the dorsal muscles joining the cranium and gill arches. Protraction and retraction probably succeed one another during the swallowing of prey. It is likely that, in the morays, the pharyngeal jaws and the muscles attached to them enable these forms to transport relatively large prey from the jaws into the esophagus, a distance which in eels is secondarily lengthened (Nelson, 1966). Thus, these structures appear to be adapted to the known predatory habits of the morays.

SUMMARY

1. Branchial muscles are described for six genera representing five eel families: *Conger* (Congridae), *Anguilla* (Anguillidae), *Moringua* (Moringuidae), *Kaupichthys* (Xenocongridae), *Uropterygius* and *Gymnothorax* (Muraenidae).

2. In the examined forms, muscles as well as gill arches suggest stages in an evolutionary sequence, with the Congridae being the most primitive and the Muraenidae being the most advanced.

3. Dorsal and ventral retractor muscles occur in all species examined. In eels of the subfamily Muraeninae they acquire secondarily an attachment to the vertebral column.

4. Gill arch muscles and pharyngeal jaws of muraenids are adaptations probably enabling these fishes to swallow large prey.

REFERENCES

BERTMAR, G. 1962. On the ontogeny and evolution of the arterial vascular system in the head of the African characidean fish *Hepsetus odoë*. Acta Zool. 43:255–294, 12 figs.

DIETZ, P. A. 1912. Vergelijkende Anatomie van de Kaak- en Kieuwboogspieren der Teleostei. Leiden. 196 pp., 25 figs.

——— 1914. Beiträge zur Kenntnis der Kiefer- und Kiemenbogenmuskulatur der Teleostier. I. Die Kiefer- und Kiemenbogenmuskeln der Acanthopterygier. Mitt. Zool. Stat. Neapel 22:99–162, 45 figs.

——— 1921. Über die systematische Stellung der Gadidae. Zugleich Nr. 2 der "Beiträge zur Kenntnis der Kiefer- und Kiemenbogenmuskulatur der Teleostier." Mitt. Zool. Stat. Neapel 22:433–457, 14 figs.

EDGEWORTH, F. H. 1935. The Cranial Muscles of Vertebrates. Cambridge Univ. Press. viii + 300 pp., 841 figs.

GREENE, C. W., and C. H. GREENE. 1913. The skeletal musculature of the king salmon. Bull. Bur. Fish. 33:25–59, 14 figs., 2 pls.

KESTEVEN, H. L. 1943. The evolution of the skull and the cephalic muscles. A comparative study of their development and adult morphology. Part I. The fishes (*continued*). Mem. Austral. Mus. 8:63–132, 69 figs.

HOLSTVOOGD, C. 1960. The importance of the retractores arcuum branchialium for the classification of teleostean fishes. Bull. Aquat. Biol. 2:49–50.

——— 1965. The pharyngeal bones and muscles in Teleostei, a taxonomic study. Proc. Konikl. Nederl. Akad. Wetens., Ser. C, 68:209–218, 12 figs.

NELSON, G. J. 1966. Gill arches of teleostean fishes of the order Anguilliformes. Pacific Sci. 20:391–408, 58 figs.

——— 1967. Branchial muscles in some generalized teleostean fishes. Acta Zool. [In press.]

PETUKAT, S. 1965. Über die arteriellen Gefässstämme bei den Teleostiern. Zool. Beitr. 11:437–515, 34 figs.

VETTER, B. 1878. Untersuchungen zur vergleichenden Anatomie der Kiemen- und Kiefermusculatur der Fische. Jena Z. Naturwiss. 12:431–550, pls. 12–14.