THE CRANIAL MUSCULATURE OF THE
TOADFISH (OPSANUS TAU).

by

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I. INTRODUCTION.

Although the toadfish (*Opsanus tau*) is well known to biologists, only a few papers are to be found that deal with its morphology. Miss Clapp, ('98) described the "Lateral Line System of *Batrachus tau*", and Gudger ('08) wrote, "The Habits and Life History of the Toadfish." A few embryological papers have been written on this aberrant teleost, latest of which is by Tracy ('26), "The Development of Motility and Behavior Reactions in the Toadfish (*Opsanus tau*)."

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The present paper aims to supply a brief account of the cranial muscles of *Opsanus tau*, which may be available for comparative purposes or for future developmental studies. Since the terminology of muscles in fishes has not been thoroughly standardized, the author deemed it desirable to construct a chart somewhat similar to Vetter's ('78). In this chart are tabulated in a comparative manner, for convenient reference, the cranial muscles of various fishes that have been described. The earliest work used in this paper is that on *Perca fluviatilis* (Owen '66). Other well known contributions to the cranial anatomy of fishes were made by Fürbringer ('75), Vetter ('78), and McMurrich ('84). Very extensive work has been done by Allis ('97, '03) on such familiar forms as *Amia calva* and *Scomber scomber*. The most recent work is that of Danforth ('13), "The Myology of *Polyodon*". At

present no group of vertebrates needs a comparative study more than do the teleosts, especially the higher and aberrant forms (Kingsley '25). Only *Esox* and *Acipenser* have been taken from Vetter's ('78) work, because they are the most representative forms. The designations used by Allis were employed as a basis, unless otherwise indicated, because *Scomber* is the nearest related teleost that has been described; and many of Allis' terms are based on the classical investigation done by Vetter ('78). Where the same name was not used by the various investigators, an attempt was made to find its homologue according to structure innervation and function.

CHART

Group	Pisces	Polyodon-spatula		Acipenser-sturio		Ama-calva		Amiurus-catus		Isos-lucius		Perca-fluviatilis		Scomber-scomber		Opsanus-tan	
		Danforth '13	N	Vetter '78	N	Allis '97	N	McMurrich '84	N	Vetter '78	N	Owen '66	N	Allis '03	N	Pankrats '27	N
Eye Muscles	Three Recti	typ.	III			typ.	III							typ.	III	typ.	III
	Lateral Rectus	+	VI			+	VI							+	VI	+	VI
	Superior Oblique	+	IV			+	IV							+	IV	+	IV
	Inferior Oblique	+	III			+	III							+	III	+	III
Mandibular	Intermandibularis	-		Hyl.	V	+	V	+	V	+	V	+	V	+	V	+	V
	Branchiomandibularis	+		+		+	1,2 3,0	-		-		-		-		-	
	Geniohyoideus	+	V	Con.sup	V	+	V	+	V	+	V	+	V	+	V	+	V
Hyoid.	Hyohyoideus	-		1 - 5	VII	+	VII	+	VII	+	VII	Lev.Br.Steg. Dep.Br.Steg.	V	+	VII	Lev.Br.Steg. Dep.Br.Steg.	V
	Pharyngo-hyoideus	-		-		-		Hyo.Br.	IX	Ph.Arc.	X	+	X	+	X	+	X
	Sterno-hyoideus	Cor.Arc.-Hyo.Cl	1,2	Cor.Arc., p.-a	1,2	+	1,2 3,4	Hyo.Pec.	3,9	+	(2)	Rot. Hyo	8	+	1,2	St.Hyo.-Rect.Ab	8
	Pharyngo-clavicularis-Ext.	+	(2)	-		+	X	+	IX	+	X	Br.Ret.Inf.	X	+	X	+	X
Pharyngeal	Pharyngo-clavicularis-Int.	or + (3)	"	-		+	X	+	X	+	X	Br.Ret.Sup.	X	+	X	+	X
	Constrictor Esophagei	+		-		Con.Ph.		-		Ph.Tr.	X	Ph.Tr.	X	+	X	+	X
Dorsal Mandibular.	Adductor Mandibularis	+	(2)	+	V	+	(3)	+	V	+	(3)	+	(3)	+	(3)	+	(3)
	Adductor Tentaculi :	-		-		-		+	V	-		-		-		+	V
	Levator Premaxillaris :	-		-		-		-		-		-		-		+	V
	Levator Maxillaris-Sup.	-		-		+	V	-		-		-		-		+	V
Opercular	Adductor Hyomandibular	P.Ret.Hyom.	VII	Ret.Hyom.	VII	+	VII	+	VII	+	VII	+	VII	+	VII	+	VII
	Dilator Opercularis	Pro.Hyom.	V	Pro.Hyom.	V	+	V	+	V	+	V	+	V	+	V	+	V
	Levator Opercularis	Op.	VII	Op.	VII	+	VII	+	VII	+	VII	+	V	+	VII	+	VII
	Adductor Opercularis	Ret.Hyom.	VII	Ret.Hyom.	VII	+	VII	+	VII	+	VII	Dep.Op.	V	+	VII	+	VII
Palatine	Levator Arcus Palatini	A.Pro.Hyom.	V	Pro.Hyom.	V	+	V	+	V	+	V	Lev.Tym.	?	+	VII	+	VII
	Adductor Arcus Palatini	Ret.Hyom.	VII	Ret.Hyom.	VII	-		+	VII	+	VII	Dep.Tym		+	VII	+	VII
	Interbranchialis	-		+	IX	-		-		-		-		+		-	
Branchial	Levator Arcum Branchialis	+	(4)	+	(5)	+	(6)	+	IX	+	(3)	Br. Lev. (4)	IX	+	(7)	+	(5)
	Interarcuales Dorsalis	-		-		-		-		-		+	?	+	(3)	-	
	Oblique Dorsalis	-		-		+	(3)	+	IX	+	(3)	Ma. B. ?	X	+	(3)	+	(2)
Dorsal	Transversus Dorsalis Ant.	Tr. Dor.		-		+	X	+	IX	+	?	+	X	+	X	+	X
	Transversus Dorsalis Post	-		-		+	X	+	X	+	?	+	X	+	X	+	X
	Retractor Arcum Br.	-		-		+	X	-		-		+	X	+	X	+	X
	Adductor Arcum Br.	-		+	(3)	+	(2)	-		-		Br.Dep.		+	(2)	-	
Ventral	Oblique Ventralis	-		-		+	(3)	+	X	Ph.Arc. (2)	X	+	(4)*	+	(2)	Ph.Arc. (2)	X
	Transversus Ventralis Ant.	-		Int.Arc.		+	X	+	IX	+	(4)	+	X	+	X	+	X
	Transversus Ventralis Post.	+	X	Vent. (5)	X	+	X	+	X	+	X	+	X	+	X	+	X
	Trapezius	+		-		-		+	1,2 3,8	+	1,2 3,8	+	1,2 3,8	-		+	1,2 3,8

* = According to other Authors

* = According to Vetter

Terminology of Allis used as a basis

CHART

Reference Letters

A. Pro. Hymd.	=	Anterior Part of M. Protractor Hyomandibularis.
Br. Dep.	=	Mm. Branchi-Depressores.
Br. Lev.	=	Mm. Branchi-Levatores.
Br. Ret. Inf.	=	Mm. Branchi-Retractores Inferioris.
Br. Ret. Sup.	=	Mm. Branchi-Retractores Superioris.
Con. Ph.	=	M. Constrictor Pharyngis.
Con. Sup.	=	M. Constrictor Superficialis.
Cor. Arc.	=	Mm. Coraco-Arcuales.
Dep. Br. Steg.	=	Mm. Depressores Branchiostegorum.
Dep. Op.	=	M. Depressor Opercularis.
Dep. Tym.	=	Mm. Depressores Tympani.
Hyo. Br.	=	M. Hyo-Branchialis.
Hyo. Cl.	=	M. Hyo-Clavicularis.
Hyo. Pect.	=	M. Hyo-Pectoralis.
Int. Arc. Vent.	=	Mm. Interarcuales Ventrals.
Lev. Br. Steg.	=	Mm. Levatores-Branchiostegorum.
Lev. Tym.	=	Mm. Levatores Tympani.
Ma. B.	=	M. Masto-Branchialis.
Myl.	=	M. Mylohyoideus.
N.	=	Nerve.
O.	=	Occipital nerve.
P. Ret.	=	Posterior Part of M. Retractor Hyomandibularis.
Ph. Arc.	=	Mm. Pharyngeus Arcuales.
Ph. Tr.	=	M. Pharyngeus Transversus.
Pro. Hymd.	=	M. Protractor Hyomandibularis.
Pty.	=	M. Pterygoideus.
Rect. Ab.	=	M. Rectus Abdominis.
Ret. Hymd.	=	M. Retractor Hyomandibularis.
Ret. Hyo.	=	M. Retractor Hyoideus.
S.	=	Spinal nerve.
St. Hyo.	=	M. Sterno-Hyoideus.
Tr. Dor.	=	M. Transversus Dorsalis.
Typ.	=	Typical.

III. METHODS AND MATERIAL

The heads of adult toadfish varying from ten to twenty centimeters in length were dissected, under the binocular when necessary, and drawings made of the different muscle layers. A number of specimens were macerated in dilute nitric acid and the nerve supply to the muscles determined. This method as used by Miss Clapp ('98), makes possible the dissection of even the very small nerves, since the acid dissolves the connective tissue sheaths. A number of heads of various sizes were also freed of all the muscles and connective tissue, and the skulls studied for origins and insertions of the muscles described. In order to clean the skulls, they were either boiled in a weak sodium carbonate solution, or allowed to macerate in tap water.

IV. DESCRIPTION AND DISCUSSION OF THE CRANIAL MUSCULATURE.

For descriptive purposes, the muscles are grouped under the following large divisions: Eye muscle, hyomandibular, opercular, branchial, and pharyngeal groups.

1. The Eye Muscle Group. The eyeball of *Opsanus tau* is large, the orbit long, and correlated with it are long and well-developed eye muscles. The number and arrangement of the muscles conforms essentially to the teleost type, as described by Allis ('03) in his work on *Scomber scomber*.

a. Mm. obliqui inferioris et superioris. The two

oblique muscles arise close together at the anterior part of the orbit, from the interorbital septum, at the junction of the ethmoid, vomer, and parasphenoid, posterior to the entrance of the nervus olfactorius into its ethmoid canal. The M. ^{Obliquus} ~~rectus~~ superioris passes lateral-ward superior to the nervus olfactorius, which lies free in the orbit for some distance. It is inserted in the bulbar fascia medial to the insertion of the M. rectus superioris, and is innervated by two small twigs from the long slender nervus trochlearis. The M. obliquus inferioris likewise passes laterally to insert near the M. rectus inferioris. It is innervated by a slender branch from the inferior division of the nervus oculomotorius. This branch passes forward under the medialis and recti inferior; and ventral to the nervus olfactorius.

b. Mm. recti medialis et lateralis et superioris et inferioris. The four recti muscles arise from a small area about the union of the interorbital septum, the basisphenoid, and the parasphenoid. Their origin is ventral to the nervus opticus which passes to the eyeball over the superior rectus and lateral to the medial rectus. They all become wide and tendinous, to insert on the fascia of the eyeball posterior to the edge of the cornea. The medial and inferior recti are innervated by branches from the inferior division of the oculomotor, and the superior rectus by the small upper division of the oculomotor. The lateral rectus is innervated by the abducens which penetrates its proximal third by two or three twigs.

2. The Hyomandibular Group.

a. M. adductor mandibularis. The M. adductor mandibularis is the most conspicuous dorsal muscle in the toadfish. It arises from the anterior surface of the preoperculum, and the antero-ventral margin of the frontal bone. The muscle appears to be composed of three well-fused parts, and forms a heavy tendinous insertion on the posterior and inner surface of the triangular process on the articular (A. figs. 1 & 3). It is innervated by four or five small branches from the nervus maxillaris inferioris, (Inf. M. fig. 11). The well-developed adductor of the mandible apposed by the large flat M. geniohyoideus functions as a very powerful adductor of the mandible. The structure of this group of muscles is well correlated with the voracious and carnivorous habits of the toadfish.

b. Mm. Pterygoidei. The M. pterygoideus anterioris lies medial to the anterior portion of the M. levator arcus palatini and the origin of the M. levator premaxillaris. It is very large at its origin arising from most of the ventral surface of the frontal bone, forming the posterior wall of the orbit. Towards its insertion it becomes small and tendinous to insert on the mesial surface of the articular ventral to the insertion of the M. adductor mandibularis (Pt. a. figs. 3, 7). It is innervated by a branch from the nervus maxillaris inferioris.

The M. pterygoideus posterioris (Pt. p. fig. 7) arises from the anterior surface of the hyomandibular bone and the ventral surface of the postorbital ossification. It is a thin triangular muscle which

becomes totally tendinous at its insertion, with the anterior on the articular. It receives its innervation from the nervus maxillaris inferioris.

The two *Mm. pterygoidei* are possibly homologous to the deeper parts of the *M. adductor mandibularis* as described by previous writers. They aid the *M. adductor mandibularis* in powerful adduction of the mandible.

c. *M. levator premaxillaris.* The *M. levator premaxillaris* is a long narrow muscle arising from the frontal, just medial to the origin of the antero-medial fibers of the *M. adductor mandibularis*. At its origin, it is a wide flat tendon and it inserts on the superior surface of the premaxillaris about one-third from its lateral extremity (L. Pr. fig. 1). It receives two or three small rami from the nervus maxillaris inferioris. The levator draws the corners of the mouth upwards and backwards.

d. *Mm. arcus palatini.* Medial to the origin of the *M. adductor mandibularis* the *M. levator arcus palatini* arises from the ventral surface of the frontal and from the postorbital ossification. It is a flat triangular muscle with the base dorsal and its apex inserted on the anterior surface of the dorsal end of the hyomandibular and the metapterygoid. The nervus maxillaris inferioris supplies this muscle with two or three small rami. It acts as a elevator of the hyomandibular and the metapterygoid, thus increasing the width of the palatine arch.

The adductor hyomandibularis et adductor arcus palatini are one continuous muscle. They arise from the lateral surface of the

parasphenoid and the vomer, and form a flat arched muscle in the roof of the mouth (Aap. Ah, fig. 8). A heavy fascia covers them dorsally and the thick and tough buccal lining ventrally. The fibers pass laterally to insert on the inner surface of the hyomandibular, maxillary and the mesial surface of the whole palatine arch. A portion of the M. adductor arcus palatini forms the ventral floor of the orbit. The nerve supply to this pair of muscles is from the nervus hyomandibularis. Their function is to adduct the palatine arch by depressing the hyomandibular and maxillary bones.

e. M. geniohyoideus. The most conspicuous muscle on the ventral surface is the long flat M. geniohyoideus that superficially covers the floor of the buccal cavity (Gh. fig. 5). Its fibers originate from most of the anterior surface of the ceratohyal (hyoid, Kingsley '25) and the base of the third branchiostegal ray. They pass medially and anteriorly to insert in a median aponeurotic band and the posterior surface of the dentary near the symphysis menti. The lateral part of the muscle near its origin is somewhat confined by a cartilaginous process on the ceratohyal (figs. 5, 6). This leaves a narrow area between the M. geniohyoideus and the mandible where the buccal floor is formed by a heavy fascia with a few transverse muscle fibers suggesting a M. mylohyoideus. The M. geniohyoideus is innervated by a large branch from the nervus mandibularis facialis externus (MeF. fig. 6). When the hyoid bone is fixed by its other muscles, the M. geniohyoideus functions as the depressor of the mandible. When the mandible is fixed or adducted, it forcefully

depresses the hyoid apparatus as in regurgitation, and expulsion of water.

f. M. hyohyoideus. The M. hyohyoideus in the toadfish is a long flat superficial muscle (Hh. fig. 5). It arises from a median aponeurosis, common to both which extends forward to the first basibranchial (copula, Gengenbaur '98). It passes posterolaterally to insert on the medial surface of the ventral branchiostegal ray at the point of its greatest curvature. A branch from the hyomandibular nerve ramifies over its middle ventral surface. The hyohyoideus in the toadfish functions as the most powerful depressor of the branchiostegal rays.

3. The Opercular Group.

a. M. dilator opercularis. The M. dilator opercularis is a large triangular muscle which lies in the dorsal temporal groove (Do. fig. 1). It also takes origin from a dorso-medial and transverse crest of the frontal, from the postorbital, squamosal, and the dorsal groove in the hyomandibular bone. The fibers converge and pass posterolaterally to insert on the superior to the articulation of the operculum with the hyomandibularis. It is innervated by small branches from the nervus maxillaris inferioris.

b. M. levator opercularis. The M. levator opercularis is a much smaller conical muscle, (Lo. fig. 1), which arises from the postero-dorsal surface and crest of the squamosal bone. As in Scomber, it is contiguous with the dilator at its origin and its anterior fibers run parallel to, and in contact with the posterior fibers of the former.

It is innervated by a small superior branch of the nervus hyomandibularis. The two muscles abduct and elevate the operculum thus increasing the capacity of the branchial cavity. This pair is apposed by the M. adductor opercularis and the ventral hyoid group.

c. M. adductor opercularis. The M. adductor opercularis, (Ah. fig. 7) is a triangular muscle arising from portions of the lateral surface of the squamosal, intercalar, petrosal, and lateral occipital bones. Its anterior fibers originate just posterior to the foramen of the facial nerve and pass postero-laterally immediately posterior to the branchial levators. The apex of the triangular muscle inserts on the inner surface of the operculum. It is innervated by the nervus hyomandibularis and acts as a strong depressor of the operculum.

4. The Branchial Group.

a. M. depressores branchiostegorum. In the second ventral layer, there are three pairs of small triangular muscles which connect the ceratohyal and the bases of the branchiostegal rays. The medial is the largest and arises from the postero-medial surface of the ceratohyal and inserts on the medial-proximal portion of the first branchiostegal ray (D. Br. fig. 6). The other two parts have their origin from the more distal part of the ceratohyal and the lateral surface of first and second rays, and insert on the medial surfaces of the second and third rays. They are innervated by the nervus hyomandibularis. This group act as depressors of the branchiostegal rays (figs. 5, 6); hence the name depressores

branchiostegorum (Owen '66) is appropriate. Owen ('66) describes this group of muscles in *Perca fluviatilis*. These muscles are not mentioned by other authors and are apparently absent in the more generalized fishes. This group with the *Mm. levatores branchiostegorum* regulate the capacity of the branchial chamber. Since the toadfish is a sluggish bottom feeder, this muscular arrangement makes possible forceful expulsions of water under asphyxial conditions.

b. *M. levatores branchiostegorum*. The muscles of the branchiostegal rays are well-developed. As in Scomber, the toadfish usually has seven branchiostegal rays (B. R. G. fig. 5). These rays are firmly bound together by a heavy fascia in whose inner layer lies embedded a layer of thin oblique muscle fibers. These muscle fibers elevate and draw the rays together, thus aiding the *Mm. depressores* in regulating the size of the branchial chamber (L. Br. fig. 1). To the writer's knowledge, similar muscles have been described only in *Perca* by Owen ('66). He calls them the *levatores branchiostegorum* which is accepted by the writer. These muscles receive small rami from the *nervus hyomandibularis*.

c. *Mm. levatores arcuum branchialium*. The *Mm. levatores arcuum branchialium* muscles consist of two interni and three externi (Labl. a-p, Labe. a. m. p. fig. 10). They arise from the base of the skull, from the ventral surface of the petrosal, intercalar, and squamosal. The posterior externus inserts on the fourth branchial arch, which has no gills, and is nearly twice as large as

the others. The third and second arches have only one levator, while the first arch has a separate muscle. The first two externi insert on the epibranchial cartilages, (suprapharyngeal processes of Allis '03), immediately proximal to the gills. The third externus inserts on the epibranchial cartilage opposite the insertion of the M. pharyngo-clavicularis. These muscles raise the gill arches and draw them slightly toward the median line. The two internal levators arise immediately medial to the three external muscles, and pass ventrally to insert on the dorsal surface of the three pharyngo-branchial cartilages near the median line (fig. 10). Allis ('03) calls these cartilages the infrapharyngo-branchials.

The nervus glossopharyngeus passes laterally between the two internal levators, its ganglion (fig. 11) lying immediately lateral to the anterior internal and medial to the anterior and middle external levators. The five levators are innervated by the branches of the ninth and tenth nerves of their respective arches. The anterior externus and internus are supplied by the nervus glossopharyngeus.

d. Mm. obliqui dorsales. The two dorsal oblique muscles (mm. adductores arcuum branchialium), have a common origin from the posterior surface of the second pharyngo-branchial cartilage between the insertion of the retractor arcuum branchialis dorsalis and the anterior levator arcus branchialis internus. The most dorsal is the larger and inserts on the epibranchial cartilage of the fourth medially to the external levator (abd. fig. 10). The deeper and smaller oblique is covered by the former and inserts on the

epibranchial cartilage of the third arch laterally to the *Mm. retractores arcuum branchialium dorsales* and in conjunction with a slip of the *M. transversus dorsalis posterioris*. They are innervated by rami from the first divisions of the nervus vagus. Their action is primarily to adduct the branchial arches, although apparently only a limited amount of adduction is possible.

e. *Mm. retractores arcuum branchialium dorsales*.

The *Mm. retractores arcuum branchialium dorsales* (Rbad. fig. 9, 10) are paired muscles lying longitudinally and dorsally to the pharynx. It arises by a continuous, tendinous slip from the bodies of the fourth, fifth, and sixth vertebrae. The muscle becomes wider and passes ventral to the *Mm. pharyngei transversi dorsales* to insert in the roof of the pharynx. Its insertion is on the first three pairs of pharyngo-branchial arches, medially to the insertion of the internal levatores and the dorsal oblique muscles. Small rami from the fourth division of the nervus vagus pierce its anterior portion. It functions as a powerful retractor of the branchial arches, causing the individual arches to separate, thus apposing the dorsal oblique muscles.

5. The Pharyngeal Group.

a. *Mm. Pharyngei transversi*. Most generalized fishes have a single muscle mass in the dorsal wall of the pharynx (*m. pharyngeus transversus ventralis, anctorum*). In *Scomber scomber*, however, these muscle masses are more specialized and divide into an anterior and posterior muscle. This condition also exists in *Opsanus tau*. The *M. pharyngeus transversus dorsalis anterioris* (Tda. fig. 10) the

larger of the two dorsal muscles, arises in common with its mate from a median raphe. It passes laterally between the two internal levators of the branchial arches to insert with the second levator arcus branchialis externus on the epibranchial cartilages of the second and third arches. The *M. pharyngeus transversus dorsalis posterioris* (Td p. fig. 10) is much smaller and is composed of two minor slips arising in the median common raphe and inserts on the epibranchial cartilages of the third and fourth branchial arches. Their innervation is from the rami of the nervus vagus supplying the arches related to each muscle. They act, as Danforth (*13) says of *Polyodon*, as constrictors of the pharynx.

The *Mm. pharyngei transversi ventrales* originate from the median aponeurosis and the ventral surfaces of the hypobranchials of the third and fourth arches. The anterior passes postero-laterally to insert on the medial surface of the cerato-branchial of the fourth arch near the insertion of the pharyngo-hyoideus. This muscle appears to be the muscle which Vetter (*78) describes as the *M. pharyngeus transversus* (Tva. Tvp. fig. 9). The posterior muscle is wide and flat, having a very extensive insertion along the mesial surface of the fourth cerato-branchial arch. Both muscles are innervated by branches from the fourth ramus of the nervus vagus. They function as constrictors of the pharynx, while the anterior also slightly pulls the pharynx forward.

b. *Mm. Pharyngo-claviculares.* In the toadfish, as in *Scomber scomber*, two muscular slips connect the pectoral arch with

the pharynx. The largest, the *M. pharyngo-clavicularis internus* (Poi. fig. 4.) originates from the anterior surface of the cleithrum, (clavicle of older writers) opposite the pelvic fin. It passes medially and forward to insert on the ventral curvature of the fifth ceratobranchial opposite the origin of the pharyngohyoideus muscle.

The *M. pharyngo-clavicularis externus* (Pce. figs. 4, 9) arises from the anterior surface of the cleithrum, just opposite the pectoral fin and passes forward somewhat dorso-medially to insert on the posterior surface of the fifth cerato-branchial arch near the internus. They are both innervated by branches from the pharyngeal root of the vagus (fig. 11). Their most important action is to draw the pharyngeal and the whole branchial apparatus backward and downward.

c. *Mm. pharyngo-abdomini.* Due to the jugular position of the pelvic fins, the ventral musculature is somewhat different from that in any of the forms tabulated on the chart. The superficial layer is a cephalad extension of the ventral abdominal musculature which continues over the cleithrum to attach on the ventral surfaces of the second, third and fourth basibranchials. A band of fascia separates the two divisions of the ventral musculature. It shows the definite segmentation of the body musculature. This layer may be called a *rectus abdominis* (R. A. fig. 4). Maurer ('94) describes a similar arrangement in various teleosts. A deeper layer arises from the anterior surface of the cleithrum and passes forward to insert on the postero-ventral surface of the last basibranchial (Sh. fig. 6). This corresponds to the *M. stenohyoideus* in Scomber, although no sternum is present. This group is innervated by the first spinal nerve. Their

usual action is to pull the hyoid bone backwards and downwards, thus depressing the floor of the mouth. With the hyoid bone fixed, they will slightly pull the cleithrum and pelvic girdle forward.

d. Mm. interacuales ventrales. Lateral to the median ventral aponeurosis and dorsal to the M. stenohyoideus lies the round M. pharyngo-hyoideus. It arises from the posterior surfaces of the first and second basibranchials (Kingsley '25) and passes postero-laterally to insert on the anterior surface of the hypobranchial of the fourth arch medially to the insertion of the M. pharyngo-clavicularis internus (Ph. figs. 4, 9). This muscle is innervated by a pharyngeal ramus of the vagus nerve. When the hyoid is fixed, it draws the pharyngeal arch forward; and when the pharynx is fixed, it depresses the buccal floor.

Dorsal to the M. pharyngo-hyoideus, there are two small oblique muscles (Ov. 1-2) called the fourth ventral oblique in Scomber by Allis ('03) and Mm. pharyngo-arcuales by Vetter ('78). To the writer, the name used by Vetter seems preferable. The larger and most ventral arises from the posterior surface of the second basibranchial and hypobranchial cartilages to insert on the anterior surface of the hypobranchial of the fourth arch dorsal to the M. pharyngo-hyoideus (P. a. 1, fig. 9). Inserting with this is the smaller and deeper muscle which arises from the third basibranchial (P. a. 2, fig. 9). These muscles are innervated by the pharyngeal ramus of the nervus vagus. Their function is like that of the pharyngo-hyoideus.

e. M. constrictor oesophagei. The M. constrictor

oesophagei is well-developed in the toadfish. The dorsal portion of the constrictor lies ventral to the *M. retractores arcuum branchialium* and the *M. transversus dorsalis posterioris*. In *Amia* and *Polyodon*, the constrictor pharyngis (oesophagei) is continuous with the transversus posterioris on both dorsal and ventral surfaces. In the toadfish, this muscle is continuous only with the *M. transversus posterioris ventralis*. It is a constrictor attached continuously to the entire inner surface of the fourth branchial arch, with strongly developed connections to the pharyngo-branchial and epibranchials of that arch (C. E. figs. 9, 10). It always presents a well-developed posterior annular portion (fig. 9). It is innervated by small rami from the pharyngeal rami of the nervus vagus. The large constrictor makes possible such forceful regurgitations as the toadfish manifests. All of the preserved specimens have an involuted oesophagus.

6. Pectoral and Pelvic Girdle Musculature. Only a very general statement can be made in this paper concerning this group. The description of the *M. trapezius* is in an unsettled state, and the two girdles need further investigation. As Vetter (*78) has stated, the trapezius in bony fishes is not present as a muscle that passes from the pectoral girdle to the cranium. The trapezius is rather represented by a layer of dorsolateral trunk musculature which inserts on the superior occipital, exoccipital, parietal, and lateral occipital bones (Tp. fig. 1). It does, however, give an attachment to the suprascapular as it passes over that bone. It is innervated by the first spinal nerves. Its action is to elevate the head slightly,

but more to aid in the lateral body movements.

The pectoral muscles have been described in such forms as *Scomber*, *Polyodon* and *Amiurus* in conjunction with the cranial musculature. The author has found that the pectoral muscles are well developed due to the large fin and conform very closely to the description given by Allis ('03) of *Scomber scomber* (figs. 1, 4, 5, 6).

The pelvic fin is small and lies antero-medially to the pectoral fin. Its musculature is the most complicated in structure of all the fins (Danforth '13). The pelvic fins and their musculature have been thoroughly described in a large number of forms by Davidoff ('78, '80).

V. DISCUSSION

In general, the cranial musculature of the toadfish is like that of *Amia* and *Scomber*, although less complex. The definite differences are: No *M. intermandibularis*; no *M. branchiomandibularis*; a long conical *M. levator premaxillaris* is present, innervated by the fifth nerve; seven branchiostegal rays connected by a heavy layer of fascia and oblique muscle fibers; and three pairs of triangular shaped muscles arising from the ceratohyal and the first two branchiostegals inserting on the proximal medial surface of the first three branchiostegals successively. The latter are called *depressores branchiostegorum* as described by Owen ('66) in *Perca fluviatilis*. Especially well-developed are the masticator muscles represented by the prominent cylindrical adductor mandibularis and two triangular shaped anterior and posterior pterygoideus muscles.

The *M. levator arcus palatini* lies between the two *Mm. pterygoidei* and the *M. adductor mandibularis*. The buccal roof is formed primarily by the flat arched *M. adductor arcus palatini* and the *M. adductor hyomandibularis*. This group is innervated by the fifth-seventh nerve complex. The large eye and long orbit are correlated with well-developed typical eye muscles.

The operculum is abducted by a large dilator and elevated and depressed by two smaller muscles, all innervated by the fifth and seventh nerves.

The gill apparatus is composed of four branchial arches, the fourth without gills and giving origin to the large *M. constrictor esophagei*. The arches are elevated by two internal and three external levator muscles; they are retracted by a pair of long *Mm. retractores arcuum branchialium*. Two transverse and oblique muscles draw the dorsal portion of the arches together. Ventrally the gill arches are adducted and the pharynx constricted by the two *Mm. pharyngo-arcuales*, *M. pharyngo-hyoideus*, and the *Mm. transverse*. The branchial and pharyngeal muscles are innervated by the ninth and tenth nerves.

The ventral segmented *M. rectus abdominis* and the smaller *M. sterno-hyoideus*, separated by a median aponeurosis connect the cleithrum and the pelvic girdle with the hyoid bone. These muscles appose the large *M. geniohyoideus* in depressing the hyoid bone and the buccal floor. The fourth branchial arch is connected with the cleithrum by a *Mm. pharyngo-clavicularis internus et externus*.

The pectoral fins are large and its muscles well-developed, while the jugular pelvic fins are small and its musculature complex.

The mandibular musculature, as a whole, is well adapted to the voracious and carnivorous habits of the toadfish. The branchial mechanism is adapted for a high degree of efficiency in the utilization of water with a low oxygen content, to which individuals of this species are often subjected. The branchial chamber is large, because of length and flexibility of the seven branchiostegal rays with their fascial connections with the operculum and their dilators and compressors (*mm. levatores et depressores branchiostegorum*). The opercular aperture is relatively small and entirely posterior, so that the water during expiration flows not only through the gill slits, but also washes along the more posterior gills on its way out. In this way, there is secured a maximal exposure of the water to the respiratory surfaces.

VI. SUMMARY.

The cranial musculature of the toadfish is more specialized than any of the teleosts which have been previously described. The eyeball is large and has long typical muscles. No intermandibularis nor branchiomandibularis is present. A levator premaxillaris muscle, innervated by the fifth nerve and not described before, is present. It has seven branchiostegal rays connected by a heavy fascia and oblique levator muscles. They are depressed by three small adductors. The innervation of the two groups is from the fifth and seventh nerves. The gill apparatus is composed of four pairs of branchial arches — the last one without gills. The arches have a complete set of levators, adductors, and retractors, innervated by the ninth and tenth nerves. Especially

well developed are the masticator muscles represented by a large adductor mandibularis and an anterior and a posterior pterygoid muscle. This group is innervated by the fifth-seventh nerve complex. The pelvic fins are small and have a jugular position, while the pectoral fins are large. Two narrow muscles connect the cleithrum with the pharynx. A short heavy median raphe joins the medial end of the cleithrum and the pelvic girdle. The ventral segmented rectus abdominis, separated by a median aponeurosis, passes over the cleithrum and attaches to the basibranchials. No sternum is present, but a sternohyoid muscle connects the cleithrum with the branchial arches. This group and the hyohyoid muscle appose the large geniohyoid in depressing the hyoid bone and the buccal floor. A large trapezius muscle is present.

The cranial anatomy of the toadfish is well-adapted to its carnivorous habits; and the structure of its branchial apparatus makes efficient respiration possible under asphyxial conditions.

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VIII. REFERENCE LETTERS AND FIGURES WITH
DESCRIPTION.

Reference Letters

A.	= M. Adductor Mandibularis.
Aap.	= M. Adductor Arcus Palatini.
Ah.	= M. Adductor Hyomandibularis.
AO.	= M. Adductor Opercularis.
Ar.	= Articular.
B. B.	= Basi-Branchial.
B. H.	= Basihyal Cartilage.
B. R. G.	= Branchiostegal Rays.
Buc. f. 1	= N. Ramus Buccalis Facialis Medialis.
Buc. f. 2	= N. Ramus Buccalis Facialis Lateralis.
C.	= Cerebrum.
C. B.	= Cerebellum.
CB. 3	= Third Ceratobranchial.
CB. 4	= Fourth Ceratobranchial.
C. E.	= M. Constrictor Esophagei.
C. H.	= Cerato-hyal (hyoid)
Cl.	= Cleithrum (clavicle of old authors).
Com. VII-X	= Commissure Between VII and X.
D.	= Dentary.
D. Br.	= Mm. Depressores Branchiostegorum.
Do.	= M. Dilator Opercularis.
Fr.	= Frontal.
F. Rec.	= Recurrens Facialis.
G.	= Gills.
GH.	= M. Genio-Hyoideus.
H. B. 1	= Hypobranchial.
Hh.	= M. Hyo-hyoideus.
HMD.	= Hyomandibular.
Hmf.	= Nervus Hyomandibularis.
Inf. M.	= Nervus Maxillaris Inferioris.
Labe-a	= M. Levator Arcus Branchialis Externus Anterioris.
Labe-m	= M. Levator Arcus Branchialis Externus Medialis.
Labe-p	= M. Levator Arcus Branchialis Externus Posterioris.
Labi-a	= M. Levator Arcus Branchialis Internus Anterioris.
Labi-p	= M. Levator Arcus Branchialis Internus Posterioris.
L. Br.	= Mm. Levatores Branchiostegorum.
Ll. V.	= Nervus Lineae Lateralis Vagi.
L. O.	= M. Levator Opercularis.
L. Pr.	= M. Levator Premaxillaris.
Md.	= Medulla Oblongata.
M e f.	= N. Ramus Mandibularis Externus Facialis.
Mx.	= Maxilla.

N. Ac.	=	Nervus Acusticus.
N. GL.	=	Nervus Glossopharyngeus.
N. OL.	=	Nervus Olfactorius.
O. B.	=	Bulbus Olfactorius.
Obd.	=	M. Obliquus Dorsalis Superficialis.
Op.	=	Operculum.
Op. f.	=	Ramus Ophthalmicus Superficialis.
Op. L.	=	Lobus Opticus.
Op. t.	=	Ramus Ophthalmicus Trigenimus. —
OS.	=	Opercular Spine.
Ov. 1-2	=	M. Obliquus Ventralis 1-2.
P. B. 1	=	Pharyngo Branchialis (First)
Pce.	=	M. Pharyngo-Clavicularis Externus.
Pci.	=	M. Pharyngo-Clavicularis Internus.
Pe. F.	=	Pelvic Fin.
P. f.	=	Nervus Palatinus Facialis.
P. F.	=	Pectoral Fin.
P. GI.	=	Nervus Palatinus Glossopharyngeus.
Ph.	=	M. Pharyngo-Hyoideus.
P. OP.	=	Preoperculum.
Pr.	=	Premaxillaris.
P. S.	=	Parasphenoid.
Pt. a.	=	M. Pterygoideus Anterioris.
Pt. p.	=	M. Pterygoideus Posterioris.
Q.	=	Quadrate.
R. A.	=	M. Rectus Abdominis.
Rbad.	=	M. Retractor Branchialium Arcuum Dorsalis.
S.	=	Skull.
Sh.	=	M. Sterno-hyoideus.
Tda.	=	M. Transversus Dorsalis Anterioris.
Tdp.	=	M. Transversus Dorsalis Posterioris.
Te. V.	=	Nervus Temporalis Vagi.
Tp.	=	M. Trapezius.
Tr. R.	=	Nervi Trematici Vagi.
Tva.	=	M. Transversus Ventralis Anterioris.
Tvp.	=	M. Transversus Ventralis Posterioris.
U. L.	=	Upper Lip.
V.	=	Vertebra.
VO.	=	Vomer.
II.	=	Nervus Opticus.
III.	=	Nervus Oculomotorius.
IV.	=	Nervus Trochlearis.
VI.	=	Nervus Abducens.

DESCRIPTION OF FIGURES

PLATE I.

- Figure 1. Dorsal view of the head showing the superficial musculature.
Figure 2. Dorsal view of skull (modified from Clapp).
Figure 3. Mesial view of the right mandible.
Figure 4. Lateral view of the right cleithrum and part of the fourth and third branchial arches with the associated muscles.

PLATE 2.

- Figure 5. Ventral view of the superficial layer of muscles.
Figure 6. Ventral view of the deeper layer of muscles.

PLATE 3.

- Figure 7. Ventral view of the Mm. pterygoidei with mandible intact.
Figure 8. Ventral view of the buccal roof (palatine arch) showing the M. adductor arcus palatine, M. Adductor hyo-mandibularis and M. adductor opercularis.
Figure 9. Ventral view of the branchial apparatus.
Figure 10. Dorsal view of the branchial apparatus.

PLATE 4.

- Figure 11. Dorsal optical view of the brain and the cranial nerves.

Plate I.

Fig. 1.

Fig. 3.

Fig 2.

Fig. 4.

Plate II.

Fig. 5.

Fig. 6.

Plate III.

V.O.

Fig. 7.

MX. P.S.

D.
Pta.
Pt.p.

Fig. 8.

M.X.

D.
Aap.
Ah.

Ao.

S.

V.

BH.

H.Bi.
Ov. 1-2.
(P.a. 1-2)

Tvp.

C.E.

Fig. 9.

BB.

CH.

Ph.

Tva.

Tda.

C.B. Labip.

L.Br. Tdp.

BR.G.

G.

Pce.

Rbad.

P.B.

Rbad.

Fig. 10.

Labi.a.

Obd.

Labe.a.

Labem.

Lbe.p.

C.E.

Plate IV.

Fig. 11.