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THE COMPARATIVE MORPHOLOGY OF
EXTRINSIC GASBLADDER MUSCULATURE
IN THE SCORPIONFISH GENUS *SEBASTES*
(PISCES: SCORPAENIDAE)

By

Leon E. Hallacher

San Francisco State University
San Francisco, California 94132¹

ABSTRACT: Phylogenetic relationships within the rockfish genus *Sebastes* (Scorpaenidae) are not well understood. Study of variation in the structure of extrinsic gasbladder musculature within this group may help clarify understanding of evolutionary relationships. Eighty-two species of rockfishes were dissected for examination of gasbladder muscles. Possible evolutionary implications are discussed. The function of the gasbladder muscles is sound production, but they may also be used for sound reception.

INTRODUCTION

The rockfish genus *Sebastes*, of the family Scorpaenidae, contains approximately 100 species, ranging in size from about 200 mm. to 1000 mm. standard length as adults (Phillips, 1957; Eschmeyer and Hureau, 1971). Unlike most species of scorpionfishes which are tropical in distribution, rockfishes inhabit cold temperate seas. They are found principally in the North Pacific from Japan to Mexico, although a few species can be found in the North Atlantic and in the temperate Southern Hemisphere (Eschmeyer and Hureau, 1971). Fifty species of rockfishes may occur at a single latitude with up to 10 species occurring at a single collecting station. This high degree of congeneric sympatry

¹Present address: Department of Zoology, University of California, Berkeley, CA 94720. This study formed the basis of a Master's thesis at California State University, San Francisco.

is of interest to community ecologists studying division of resources and isolating mechanisms.

Although rockfishes are important to commercial and sports fisheries, little is known about their biology. All rockfishes are believed to be generalized large-mouthed carnivores. They vary from benthic hole-dwelling solitary species to schooling species that live off the bottom in the kelp canopy or in open water. They are ovoviparous, giving birth to large numbers of yolk-sac larvae (Moser, 1967).

Field observations made in 1970 by the author indicated that several species can be stimulated to produce sounds under stress. Recent work by McInerney and Yearsley (in press) shows that rockfishes produce sounds during agonistic encounters. The sound producing mechanism consists of a pair of muscles, one on each side of the midline, originating on the occipital portion of the cranium and inserting on the gasbladder. Gasbladder muscles of this sort were first called "extrinsic" by Dufosse (1874) because they inserted on the gasbladder at one end and elsewhere at the other end. Muscles with both points of insertion on the gasbladder wall, such as those found in triglids (Tower, 1908), were labeled by Dufosse as "intrinsic." In this paper, muscles originating on the cranium and inserting on or near the gasbladder will be called extrinsic gasbladder muscles or, simply, gasbladder muscles.

The first major work which described these gasbladder muscles for a variety of scorpaenid fishes was that of Matsubara (1943). All the scorpaenids dissected by Matsubara have some type of muscle associated with the gasbladder, although a variety of morphological patterns exist. For Oriental rockfishes, he showed that intrageneric variations in the structure of these muscles do exist. Dissections made on 82 species of rockfishes in the present study also reveal great variations in the patterns of the gasbladder muscles within *Sebastes*.

The species in the genus *Sebastes* are well known from several regional works (Matsubara, 1943; Phillips, 1957; Barsukov, 1964), but a worldwide review has not yet been attempted. One character that may be useful in an attempt to clarify phylogenetic relationships within this genus is the variation in the structure of the extrinsic gasbladder musculature.

As a result of the attempt to clarify the possible origin and evolution of the various rockfish muscle patterns, dissections were made on representatives from 23 other genera in the family Scorpaenidae and on fishes from 9 other families in the order Scorpaeniformes. The classification of groups within this order is uncertain (Greenwood *et al.*, 1966), and it is possible that an eventual overall survey of gasbladder musculature will aid in the understanding of phylogenetic relationships in the so-called mail-cheeked fishes.

Another character not surveyed in this study that may also prove useful

in clarifying phylogenetic relationships within *Sebastes* is variability in gasbladder structure itself. The morphology of rockfish gasbladders appears to be diverse. Variability in the thickness of gasbladder walls, in attachment of the bladder, and in division of the bladder into two chambers is apparent (see also Matsubara, 1943, p. 126-147).

ACKNOWLEDGMENTS

Specimens used in this study were obtained from a variety of sources. Eastern Pacific material came principally from the California Academy of Sciences fish collection, although some material was obtained from the collection at California State University at San Diego and the Scripps Institution of Oceanography. Western Pacific material came from the California Academy of Sciences fish collection and from the Museum of Zoology of the University of Michigan.

Field collections were made during the course of this study to provide fresh material. I wish to thank the following people for their aid: Dr. George W. Barlow of the University of California at Berkeley who first advised the author of sound production by rockfishes; Dr. John S. Stevens of Occidental College and the crew of the research vessel *Van Tuna*, who provided specimens from Catalina Island off southern California; Dr. Lo-chai Chen of California State University at San Diego and the Scripps Institution of Oceanography for supplying a boat for collections made off La Jolla, California; Dr. Tomio Iwamoto of the California Academy of Sciences, who collected specimens off British Columbia from the research vessel *G. B. Reed*; Dr. William N. Eschmeyer of the California Academy of Sciences, who collected specimens off the Oregon coast from the Oregon State University vessel *Yaquina*; Dr. Eschmeyer, Dr. Chen, Christopher Tarp, Frederick Jones, and Ernest W. Iverson, who assisted in making collections from sportfishing boats; David W. Behrens, Kenneth R. McKaye, and divers from the University of California at Berkeley Diving Program, who aided the author in netting and spearing shallow water species; Daniel J. Miller and Robert N. Lea of the California Department of Fish and Game, who donated specimens; Dr. Reeve M. Bailey, Dr. Robert R. Miller, and staff of the Museum of Zoology of the University of Michigan, who provided the assistance to Dr. William N. Eschmeyer which resulted in the loan of Oriental specimens from their University collection; Dr. John E. McInerney and Dr. John H. Yearsley for allowing me to read their manuscript on sound production by rockfishes.

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METHODS

In this paper the term gasbladder has been applied to the structure more commonly referred to as the airbladder or swimbladder. This follows the terminology suggested by Lagler, Bardach, and Miller (1962). Since the gasbladder in rockfishes is physoclistous (no duct connects the gasbladder to the alimentary canal) and inflated by means of a gas gland, the term gasbladder seems more appropriate than either alternative expression. In accordance with this terminology, any specialized muscles associated with the gasbladder have been referred to by this author as gasbladder muscles rather than the more commonly used 'swimbladder muscles'.

Extrinsic gasbladder muscles were exposed for examination by dissection. These muscles appear to have arisen from the ventral fibers of the epaxialis (the dorsal half of the lateral body musculature). All species have a pair of muscles, one on each side of the midline. They extend posteriorly from their origin on the occipital region of the cranium to the gasbladder or vertebral parapophyses where they insert by means of tendons. Since their position relative to skeletal structures is constant throughout the genus, one standard dissection technique was sufficient for all rockfish species and could be done with a scalpal and forceps. In preliminary dissections, the muscles from both sides of specimens were examined with no structural differences being observed. All subsequent dissections were made on the right side of specimens, with only the muscle on the right side being examined. A large patch of skin was removed, its perimeter extending along the rear of the cranium and pectoral girdle, posteriorly along the base of the spinous dorsal fin to its end, downward to the ventral half of the fish's side and forward to the pectoral fin axil.

All exposed muscle tissue lying dorsal to the right dorsal ribs was removed. The right gasbladder muscle was exposed to view by gently breaking away the dorsal ribs. Care was taken while removing the first two dorsal ribs since the

gasbladder muscle lies just ventral to them. In most species of rockfishes the muscle passes between the second and third ventral ribs so that it is found on the visceral cavity side of the third through eighth ventral ribs.

Once the gasbladder muscle was exposed, all skeletal muscle tissue surrounding it was plucked away cautiously to expose the muscle from its point of origin on the cranium to its points of insertion on the gasbladder or vertebral parapophyses. The insertion points were determined by clearing away all intercostal muscle between the ventral ribs. Once the first eight or nine ribs were exposed, the dense tendon tissue of the gasbladder muscle was seen extending laterally just under the ribs. These whitish tendons were followed to their points of insertion on the vertebral parapophyses. In species where these tendons inserted first upon the gasbladder, an incision into the body cavity was made to examine posterior insertion sites.

Another method was sometimes used in species where the insertion points on the vertebral parapophyses were not readily determined from a dissection of lateral body musculature. The body cavity was entered from the ventral side and the viscera and the gasbladder were removed. Once the gasbladder was removed, the whitish tendons of the gasbladder muscle could be seen inserting on the vertebral parapophyses.

Dissections of other members of the order Scorpaeniformes were conducted in much the same manner since their gasbladder muscles were located in the same general area of the lateral skeletal musculature. The notable exceptions were members of the suborder Cottoidei. In species of this group, muscles termed "cranioclavical muscles" by Barber and Mowbray (1956) extend from the posterior cranium to the pectoral girdle. To expose these cranioclavical muscles, only musculature situated directly behind the cranium was removed.

At the onset of the study, radiographs were taken of dissected specimens to clarify the topographic relationships of the origin and insertion points of the extrinsic gasbladder musculature. Once the anatomy of these fishes became familiar, radiography was no longer required for the majority of species.

Specimens used in the study are listed in the appendix.

RESULTS

Dissection of 82 species of rockfishes reveals considerable variation among species in gross morphology of the extrinsic gasbladder musculature. In species where both sexes were examined no sexual dimorphism was observed. Several insertion points may be listed for one muscle because of the fact that in most cases, the striated muscle tissue of the gasbladder muscle ends in one to several tendons after the muscle passes under the third rib. In several species, only one or two tendons develop from the muscle, but later branch to insert on several different vertebral parapophyses. Table 1 summarises origin and insertion points for the gasbladder muscles of all rockfishes examined.

TABLE 1. *Muscle type and points of insertion of the gasbladder muscle for all species of Sebastes examined. Where more than one specimen of a species was examined, the information on each specimen examined is listed. Abbreviations for the points of insertion are as follows: gb represents the gasbladder, r-1 thru r-4 represent the first through the fourth ventral ribs, and v-7 through v-11 represent the seventh through the eleventh vertebrae. Muscle category includes major type (either Type I or Type II) and the subdivision within a type: a-z = aleutianus-zacentrus, a-v = atrovirens-vexillaris, i-v = ijimae-vulpes, p = paucispinis, s = serriceps, t = taczanowskii, m = marinus.*

Species	Muscle Category	Points of Insertion									
		gb	r-1	r-2	r-3	r-4	v-7	v-8	v-9	v-10	v-11
<i>aleutianus</i>	I a-z						×	×	×		
<i>alutus</i>	I a-z			×		×	×	×			
"	I a-z			×		×	×	×	×		
<i>auriculatus</i>	I a-z							×	×	×	
"	I a-z							×	×	×	
"	I a-z							×	×	×	
<i>aurora</i>	I a-z			×		×	×				
<i>atrovirens</i>	II a-v	×						×	×	×	
"	II a-v	×						×	×	×	
<i>babcocki</i>	I a-z		×	×		×					
<i>baramenuke</i>	I a-z						×	×	×	×	
<i>borealis</i>	I a-z						×	×	×		
<i>brevispinis</i>	I a-z			×		×	×				
<i>capensis</i>	I a-z							×	×		
<i>carnatus</i>	II a-v	×						×	×	×	
<i>caurinus</i>	II a-v	×							×	×	
"	II a-v	×						×	×	×	
<i>chlorostictus</i>	I a-z						×	×	×		
<i>chrysomelas</i>	II a-v	×							×	×	
<i>ciliatus</i>	I a-z				×			×	×	×	
<i>constellatus</i>	I a-z						×	×	×		
<i>crameri</i>	I a-z						×	×	×		
<i>dallii</i>	I a-z			×				×	×		
"	I a-z						×	×	×		
<i>diploproa</i>	I a-z					×		×	×		
<i>elongatus</i>	I a-z			×			×	×	×		
<i>emphaeus</i>	I a-z									×	
"	I a-z						×	×	×		
<i>ensifer</i>	I a-z							×	×		
<i>entomelas</i>	I a-z								×	×	
<i>eos</i>	I a-z							×	×		
<i>exsul</i>	I a-z						×	×	×	×	
<i>flameus</i>	I a-z			×		×	×				
<i>flavidus</i>	I a-z						×		×	×	
<i>gilli</i>	I a-z					×	×	×			
<i>glaucus</i> *	I a-z							×	×	×	
<i>goodei</i>	I a-z		×	×	×						

* Not examined. Information from Matsubara (1943).

TABLE 1. *Continued*

Species	Muscle Category	Points of Insertion									
		gb	r-1	r-2	r-3	r-4	v-7	v-8	v-9	v-10	v-11
<i>helvomaculatus</i>	I a-z					×		×	×		
"	I a-z						×	×	×		
<i>hopkinsi</i>	I a-z								×	×	
<i>hubbsi</i>	I a-z							×	×		
<i>ijimae</i>	II i-v								×	×	
<i>inermis</i>	II i-v							×	×	×	×
"	II i-v							×	×	×	×
<i>iracundus</i> *	I a-z				×	×	×				
<i>itinus</i> *	I a-z							×	×	×	
<i>jordani</i>	I a-z			×		×					
<i>joyneri</i>	I a-z						×	×	×		
<i>kawaradae</i> *	I a-z				×		×	×	×		
<i>lentiginosus</i>	I a-z						×	×	×		
<i>levis</i>	I a-z		×	×			×	×	×		
<i>longispinis</i>	I a-z							×	×	×	
<i>macdonaldi</i>	I a-z		×	×	×	×	×	×	×		
<i>maliger</i>	II a-v	×							×	×	
"	II a-v	×							×	×	
<i>marinus</i>	I m				×			×	×	×	
"	I m							×	×	×	×
"	I m								×	×	×
<i>matsubarae</i>	I a-z			×	×		×	×	×	×	
<i>melanops</i>	I a-z						×	×	×		
<i>melanostictus</i> *	I a-z				×		×	×	×		
<i>melanostomus</i>	I a-z		×	×			×	×	×		
"	I a-z						×	×	×		
<i>miniatus</i>	I a-z						×	×	×		
<i>mystinus</i>	I a-z					See Table 2					
<i>nebulosus</i>	II a-v	×						×	×		
<i>nigrocinctus</i>	I a-z			×	×		×				
<i>nivosus</i>	II i-v								×	×	
<i>oblongus</i>	II i-v							×	×		
<i>ovalis</i>	I a-z						×	×	×	×	
<i>owstoni</i>	I a-z			×	×			×			
<i>pachycephalus</i>	II i-v							×	×	×	
<i>paucispinis</i>	II p	×								×	
"	II p	×								×	
<i>phillipsi</i>	I a-z					×	×				
<i>pinniger</i>	I a-z						×	×	×	×	
<i>proriger</i>	I a-z					×		×	×	×	
<i>rastrelliger</i>	I a-z							×	×		
<i>reedi</i>	I a-z					×	×	×	×		
<i>rosaceus</i>	I a-z							×	×	×	
<i>rosenblatti</i>	I a-z					×	×	×			

* Not examined. Information from Matsubara (1943).

TABLE 1. *Continued*

Species	Muscle Category	Points of Insertion									
		gb	r-1	r-2	r-3	r-4	v-7	v-8	v-9	v-10	v-11
<i>ruberrimus</i>	I a-z						×	×	×	×	
<i>rubrivinctus</i>	I a-z			×	×	×	×				
<i>rufus</i>	I a-z						×	×	×	×	
<i>saxicola</i>	I a-z			×		×	×				
<i>schlegelii</i>	II i-v								×	×	×
"	II i-v								×	×	×
<i>scythropus</i>	I a-z				Points of insertion decayed						
<i>serranoides</i>	I a-z					×	×	×			
<i>serriceps</i>	I s			×			×				
<i>simulator</i>	I a-z							×	×		
<i>sinensis</i>	I a-z							×	×		
<i>steindachneri</i>	I a-z									×	×
<i>taczanowskii</i>	II t	×							×	×	×
<i>thompsoni</i>	II i-v						×	×	×		
<i>trivittatus</i>	II i-v								×	×	×
<i>umbrosus</i>	I a-z						×	×	×		
<i>variegatus</i>	I a-z						×	×	×	×	
<i>vexillaris</i>	II a-v	×							×	×	
<i>vulpes</i>	II i-v							×	×		
<i>wakiyai</i> *	I a-z						×			×	×
<i>wilsoni</i>	I a-z								×	×	
<i>zacentrus</i>	I a-z							×	×	×	
"	I a-z							×	×	×	

* Not examined. Information from Matsubara (1943).

For the purpose of determining the extent of variation within a species, dissections were done on 17 specimens of the blue rockfish, *Sebastes mystinus*. These dissections revealed only slight variations in the size and shape of the extrinsic gasbladder muscles, but they did indicate great intraspecific variation in posterior insertion points (table 2). No apparent sexual dimorphism was found. The size range of this series, consisting of eight males and nine females, was 70 mm. to 376 mm.

On the basis of morphological variations, two basic divisions in gasbladder muscle structure are recognized for the genus *Sebastes*. These divisions have arbitrarily been designated Type I and Type II. Type I consists of all muscle variations that attach firmly to the pectoral girdle as they pass posteriorly from their origin on the occipital cranium to their points of insertion on the vertebrae (fig. 1). Type II is comprised of muscle variations that *bypass* the pectoral girdle as they pass posteriorly from their origin on the occipital cranium to their points of insertion on the gasbladder or vertebrae (fig. 2). Each division is further subdivided into subtypes on the basis of additional structural variations.

TABLE 2. Muscle type and points of insertion of the gasbladder muscle for 17 specimens of the blue rockfish, *Sebastes mystinus*. Sex and standard length (S.L.) are listed for each specimen. Abbreviations for the points of insertion are the same as in table 1.

Sex	S.L.	Muscle	Points of Insertion				Sex	S.L.	Muscle	Points of Insertion			
			v-7	v-8	v-9	v-10				v-7	v-8	v-9	v-10
♂	222 mm.	I a-z			×	×	♀	112 mm.	I a-z			×	×
♂	231 mm.	I a-z		×	×	×	♀	157 mm.	I a-z			×	×
♂	251 mm.	I a-z		×	×	×	♀	191 mm.	I a-z			×	×
♂	258 mm.	I a-z			×	×	♀	264 mm.	I a-z	×	×	×	
♂	260 mm.	I a-z				×	♀	265 mm.	I a-z				×
♂	267 mm.	I a-z		×	×	×	♀	294 mm.	I a-z			×	×
♂	275 mm.	I a-z		×	×		♀	342 mm.	I a-z			×	×
♂	289 mm.	I a-z			×	×	♀	376 mm.	I a-z			×	
♀	70 mm.	I a-z		×	×	×							

Type I contains three subdivisions that are nominally denoted: aleutianus-zacentrus, serriceps, and marinus. Type II contains four subdivisions: paucispinis, ijimae-vulpes, atrovirens-vexillaris, and taczanowskii.

Subdivision nomenclature was determined by simply listing all species with a particular type of musculature in alphabetical order. The first and last species names on the list were taken to denote the subdivision name for that particular muscle type. Hence, the aleutianus-zacentrus subdivision is the pattern in all species in alphabetical order from *Sebastes aleutianus* through *Sebastes zacentrus* that possess dorsoventrally flattened muscles, originating on the cranium, attaching to the cleithrum, and inserting on the vertebral parapophyses. Four of the subdivisions are found in only one species each, so only one species name is listed for each of these four systems.

TYPE I

All species with musculature of this major category have extrinsic gasbladder muscles that attach firmly to the pectoral girdle as the muscles pass posteriorly from their origin on the occipital cranium to their insertion points on the vertebral parapophyses. Subdivisions of this major category have been formed on the basis of additional structural variations.

ALEUTIANUS-ZACENTRUS SUBDIVISION. This was the basic muscle structure found in the genus *Sebastes* with 62 of the 82 species dissected having this morphology. (See fig. 1A). Unlike some of the other muscle types which are found only in one geographic region, this type occurred in species taken throughout the geographic range of the genus.

The gasbladder muscles of this group are dorsoventrally flattened with the point of origin being the cranium. The specific site of attachment to the cranium is only slightly variable, and is usually around the exoccipital-opisthotic suture,

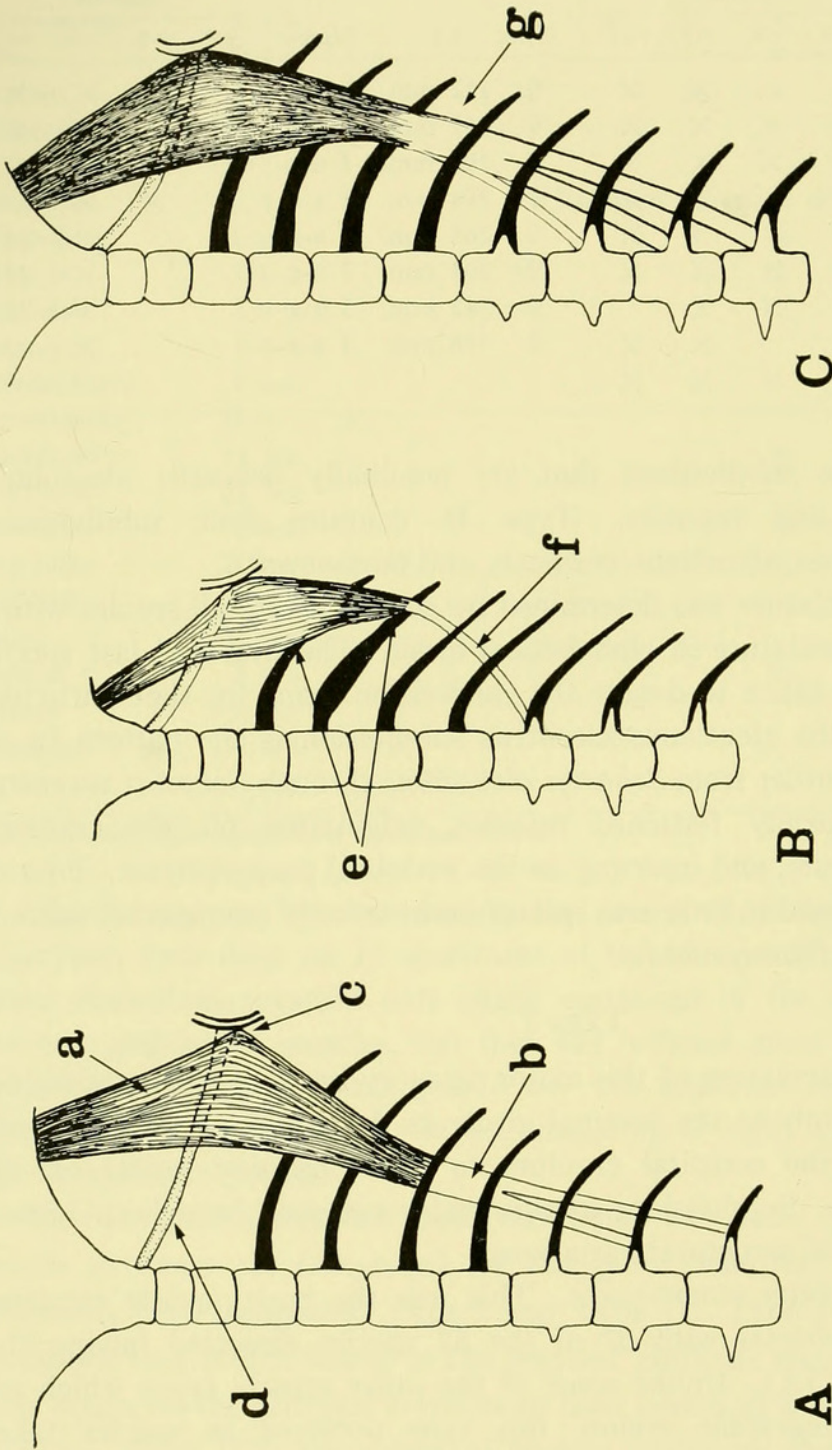


FIGURE 1. *Sebastes* Type I gasbladder muscles (right side only) showing characteristic attachment to the pectoral girdle as the muscles pass posteriorly from their origin on the occipital cranium to their insertion on the ribs or vertebrae. The tendons do not attach to the gasbladder in these subtypes. A: Dorsal view of aleutianus-zacentrus subtype vertebral column and gasbladder muscles showing (a) striated muscle portion, (b) tendon portion, (c) attachment to pectoral girdle, and (d) Baudelot's ligament. Drawing made from *Sebastes rastrelliger*, 198 mm. standard length. B: Dorsal view of serriceps subtype showing (e) attachment of striated muscle to the ribs, and (f) the single tendon inserting on the parapophysis of the seventh vertebrae. Drawing made from *Sebastes serripes*, 251 mm. standard length. C: Dorsal view of marinus subtype showing (g) muscle passing between the third and fourth ribs as opposed to between the second and third ribs in all other 81 species of *Sebastes* dissected. Drawing made from *Sebastes marinus*, 205 mm. standard length.

although in some species the attachment site seems wholly on one or the other of these two bones, or on the opisthotic. As the muscle passes posteriorly, some of its fibers attach to the supracleithral bone near the distal attachment site of Baudelot's ligament. Insertion by tendons occurs on the ribs or vertebral parapophyses.

The points of insertion, which tend to vary interspecifically, are listed in table 1 for all 62 species included in this muscle category. Unless otherwise stated in table 1, only one specimen of each species was dissected. The species of *Sebastes* examined, listed alphabetically, are as follows: *aleutianus*, *alutus*, *auriculatus*, *aurora*, *babcocki*, *baramenuke*, *borealis*, *brevispinis*, *capensis*, *chlorostictus*, *ciliatus*, *constellatus*, *crameri*, *dallii*, *diploproa*, *elongatus*, *emphaeus*, *ensifer*, *entomelas*, *eos*, *exsul*, *flameus*, *flavidus*, *gilli*, *goodei*, *helvomaculatus*, *hopkinsi*, *hubbsi*, *jordani*, *joyneri*, *lentiginosus*, *levis*, *longispinis*, *macdonaldi*, *matsubarae*, *melanops*, *melanostomus*, *miniatus*, *mystinus*, *nigrocinctus*, *ovalis*, *owstoni*, *phillipsi*, *pinniger*, *proriger*, *rastrelliger*, *reedi*, *rosaceus*, *rosenblatti*, *ruberrimus*, *rubrivinctus*, *rufus*, *saxicola*, *scythropus*, *serranoides*, *simulator*, *sinensis*, *steindachneri*, *umbrosus*, *variegatus*, *wilsoni*, and *zacentrus*.

Species of *Sebastes* dissected by Matsubara (1943) possessing this type of musculature are as follows: *baramenuke*, *flameus*, *hubbsi*, *longispinis*, *matsubarae*, *owstoni*, *scythropus*, and *steindachneri*; plus those examined by Matsubara but not by the author (Matsubara's results are included in table 1): *glaucus*, *iracundus*, *itinis*, *kawaradae*, *melanostictus*, and *wakijai*.

SERRICEPS SUBDIVISION. This muscle arrangement is found only in the treefish, *Sebastes serriceps*, an eastern Pacific species. The gasbladder muscles of this species are very similar to those of the aleutianus-zacentrus subdivision, being dorsoventrally flattened muscles with the point of origin on the cranium. As the muscles in this species pass posteriorly, a portion of the muscle fibers attach to the supracleithral bone. The mode of insertion of the gasbladder muscles in *S. serriceps* is however quite different from that found in the species listed in the aleutianus-zacentrus group. In the treefish, the posterior margin of the gasbladder muscle inserts primarily on the second rib, without first becoming a tendon. Careful examination revealed one small tendon coming off the muscle that passed between the second and third ventral ribs and inserted to the parapophysis of the seventh vertebra (see fig. 1B).

MARINUS SUBDIVISION.¹ The extrinsic gasbladder muscles of *Sebastes marinus* are similar in overall structure to those found in the aleutianus-zacentrus group (fig. 1C). Each muscle originates on the occipital region of the cranium and attaches to the pectoral girdle as it passes posteriorly to insert by means of tendons to the vertebral parapophyses. The major difference between this species and all other rockfishes is that the muscle crosses between the third and fourth

¹ See addendum.

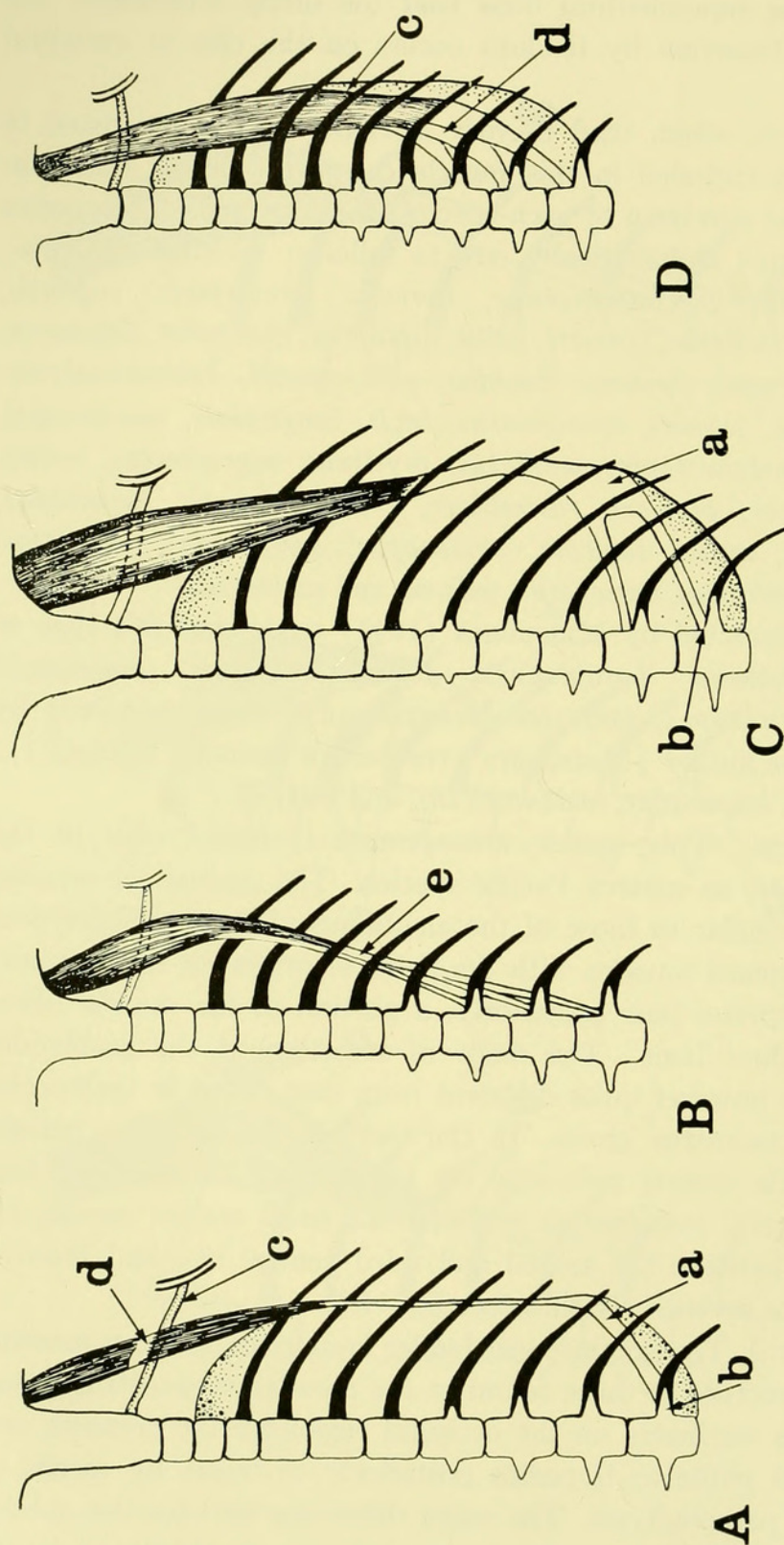


FIGURE 2. *Sebastes* Type II gasbladder muscles (right side only) showing the characteristic bypass of the pectoral girdle as the muscles pass posteriorly from their origin on the occipital cranium to their insertion on the vertebrae or gasbladder. A: Dorsal view of *paucispinis* subtype vertebral column and gasbladder muscle showing (a) the single tendon's attachment to the gasbladder, (b) the insertion of this tendon to the parapophysis of the tenth vertebra, (c) Baudelot's ligament, and (d) fascia that divides the striated muscle tissue into two parts. Drawing made from *Sebastes paucispinis*, 259 mm. standard length. B: Dorsal view of *ijimae-vulpes* subtype showing (e) the tendon portion that inserts on the vertebrae. No attachment to the gasbladder in these species. Drawing made from *Sebastes vulpes*, 161 mm. standard length. C: Dorsal view of *atrovirens-vexillaris* subtype showing (a) the attachment of the tendon portion to the gasbladder, and (b) insertion of the tendons to the vertebral parapophyses. Drawing made from *Sebastes caurinus*, 330 mm. standard length. D: Dorsal view of *taczanowskii* subtype showing (c) the attachment of the striated muscle tissue directly to the gasbladder, and (d) the three short tendons that insert to the parapophyses of the ninth, tenth, and eleventh vertebrae. Drawing made from *Sebastes taczanowskii*, 122 mm. standard length.

ventral ribs as it passes posteriorly towards the vertebrae, instead of passing between the second and third ventral ribs as in all other rockfish species examined. See table 1 for points of insertion in all *Sebastes marinus* dissected.

TYPE II

All species having muscular of this major category have extrinsic gasbladder muscles that *bypass* the pectoral girdle as the muscles pass posteriorly from their origin on the occipital cranium to their insertion points on the gasbladder or vertebral parapophyses. The muscles of this category tend to be more massive and cylindrical than those of the Type I category. Subdivisions of this Type II category are delineated by the author on the basis of additional structural variations.

PAUCISPINIS SUBDIVISION. This muscle arrangement is found only in the bocaccio, *Sebastes paucispinis*, an eastern Pacific species. In this species the gasbladder muscles have the point of origin on the cranium. As the muscles pass posteriorly, they do not make a connection with the pectoral girdle. This species, unlike any others in the genus, has the striated muscle tissue of the gasbladder muscles divided into two parts by a thin fascia (fig. 2A). The gasbladder muscles insert, each by means of a single tendon, on the posterior portion of the gasbladder. This tendon, while firmly fastened to the gasbladder wall, curves dorsally to anchor the gasbladder to the parapophysis of the tenth vertebra.

IJIMAE-VULPES SUBDIVISION. The gasbladder muscle pattern included in this group was found in nine species, all from the Orient. In these fishes, as in the rest of the genus, the extrinsic gasbladder muscles have the area of origin on the cranium, near the suture of the opisthotic and exoccipital. Like the muscles found in *Sebastes paucispinis*, these do not make a connection to the pectoral girdle as they pass posteriorly. The muscles have a striated portion that is slightly more massive than those described in previous groups. They are not quite as broad as the dorsoventrally flattened muscles of the aleutianus-zacentrus or serriceps subdivisions, but are of greater girth, being more cylindrical in shape. They appear to insert by tendons to the vertebral parapophyses without first attaching to the gasbladder (fig. 2B). Points of insertion for all species in this group are listed in table 1. The species of *Sebastes* falling into this group are as follows: *ijimae*, *inermis*, *nivosus*, *oblongus*, *pachycephalus*, *schlegeli*, *thompsoni*, *trivittatus*, and *vulpes*.

ATROVIRENS-VEXILLARIS SUBDIVISION. The muscles of this grouping and the next (*taczanowskii* subdivision) are the largest in the genus *Sebastes*. These gasbladder muscles originate on the cranium. As they pass posteriorly they do not make a connection to the pectoral girdle. They insert as tendons that attach firmly to the gasbladder before swinging up and attaching to the vertebral parapophyses (figs. 2C and 3). In several of the species, one of the two tendons

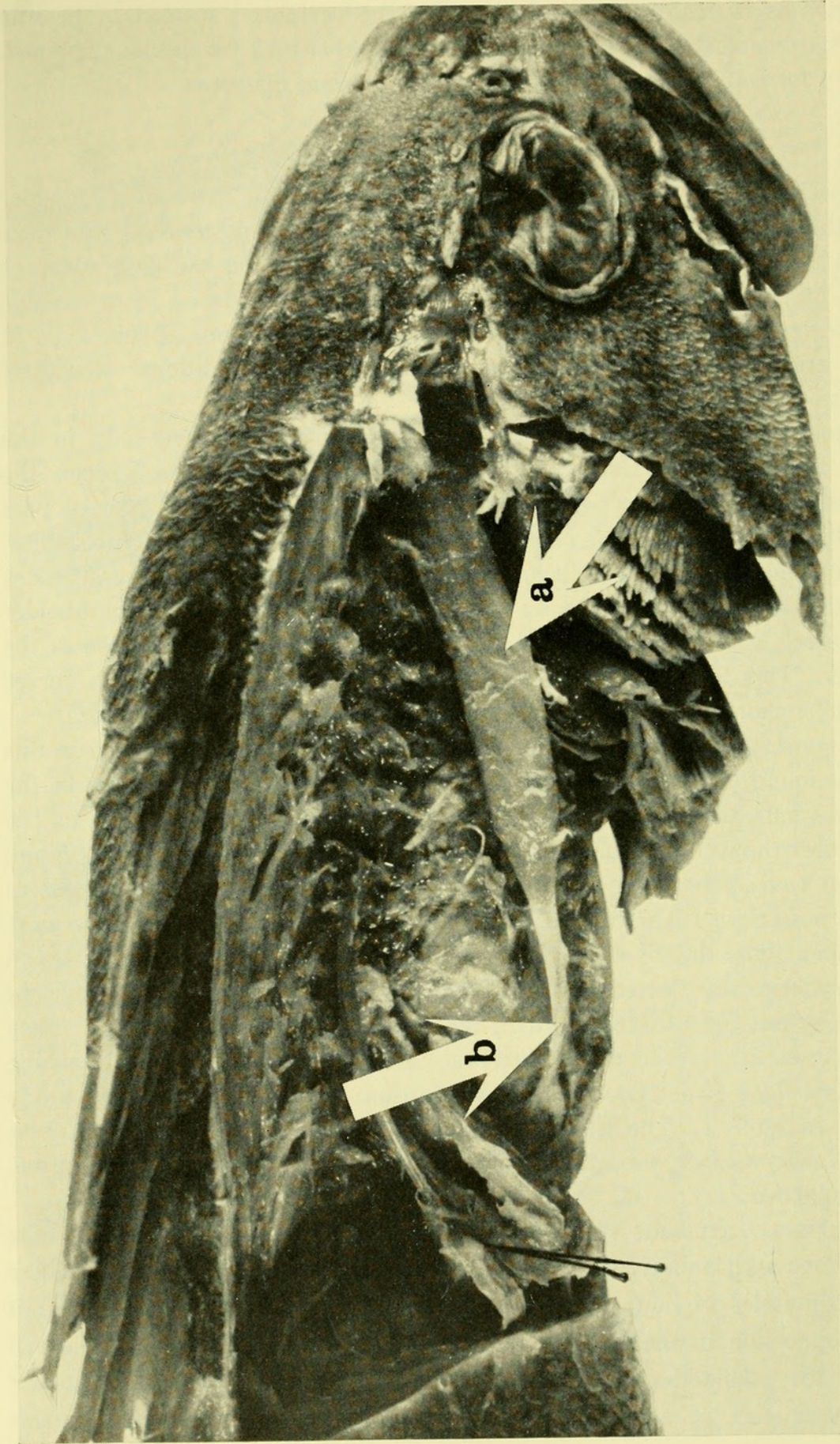


FIGURE 3. Right extrinsic gasbladder muscle of atrovirens-vexillaris subtype (*Sebastes* Type II) showing (a) the large cylindrical striated muscle band, and (b) the attachment of the muscle tendons to the side of the gasbladder. Photograph is of copper rockfish, *Sebastes caurinus*, 250 mm. standard length.

initially attaching to the gasbladder diverges so that three tendons are firmly attached to the gasbladder wall and anchor the gasbladder to three vertebral parapophyses. Points of insertion for all species in this group are listed in table 1. The species of *Sebastes* characterized by this muscle pattern are as follows: *atrovirens*, *carnatus*, *caurinus*, *chrysomelas*, *maliger*, *nebulosus*, and *vexillaris*.

TACZANOWSKII SUBDIVISION. This type is represented by one species, *Sebastes taczanowskii*, an Oriental form. It is much like that of the previous group (*atrovirens-vexillaris*) except that the muscle attaches to the gasbladder wall as muscle rather than as tendon. Originating on the cranium, the muscle passes posteriorly to attach to the outer wall of the gasbladder. No connection to the pectoral girdle occurs. While connected to the gasbladder, the muscle passes posteriorly along the gasbladder to a point approximately under the sixth rib where it then diverges to form three tendons. These three tendons, while firmly attached to the gasbladder wall, curve dorsally to anchor the gasbladder to the parapophyses of the ninth, tenth, and eleventh vertebrae (fig. 2D).

OTHER SCORPAENIFORM DISSECTIONS

Dissection of specimens from 23 other genera within the family Scorpaenidae and nine other families within the order shows many to have muscles similar to the extrinsic gasbladder muscles found in the genus *Sebastes*. As might be expected, the highest degree of similarity in structure of these muscles occurs within families, but general similarity in structure does occur even between some families in different suborders, as is the case of the first group listed below. Dissections of scorpaeniform representatives were made primarily for general comparison and were not as precise as those done on rockfish specimens.

MUSCLE TYPES SIMILAR TO *SEBASTES* TYPE I. All fishes placed in this group have two lateral muscles similar in structure to those found in Type I muscles as defined for the genus *Sebastes*. This structural form is the most widespread and common in the order, being predominant in four of the five suborders examined. The notable exceptions were members of the suborder Cottoidei.

The species listed below possess muscles that are dorsoventrally flattened like those in the *Sebastes* Type I category. These muscles, like those in the rockfish group have the point of origin on the occipital cranium. As the muscles pass posteriorly, they make a connection with the pectoral girdle. The points of insertion in all cases appeared to be the vertebral parapophyses. Unless the precise points of insertion were determined, however, species in the group are simply listed. The species examined are as follows:

Scorpaenidae: *Ectreposebastes imus*; *Gymnapistes marmoratus*; *Helicolenus dactylopterus*; *Inimicus cuvieri*; *Iracundus signifer*; *Minous monodactylus*; *Minous pictus*; *Neomerinthe beanorum*; *Parascorpaena* species; *Plectrogenium nanum*;

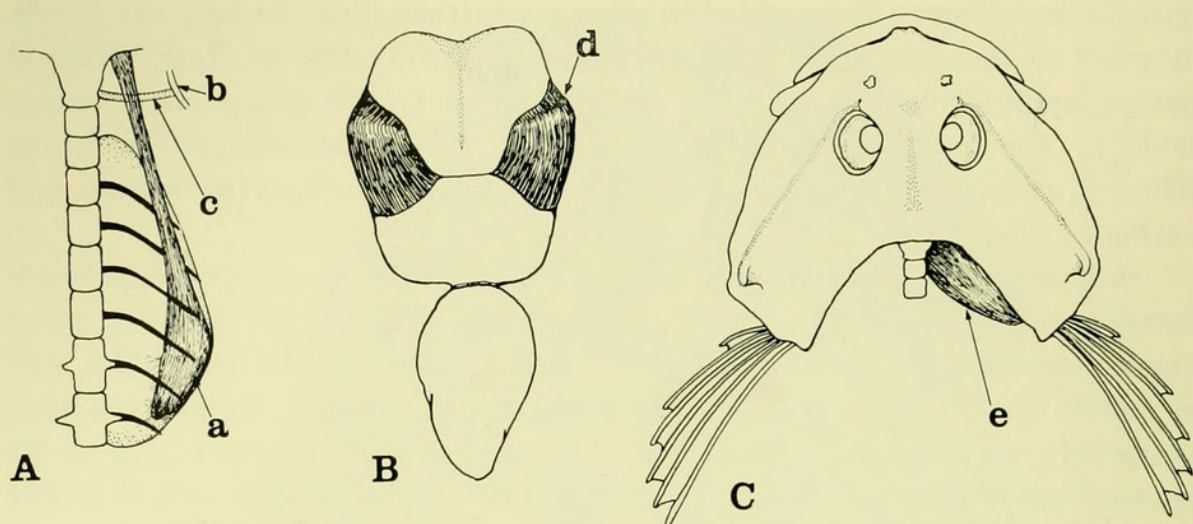


FIGURE 4. Other types of gasbladder musculature found in the order Scorpaeniformes. A: Dorsal view of the right extrinsic gasbladder muscle of *Sebastiscus marmoratus* showing (a) the broadened striated muscle tissue that inserts directly onto the gasbladder, (b) the pectoral girdle, and (c) Baudelot's ligament. This muscle system is similar in morphology to the *Sebastes* Type II muscles. Drawing from specimen 131 mm. standard length. B: Dorsal view of gasbladder from *Apistes* species showing (d) the fully intrinsic muscle tissue on the anterior lobe of the gasbladder. Drawing made from specimen 109 mm. standard length. C: Dorsal view of right cranioclavical muscle in *Cottus asper* showing (e) the short striated muscle band. Drawing from specimen 110 mm. standard length.

Pontinus longispinis; *Scorpaena agassizi*, *Scorpaena albobrunnea*, *Scorpaena brasiliensis*, *Scorpaena elongata*, *Scorpaena guttata*, *Scorpaena mystes*, *Scorpaena porcus*, and *Scorpaena russula*, all with four tendons, one attaching to each of the parapophyses of the sixth, seventh, eighth, and ninth vertebrae; *Scorpaenopsis* species; *Sebastosemus* species; *Setarches longimanus*; *Synanceia verrucosus*.

Hexagrammidae: *Hexagrammos decagrammus*

Platycephalidae: *Platycephalus* species

Hoplichthyidae: *Hoplichthys langsdorfi*

MUSCLE TYPES SIMILAR TO *SEBASTES* TYPE II (TACZANOWSKII SUBDIVISION).

The species listed in this group have two large gasbladder muscles similar in overall structure to the muscle system listed for *Sebastes taczanowskii*. These muscles are in most cases rather large and cylindrical, originating on the occipital portion of the cranium and inserting usually on the bladder (fig. 4A). No connection to the pectoral girdle occurs. Species listed below are from the family Scorpaenidae. Once again, dissections were not as exact as for the genus *Sebastes*, and precise posterior attachment sites were not exactly determined. The species listed in this group are as follows:

Scorpaenidae: *Brachypterois serrulifer*, *Dendrochirus zebra*, *Macroscorpius pallidus*, *Scorpaenodes parvipinnis*, *Pterois radiata*, *Sebastiscus marmoratus*, *Setarches guentheri*.

INTRINSIC GASBLADDER MUSCLES

Dissections revealing gasbladders containing fully intrinsic gasbladder muscles were made on two species, *Leptotrigla alata* (Triglidae) and *Apistes* species (Scorpaenidae). Intrinsic gasbladder muscles have been widely examined in triglids (Tower, 1908; Fish, 1954; Tavalga, 1964; Evans, 1973), and Matsubara (1943) in his review of Japanese scorpaenids reported intrinsic musculature for *Apistes carinatus*. Figure 4B is a diagram of an *Apistes* gasbladder.

CRANIOCLAVICAL MUSCLE SYSTEMS

The muscles of this group, found in members of the suborder Cottoidei, are stout cylindrical muscles connecting the pectoral girdle to the occipital region of the skull (fig. 4C). The point of attachment to the skull seems to correspond to the point of attachment of the extrinsic gasbladder muscles described for scorpaenids. Likewise, the point of attachment to the pectoral girdle seems to correspond to that in the scorpaenids. Species dissected are as follows:

Zaniolepididae: *Zaniolepis latipinnis*

Cottidae: *Clinocottus analis*, *Cottus asper*, *Hemilepidotus jordani*, *Leptocottus armatus*, *Myoxcephalus quadricornis*, *Scorpaenichthys marmoratus*

Cottunculidae: *Cottunculus thompsoni*

Agonidae: *Occella verrucosa*

Cyclopteridae: *Liparis florum*.

DISCUSSION

TAXONOMIC VALUE OF GASBLADDER MUSCLE SYSTEMS. In all rockfish species examined, only one mode of origin for the gasbladder muscles was observed, that being on the occipital region of the cranium. In some species fibers of the striated muscle tissue attached to the supracleithral bone as the gasbladder muscles passed posteriorly, while in others no such attachment occurred. Two major muscle categories were recognized on the basis of the presence (Type I) or absence (Type II) of a pectoral girdle attachment. A total of seven subdivisions were recognized, three for Type I and four for Type II, on the basis of additional structural variations.

Because of the high degree of intraspecific variability (see table 2) and interspecific overlap in insertion sites (see table 1), these muscles were in most cases not useful in species delineations. However, of the 82 species examined, four had unique muscle types. These species are *Sebastes serriceps*, (Type I), *S. marinus* (Type I), *S. paucipinis* (Type II), and *S. taczanowskii* (Type II), and could easily be separated from other species on the basis of the morphology of their gasbladder muscles.

The use of these various muscle types in conjunction with other characters as a means of delineating subgenera seems in some instances useful. For example,

in the eastern Pacific subgenus *Pteropodus*, all species with the exception of one, had gasbladder muscles that were found only in this small group (*atrovirens-vexillaris* subdivision of Type II). Muscle morphology seems to support the subgeneric classification for the *Pteropodus* group. The one species in the *Pteropodus* complex that did not possess an *atrovirens-vexillaris* muscle system was *S. rastrelliger*. It had instead the more common *aleutianus-zacentrus* bladder muscles (Type I). Workers dealing with phylogenetic relationships in *Sebastes* should perhaps consider separating *S. rastrelliger* from the other species (*S. atrovirens*, *S. carnatus*, *S. caurinus*, *S. chrysomelas*, *S. maliger*, *S. nebulosus*, and *S. vexillaris*) in this group.

Two species of the subgenus *Sebastodes*, *S. brevispinis* and *S. paucispinis*, which are usually considered to be closely related, have major differences in the structure of the gasbladder musculature. *Sebastodes brevispinis* has the *aleutianus-zacentrus* muscles (Type I), and *S. paucispinis* (Type II) possesses a unique form. These species seem to occur in similar habitats, so their general similarity may indicate ecological convergence from different ancestral lines.

The considerations given to the taxonomy of eastern Pacific subgenera in this section are in fact only brief speculations. Rearrangement of eastern Pacific subgenera lies far beyond the scope of this paper. Speculations about Oriental subgenera were completely omitted due to insufficient numbers of dissections on Japanese forms. It is probable that other workers, correlating the structure of gasbladder muscles with a variety of other taxonomic characters, will find the morphology of these gasbladder muscles useful in phylogenetic studies on the rockfish genus *Sebastes*.

ORIGIN AND EVOLUTION OF GASBLADDER MUSCULATURE WITHIN THE GENUS *SEBASTES*. In the course of a study in which one particular character is reviewed throughout a group, it is worthwhile to give consideration to the possible evolutionary origin and diversification of the structure concerned. The first worker to extensively examine the extrinsic gasbladder musculature of scorpaenids was Matsubara (1943). His hypothesis concerning the successive changes of the muscle bands was that "... the existence of well developed muscle is a primitive feature in the scorpaenoid fish." Matsubara speculated that species such as *Sebastes taczanowskii* possessing well developed extrinsic gasbladder muscles represented the ancestral muscle condition. Conversely, species having muscles small in size and connected posteriorly to the axial skeleton by tendons as in the *aleutianus-zacentrus* subdivision were thought by him to possess the more recent evolutionary structure.

It is possible that these structures may have followed a mode of evolutionary differentiation opposite to that shown by Matsubara. This speculation is based upon the preponderance of small gasbladder muscles throughout the order.

If one assumes that the structural condition of the gasbladder muscle occurring

most frequently in these rockfishes is the type most likely to be the primitive state for the genus, then the Type I division, found in 62 of the 82 species examined, is representative of the ancestral condition for the genus. The gasbladder muscles in these species are dorsoventrally flattened, originating on the cranium, passing posteriorly to make a strong attachment to the pectoral girdle, and finally inserting by tendons to ribs or vertebrae. The other structural variants (Type II) which occurred much less frequently are probably derived states.

However, another interpretation of the widespread occurrence of the Type I muscle pattern is that this pattern arose originally from one of the less frequently occurring patterns. This seems unlikely, though, in view of the widespread occurrence of this Type I pattern throughout the rest of the family. A total of 24 species belonging to 15 genera in the family Scorpaenidae also display a similar structural condition. This suggests that the pattern did not arise in the genus *Sebastes* and that it is the primitive condition for the family.

The selective pressures that have caused this divergence of gasbladder muscle structure within the rockfishes are unknown. The work of McInerney and Yearsley (in press) indicates that rockfishes possessing the smaller gasbladder muscles that attach only to the ribs or vertebrae produce sounds that are very similar to those produced by rockfishes possessing the larger gasbladder muscles that attach directly to the gasbladder. In light of this information it does not seem probable that selection for increased sound producing ability was an important evolutionary force involved in the divergence of gasbladder muscles within this lineage, although it may have been an important factor in the general elongation of gasbladder musculature in this group. What factors were involved in their subsequent divergence is a question open to speculation.

SPECULATIONS ON THE ORIGIN AND EVOLUTION OF GASBLADDER MUSCULATURE WITHIN THE ORDER SCORPAENIFORMES. It is of interest to look beyond the generic level to speculate on the possible stages of evolution of gasbladder musculature within the order Scorpaeniformes. The muscle pattern of most widespread occurrence in the genus *Sebastes* and the family Scorpaenidae is that in which the muscles are dorsoventrally flattened, inserting on the vertebrae by tendons. This muscle pattern (similar to the *Sebastes* Type I) is found in four of the six suborders recognized by Greenwood *et al.* (1966) for the order Scorpaeniformes. Again if one assumes that the structural condition of the gasbladder muscles that occurs most frequently in this group is the type most likely to be the primitive state for the order, then the dorsoventrally flattened muscles that insert to ribs of vertebrae by tendons are representative of the ancestral condition for the order.

A muscle condition exists within the order, however, that complicates the

picture somewhat. All species examined from the suborder Cottoidei were found to possess lateral musculature different in structure from the long gasbladder muscles found in other scorpaeniform fishes. They possess, instead, two stout cylindrical muscles that originate on the occipital portion of the cranium and insert on the pectoral girdle. These structures were referred to by Barber and Mowbray (1956) as cranioclavical muscles (fig. 4c), and these workers demonstrated that sounds are produced when these structures are vibrated. The points of attachment to the cranium and pectoral girdle are similar to those points of attachment of gasbladder muscles in scorpaenids. Both systems seem to have evolved from modifications of the ventral fibers of the epaxialis, the dorsal half of the lateral body musculature. Homologies between the cranioclavical muscles of cottoids and the elongate muscles of other scorpaeniform fishes are not clear.

A variety of possible evolutionary schemes can be envisioned to explain possible differences between cottoid musculature and that found in other scorpaeniform groups. For example, the members of the suborder Cottoidei may have retained muscles similar to original ancestral structures from which other scorpaeniform groups eventually developed elongate gasbladder muscles. What selection pressures might be involved in this process of muscle elongation are not clear. Perhaps the lengthening of lateral musculature increased mobility of the pectoral girdle in scorpaenidlike fishes, aiding them in movements associated with swimming or moving around on the bottom. After this primary elongation, the gasbladder muscles in some species increased in size possibly to become efficient sound-producing structures.

It is possible, however, that the situation may have been the opposite. The loss of the gasbladder in members of the suborder Cottoidei suggests that they may be derived forms. Perhaps cottoid ancestors once possessed elongate gasbladder muscles similar to those in scorpaenids. With the loss of the gasbladder, this group of benthic fishes may have evolved a modified pair of muscles that are in some way adaptive to a benthic existence. This picture, in which cottids evolved from a scorpaenoid ancestor, coincides with that proposed by Quast (1965) on the basis of osteological evidence.

Another possibility is that the common ancestor of cottoids and scorpaenids had some sort of gasbladder musculature different from that found in either of the present-day groups. It is also possible that this major difference in gasbladder musculature between the cottoids and the scorpaenids reflects different phylogenetic origins for these two groups. In any event, the picture is at present hazy, and none of the previous hypotheses can be firmly defended. For the present this author must agree with the views expressed by Greenwood *et al.* (1966) and Gosline (1971). The former stated, "The scorpaeniform fishes represent a more or less typical example of the work that needs still to be done.";

the latter, "The classification of the group appears to be in an advanced state of confusion."

FUNCTION OF THE EXTRINSIC GASBLADDER MUSCLE IN *SEBASTES*. The function of extrinsic and intrinsic gasbladder musculature in a wide variety of fish groups is that of sound production. Two review papers covering sound-producing mechanisms in fishes are those by Tavolga (1971) and Courtenay (1971).

The morphology of extrinsic gasbladder musculature in rockfishes suggests that most species are probably capable of producing sounds. Sound production has been reported for the western Pacific species, *Sebastes schlegeli* (Protasov *et al.*, 1965). Sounds have recently been recorded and analyzed for nine eastern Pacific forms, *Sebastes caurinus*, *S. flavidus*, *S. maliger*, *S. melanops*, *S. mystinus*, *S. nebulosus*, *S. nigrocinctus*, and *S. paucispinis* (McInerney and Yearsley, in press). These workers found that sounds were commonly produced during agonistic encounters between conspecifics, both in the laboratory and under natural conditions in the field. This author has heard sounds produced in the field by *Sebastes atrovirens*, *S. carnatus*, *S. caurinus*, *S. chrysomelas*, and *S. nebulosus*, but only under unnatural conditions of stress.

The morphology of gasbladder musculature in several other scorpaenid species suggests that these fishes may also produce sounds. Sound production has been reported in *Sebastiscus marmoratus* (Dotu, 1951), a species which possesses extrinsic gasbladder muscles that originate on the occipital region of the cranium and insert upon the swimbladder wall (fig. 4A).

The gasbladder muscles of rockfishes and other scorpaenids may also aid in sound reception. This seems possible in view of the large otoliths possessed by rockfishes, as well as the origin of the gasbladder muscles on the cranium in the general proximity of the otoliths. Whether rockfishes are receptive to sounds is not known at this time, and work remains to be done in this regard.

POSSIBLE ECOLOGICAL SIGNIFICANCES OF SOUND PRODUCTION. Field observations made by the author indicate that some species of the subgenus *Pteropodus* are territorial at least part of the year, unlike other rockfishes occurring sympatrically. These species are usually solitary although field observations by the author suggests that they aggregate in pairs or small intraspecific groups during certain times of the year. The work of McInerney and Yearsley (in press) indicates that these territorial, hole-dwelling fishes, which possess the large Type II atrovirens-vexillaris gasbladder muscles (see figs. 2C and 3), produce sound during territorial defense, and as a fright response. Such uses of sound have been demonstrated for squirrelfishes (Winn and Marshall, 1963; Bright, 1972), and toadfishes (Gray and Winn, 1961; Winn, 1964, 1967).

Sounds produced by rockfishes might be species-specific and thus serve as isolating mechanisms between sympatric species. A high degree of congeneric

sympatry exists among rockfishes, with as many as 10 species being captured at one collecting station. One method used in species isolation might be species-specific sound emissions. The work of McInerney and Yearsley indicates that this is possible, but interestingly, they found that structurally similar species produce sounds that appear to be indistinguishable from each other. Additional audio-isolation studies by species of *Sebastes* would be valuable.

SUMMARY

Rockfishes from the large scorpionfish genus *Sebastes* have been studied only regionally. One morphological feature that may prove useful for clarification of phylogenetic relationships within *Sebastes* is variation in the structure of extrinsic gasbladder musculature. Eighty-two species of rockfishes were dissected for examination of their gasbladder muscles. For the purpose of clarifying gasbladder muscle relationships within the genus, dissections were made on representatives from 23 other genera in the family Scorpaenidae, and fishes from 9 other families in the order Scorpaeniformes.

Dissections revealed considerable intrageneric variation in gross morphology of the extrinsic gasbladder musculature. On the basis of these structural variations, two major structural divisions in gasbladder musculature have been recognized for the rockfish genus *Sebastes*, and have been designated Type I and Type II. Type I have been divided into 3 subdivisions (aleutianus-zacentrus, serriceps, and marinus) and Type II has been divided into 4 subdivisions, (paucispinis, ijimae-vulpes, atrovirens-vexillaris, and taczanowskii).

In most cases these muscles were not especially useful for characterizing species because of a high degree of intraspecific variability and interspecific overlap in insertion sites. However, four species (*Sebastes marinus*, *S. paucispinis*, *S. serriceps*, and *S. taczanowskii*) had species-specific gasbladder musculature, and therefore could be separated from other rockfish species on the basis of morphology of their gasbladder muscles.

Delineations of subgenera through the use of the various muscle types is in most cases not practical since the muscle patterns exhibit considerable overlap between proposed subgenera. However, in the case of the subgenus *Pteropodus*, gasbladder muscles morphology supports the subgeneric classification of this group.

Within the genus *Sebastes* the presence of large cylindrical gasbladder muscles may represent the more recent evolutionary condition. Conversely, the small dorsoventrally flattened gasbladder muscles found most commonly are probably more representative of the ancestral form for the genus. Possible explanations for the occurrence of cranioclavical muscles in fishes of the suborder Cottoidei are discussed.

The function of the large cylindrical gasbladder muscles found in several

rockfish species seems to be primarily for the production of sound (McInerney and Yearsley, in press). Gasbladder muscles may also be used for sound reception.

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APPENDIX

Specimens examined in the course of this study are listed below by family. Abbreviations of depositories of specimens are as follows: CAS—California Academy of Sciences, San Francisco, California. BC—University of British Columbia, Vancouver, B.C. UMMZ—University of Michigan Museum of Zoology, Ann Arbor, Michigan. SIO—Scripps Institution of Oceanography, La Jolla, California. SU—Stanford University, collection now incorporated in the CAS collection. ZMK—Zoologisk Museum, Copenhagen, Denmark. The number of specimens examined from a particular lot and standard length in mm. are given in parentheses.

ORDER SCORPAENIFORMES

SCORPAENIDAE

Sebastes

- aleutianus*: CAS 15271 (1 specimen, 410 mm.), British Columbia, Vancouver Island, 10 September 1972.
- alutus*: CAS 15314 (1, 227), British Columbia, Vancouver Island, 11 September 1972; CAS 14888 (1, 341), southern Oregon, 26–28 April 1972.
- atrovirens*: CAS 14861 (1, 280), California, 3 April 1972; CAS 15061 (1, 232), California, 21 August 1972.
- auriculatus*: CAS 14472 (2, 229–357), California, 20 May 1972; CAS 14870 (1, 284), California, 15 April 1972.
- aurora*: CAS 15301 (1, 261), British Columbia, 10 September 1972.
- babcocki*: CAS 15286 (1, 362), British Columbia, 10 September 1972.
- baramenuke*: CAS 30088 (1, 300), Japan, 12–13 August 1929.
- borealis*: CAS 15272 (1, 406), British Columbia, 10 September 1972.
- brevispinis*: CAS 14431 (1, 230), Alaska, Summer 1971.
- capensis*: CAS 17644 (1, 198), Chile, 21 September 1966.
- carnatus*: CAS 14732 (1, 249), California, 23 April 1972.
- caurinus*: CAS 14869 (1, 330), California, 15 April 1972.
- chlorostictus*: CAS 14705 (1, 269), California, 26 May 1972.
- chrysomelas*: CAS 14896 (1, 271), California, 30 July 1972.
- ciliatus*: CAS 30089 (1).
- constellatus*: CAS 14724 (1, 266), California, 27 May 1972.
- cramerii*: CAS 15292 (1, 258), British Columbia, 11 September 1972.
- dallii*: CAS 14708 (1, 139), California, 27 May 1972; SU 4377 (1, 159), California, no date.
- diploproa*: CAS 14889 (1, 284), Oregon, 26–28 April 1972.
- elongatus*: CAS 14713 (1, 221), California, 26 May 1972.
- emphaeus*: CAS 15153 (1, 110), Oregon, 21 August 1972; BC66–135 (1, 122), British Columbia, 7 September 1966.
- ensifer*: CAS 17609 (1, 141, paratype), California, 26 May 1965.
- entomelas*: CAS 14865 (1, 207), California, 5 March 1972.
- eos*: CAS 17611 (1, 378), California, 3 August 1968.
- exsul*: CAS 17605 (1, 191), Gulf of California, 29 April 1969.
- flameus*: CAS 30090 (1, 290), Japan, Spring 1929.
- flavidus*: CAS 14880 (1, 343), California, 8 April 1972.
- gilli*: SIO 65-1-53B (1, 488), California, 9 January 1965.
- goodei*: SU 87 (1, 161), California, Santa Cruz Island, 7 February 1888.
- helvomaculatus*: CAS 15302 (1, 256), British Columbia, off Vancouver Island, 10 September 1972; CAS 17606 (1, 180), British Columbia, off Vancouver Island, 9–10 February 1967.
- hopkinsi*: CAS 15300 (1, 221), California, Santa Monica Bay, 16 September 1972.
- hubbsi*: CAS 30091 (1, 151), Japan, station H29-240, 9 August 1929.
- ijimae*: CAS 30080 (1, 192), Japan, no date.
- inermis*: CAS 30081 (1, 159), Korea, Seiskin, 15 September 1924; SU 7413 (1, 140), Japan, Misaki, no date.
- jordani*: CAS 26448 (1, 201), California, off Gaviota, 7 June 1953.

- joyneri*: SU 7604 (1, 133), Japan, Tokyo, no date.
- lentiginosus*: CAS 17614 (1, 175, paratype), California, Cortes Bank, 16 May 1963.
- levis*: CAS 26594 (1, 123), California, Santa Monica, 21 June 1953.
- longispinis*: CAS 14281 (1, 136), Korea, 23 July 1959.
- macdonaldi*: CAS 17610 (1, 163), Baja California, off west coast, 16 January 1970.
- maliger*: CAS 14890 (1, 312), California, Farallon Islands, 15 July 1972; CAS 15410 (1, 275), British Columbia, spring 1972.
- marinus*: SU 34329 (3, 205-232), Nova Scotia, Sable Island Gulley, 18-20 July 1939; SU 1770 (1, 126), no data; SU 9870 (1, 203), Norway, no date.
- matsubarae*: SU 7393 (1, 231), Japan, Misaki, no date.
- melanops*: CAS 14726 (1, 332), California, off Point Reyes, 7 June 1972.
- melanostomus*: SIO 67-79-53 (1,194), Mexico, Baja California, 3 May 1967; SU 2459 (1, 95), southern California, no date.
- miniatus*: CAS 14878 (1, 396), California, off Farallon Islands, 8 April 1972.
- mystinus*: CAS 14712 (1, 342), California, off Santa Catalina Island, 26 May 1972; CAS 14474 (1, 222), California, Halfmoon Bay, 20 May 1972; CAS 14712 (1, 258), California, Santa Catalina Island, 26 May 1972; CAS 14717 (3, 231-294), California, Fort Ross Cove, 11 June 1972; CAS 14727 (1, 265), California, Point Reyes, 7 June 1972; CAS 14863 (1, 376), California, Halfmoon Bay, 5 March 1972; CAS 14871 (2, 260-289), California, Halfmoon Bay, 15 April 1972; CAS 14882 (2, 267-275), California, Farallon Islands, 8 April 1972; CAS 14894 (1, 251), California, Farallon Islands, 15 July 1972; CAS 15440 (2, 157-191), California, Santa Rosa Island, 21 September 1972; CAS 25900 (1, 112), California, Monterey Bay, 7 October 1953; SU 15097 (1, 70), California, Pacific Grove, 31 July 1948.
- nebulosus*: CAS 14720 (2, 277-278), California, Fort Ross Cove, 11 June 1972; CAS 14731 (1, 288), California, Farallon Islands, 8 April 1972.
- nigrocinctus*: CAS 28877 (1, 224), Canada, British Columbia, 10 June 1963.
- nivosus*: CAS 30082 (1, 175), Japan, station H29-299, Spring 1929.
- oblongus*: SU 7421 (1, 202), Japan, Matsushima, no date.
- ovalis*: CAS 14710 (1, 278), California, off Santa Catalina Island, 26 May 1972.
- owstoni*: CAS 30083 (1, 145), Japan, Toyama Bay, station H29-249, 12-13 August 1929.
- pachycephalus*: CAS 30241 (1, 157), Japan, Sea of Japan, station H29-224, 4 August 1929.
- paucispinis*: CAS 15299 (1, 259), California, Santa Monica Bay, 16 September 1972; CAS 14864 (1, 453), California, Halfmoon Bay, 5 March 1972.
- phillipsi*: SIO 65-153-53A (1, 320), California, off Newport Beach, 17 June 1965.
- pinniger*: CAS 15057 (1, 315), Oregon, Stonewall Bank, 21 August 1972.
- proriger*: CAS 15289 (1, 329), British Columbia, off Vancouver, 11 September 1972.
- rastrelliger*: CAS 14895 (1, 198), California, Halfmoon Bay, 28 July 1972.
- reedi*: CAS 15290 (1, 332), British Columbia, off Vancouver, 11 September 1972.
- rosaceus*: CAS 14875 (1, 227), California, Farallon Islands, 8 April 1972.
- rosenblatti*: CAS 14703 (1, 347), California, La Jolla, 25 May 1972.
- ruberrimus*: CAS 14560 (1, 288), California, off Point Reyes, 28 May 1972.
- rubrivinctus*: CAS 14704 (1, 287), California, La Jolla, 25 May 1972.
- rufus*: CAS 17612 (1, 339), California, Santa Catalina Island, 3 May 1968.
- saxicola*: CAS 14885 (1, 269), southern Oregon, 26-28 April 1972.
- schlegelii*: SU 7428 (1, 223), Japan, Hakodate, no date; SU 6274 (1, 88), Japan, Hakodate, no date.
- scythropus*: SU 7169 (1, 147), Japan, Misaki, no date.
- serranoides*: CAS 15806 (1, 285), California, Farallon Islands, 15 July 1972.
- serriceps*: CAS 17613 (1, 251), California, San Diego, 13 December 1972.

- simulator*: CAS 17607 (1, 235, paratype), Mexico, Guadalupe Island, 29 August 1956.
sinensis: CAS 17608 (1, 115), Gulf of California, Ballenas Channel, 18 January 1968.
steindachneri: SU 7422 (1, 166), Japan, Hakodate, no date.
taczanowskii: CAS 30084 (1, 122), Japan, Mutsu Bay, summer 1929.
thompsoni: CAS 30085 (1, 188), station H29-185-63.
trivittatus: CAS 30086 (1, 160), Japan, station H29-292C, 1 September 1929.
umbrosus: CAS 14707 (1, 194), California, La Jolla, 25 May 1972.
variegatus: SIO 63-946-53 (1, 220), Gulf of Alaska, 14 August 1960.
veixillaris: CAS 18461 (1, 245), California, La Jolla, 5 April 1945.
vulpes: CAS 30087 (1, 161), Japan, station H29-292C, 1 September 1929.
wilsoni: SU 2443 (1, 116), Oregon, no date.
zacentrus: CAS 15309 (1, 210), British Columbia, off Vancouver Island, 11 September 1972.

OTHER GENERA AND SPECIES

- Apistes* species: CAS 15975 (1, 109), Hong Kong, off Lema Island, 25 July 1958.
Brachypterois serrulifer: CAS 15973 (1, 79), Hong Kong, off Lema Island, 25 July 1958.
Dendrochirus zebra: CAS 15971 (1, 100), Palau Islands, 23 September 1957.
Dendroscorpaena species: CAS 15965 (1, 107), Gulf of Thailand, 18 June 1961.
Ectreposebastes imus: CAS 30092 (1, 154), 300 miles west of Sumatra, 26 May 1966.
Gymnapistes marmoratus: CAS 30093 (1, 71), Western Australia, 8 February 1970.
Helicolenus dactylopterus: CAS 13941 (1, 137), Morocco, 15 July 1969.
Inimicus cuvieri: CAS 13553 (1, 131), Gulf of Thailand, 17-21 December 1960.
Iracundus signifer: CAS 24990 (1, 93), Hawaiian Islands, Oahu, 20 July 1969.
Macroscorpius pallidus: Fisheries Research Station Hong Kong, uncat. (1, 93), Indonesia, off Borneo, 6 June 1964.
Minous monodactylus: CAS 13907 (1, 79), Gulf of Thailand, 14 December 1960.
M. pictus: CAS 13894 (1, 89), Hong Kong, 24 July 1958.
Neomerinthe beanorum: CAS 24386 (1, 105), Gulf of Mexico, 4 February 1967.
Parascorpaena armatus: CAS 15967 (1, 100), Gulf of Thailand, 27 May 1960.
Plectrogenium nanum: CAS 15704 (1, 51), Hawaiian Islands, Lanai, November 1967.
Pontinus longispinis: CAS 15968 (1, 157), Gulf of Mexico, off Yucatan Peninsula, 22 January 1969.
Pterois radiata: CAS 15970 (1, 115), Society Islands, Moorea, 15 May 1957.
Scorpaena agassizii: CAS 24380 (1, 127), South Atlantic, 27 April 1966. *S. albobrunnea*: CAS 15969 (1, 46), Palau Islands, 29 September 1958. *S. brasiliensis*: CAS 15964 (1, 119), Colombia, Gulf of Morrosquillo, 28 November 1968. *S. elongata*: CAS 24399 (1, 192), Angola, 18 March 1968. *S. guttata*: CAS 2463 (1, 193), Mexico, Guadalupe, 16 March 1932. *S. mystes*: SU 50171 (1, 106), Mexico, Sonora, 30 December 1955. *S. porcus*: CAS 13924 (1, 153), Yugoslavia, Piran Bay, 5 October to 1 December 1968. *S. russula*: CAS 13955 (1, 116), Peru, 7 September 1966.
Scorpaenodes parvipinnis: CAS 15972 (1, 71), Mariana Islands, Guam, 4 April 1959.
Scorpaenopsis species: CAS 15966 (1, 108), Mariana Islands, Guam, 25 January 1959.
Sebastiscus species: CAS 17643 (1, 186), Taiwan Strait, Formosa Bank, February 1972.
Sebastosemus species: ZMK uncat. (1, 100), Kermadec Island, Galathea-Ekspeditionen 1950-52 Station Number 675, 3 March 1952.
Setarches guentheri: CAS 15974 (1, 101), Caribbean, off San Andrés Islands, 20 November 1968. *S. longimanus*: Fisheries Research Station Hong Kong, uncat. (1, 118), Hong Kong, 23 August 1964.
Synanceia verrucosa: CAS 14966 (1, 134), Mariana Islands, Guam, 26 April 1959.

OTHER SCORPAENIFORM FISHES

TRIGLIDAE

Leptotrigla alata: SU 21270 (1, 142), Japan, Nagasaki, no date.

HEXAGRAMMIDAE

Hexagrammos decagrammus: SU 55245 (1, 194), California, Moss Beach, 3 July 1949.

Ophiodon elongatus: CAS 21750 (2, 187-202), California, San Pablo Bay, 28 July 1953.

ZANIOLEPIDIDAE

Zaniolepis latipinnis: CAS 15979 (1, 160), California, off Avila, 19-20 October 1970.

PLATYCEPHALIDAE

Platycephalus species: SU 60950 (1, 166), Hong Kong, Plover Cove, 6 January 1958.

HOPLICHTHYIDAE

Hoplichthys langsdorfi: SU 49455 (1, 145), Formosa, no date.

COTTIDAE

Clinocottus analis: CAS 15980 (1, 124), California, off Santa Rosa Island, 25 January 1949.

Cottus asper: CAS 20857 (1, 110), California, Waddell Creek, 24 February to 2 March 1935.

Hemilepidotus jordani: CAS 15568 (1, 149), Alaska, Shumagin Island, 10 August 1962.

Leptocottus armatus: CAS 18110 (1, 157), California, Marin County, 27 May 1945.

Myoxcephalus quadricornis: SU 49209 (1, 134), Alaska, near Barrow, 19 July 1951.

Scorpaenichthys marmoratus: SU 19391 (2, 125-198), California, Moss Beach, 27 November 1951.

COTTUNCULIDAE

Cottunculus thompsoni: SU 9458 (1, 131), Off Delaware, no date.

AGONIDAE

Ocella verrucosa: CAS 15149 (1, 142), Oregon, 19 August 1972.

CYCLOPTERIDAE

Liparis florum: SU 63602 (1, 153), California, Monterey County, 14 October 1955.

ADDENDUM

Recently William Eschmeyer was able to examine additional specimens from the North Atlantic. He informs me that two structural conditions exist for gasbladder musculature in North Atlantic species of *Sebastes*. The gasbladder muscles pass between ventral ribs 2-3 in *S. marinus* and *S. mentella* and between ventral ribs 3-4 in *S. fasciatus* and *S. viviparus*. Therefore the specimens reported here as *S. marinus* are probably *S. fasciatus*, and the muscle type here referred to as the marinus subdivision should be termed the fasciatus-viviparus subdivision.



Hallacher, Leon E. 1974. "The comparative morphology of extrinsic gasbladder musculature in the scorpionfish genus *Sebastes* (Pisces: Scorpaenidae)." *Proceedings of the California Academy of Sciences, 4th series* 40, 59–86.

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