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THE VENOM APPARATUS
OF CALIFORNIA ROCKFISHES
(FAMILY SCORPAENIDAE)

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ABSTRACT

The family Scorpaenidae contains more known venomous fishes than any other bony fish family. The venom apparatus of an American representative of this family, the California sculpin or scorpionfish, has been described previously by several authors.

The rockfish genus *Sebastes* is represented in California waters by over 50 species. Several species of *Sebastes* from European and Asiatic waters are known to possess a venom apparatus, but no previously published literature describes such an apparatus in American rockfishes. The gross anatomy of the spines, pelvic girdle, and musculature and the microscopic anatomy of the spines, associated venom glands, and integument in the brown rockfish, *Sebastes auriculatus*, are described.

The microscopic anatomy of the spines and venom glands in five other species of *Sebastes* is described and compared to that of the brown rockfish. The presence of venom tissue in at least one dorsal spine of eight additional species of *Sebastes* is reported.

Symptoms resulting from human envenomation by several species of *Sebastes* are described and compared to those resulting from the stings of other scorpaenids.

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INTRODUCTION

The teleost family Scorpaenidae enjoys the dubious distinction of containing more venomous species than any other family of bony fishes. Fifty-seven species from the 23 genera *Apistus*, *Brachirus*, *Centropogon*, *Choridactylus*, *Erosa*, *Gymnapistes*, *Helicolenus*, *Hypodytes*, *Inimicus*, *Leptosynanceja*, *Minous*, *Notesthes*, *Pterois*, *Ruboralga*, *Scorpaena*, *Scorpaenodes*, *Scorpaenopsis*, *Sebastapistes*, *Sebastes*, *Sebastodes*, *Sebastolobus*, *Snyderina*, and *Synanceja* have been mentioned or described in the literature as possessing venomous properties (Halstead, 1970). The several species of stonefishes, *Synanceja*, are among the most venomous fishes yet described.

This paper describes the venom apparatus of several rockfish species of the genus *Sebastes* found along the Pacific coast of the United States. Results of this study are of particular interest to marine venomologists since fishes in this genus generally are considered non-venomous.

The genus *Sebastes* Cuvier and the genera *Sebastodes* Gill and *Sebastolobus* Gill are known by the common names rockfish or rock cod. They constitute an important part of the offshore fishery of the Pacific coast.

The first significant work on the venom organs of scorpaenids was published by Bottard in 1879. In his publication of 1889, Bottard created several arbitrary "types" of venomous fishes based on the structure of the venom apparatus, especially on how much of the venom gland was exposed to the outside environment. Two of the groups thus created were the *Synanceja* (stonefish) type and the *Scorpaena* (scorpionfish) type. Bottard denied the existence of venom organs in *Sebastes*.

One of the most important early contributors to the general field of piscine venomology, and to scorpaenid venomology in particular was Pawlowsky (also cited as Pavlovsky, Pavlovskii, and Pavlovskiy by various authors). During the period from 1906 to 1929, this worker published numerous books and papers concerning the venom apparatus of fishes. Two of his publications appearing in 1909 and 1911 were of particular importance to this investigation. In 1909 Pawlowsky described the venom apparatus of the redfish *Sebastes norwegicus*, now *Sebastes marinus* (Linnaeus), and reported the absence of both glandular grooves and venom glands in the spines of two specimens of a closely related dusky rockfish, *Sebastodes ciliatus* (Tilesius), from the North Japan Sea. In his 1911 publication, Pawlowsky described the venom organs of the Joyner stingfish, *Sebastodes joneri*, now *Sebastes joyneri* (Günther). In the same work, he described these organs in a species of the closely related genus *Sebasticus*.

Pawlowsky used the venom apparatus of *Scorpaena* as a prototype. On this basis, he characterized the organs of *Sebastes*, *Sebastodes*, and *Sebasticus* as very poorly developed, although very similar in structure to those found in *Scorpaena* and several other genera of scorpaenids. In his 1911 publication, he presented an interesting drawing illustrating a generalized, diagrammatic scorpaenid spine, accompanied by accurate drawings showing the relative amount and linear extent of the venom gland in the dorsal spines of five scorpaenid species. In this series

of drawings, the ratio of length of venom gland to total length of the spine is 1:2 in *Scorpaena*, 1:3 in *Sebastes joyneri*, and 1:4 in *Sebastes marinus*.

After Pawlowsky, no new publications on the venom organs of rockfishes appeared until the work of Tange. Between 1953 and 1961, Tange produced a series of at least 18 papers concerned with venom organs of Japanese fishes. In his 1954 publication, Tange described the anatomy of the Japanese stingfish, *Sebastes inermis* (Cuvier and Valenciennes), which was of special interest to our investigation.

Phillips (1957) provided the major source of taxonomic information. He discussed 49 species of *Sebastes*, two species of *Sebastes*, and one species of *Scorpaena*, all found in California waters. Phillips recognized the confused state of taxonomy in this group, and indicated that fishes he assigned to the genus *Sebastes* had been assigned to as many as 15 genera prior to his revision. He reviewed the group's taxonomic history beginning with the original description of the genus *Scorpaena* in 1738 and concluding with the studies of later systematists who concurred with placing all eastern North Pacific rockfishes with 13 dorsal spines in the genus *Sebastes*. While Phillips followed this system in his 1957 review, he reported the claims of other contemporary workers that there were insufficient grounds for the existence of the genus *Sebastes*, and that all species assigned to this genus should revert to the genus *Sebastes*. Chen (1971) indicated that this reassignment was valid. In the present paper, all those rockfishes previously assigned to the genus *Sebastes* by Phillips and others will be considered as species of the genus *Sebastes*.

This is the first published description of the venom apparatus of any American *Sebastes* (*Sebastes*).

TERMINOLOGY

The anatomical terminology used in this work is essentially the same as that presented by Halstead, Chitwood, and Modglin (1955a,b). The terms germane to this paper are listed in the glossary.

MATERIALS AND METHODS

Rockfish used in this study were collected with hook and line at San Clemente Island and off Newport Beach, and by otter trawl off Newport Beach and Dana Point, California.

In cases where field identification was not possible, the entire fish was placed in 10% formalin for taxonomic study. When field identification was possible the entire dorsal, pelvic, and anal fins were removed and placed in 10% formalin. Some whole specimens were transferred later from formalin to 30% isopropyl alcohol, while others remained in formalin until needed. No significant difference was noted in stained sections prepared from specimens which had been treated in these different ways.

Spines from either alcohol or formalin storage were washed in running water for several hours and placed in 8% formic acid to decalcify. Decalcification usually was accomplished within 48 hours. The formic acid was changed at least twice during this period. Decalcified spines were washed several hours in running water and transferred to a warm

solution of 10% gelatin and 0.1% Zephiran. Spines were infiltrated with this solution for 24 hours at 37–39°C. Those spines not destined for immediate sectioning were removed from the infiltrating oven and stored at room temperature in the solidified gelatine matrix.

Successive 3–4 mm sections of each spine were cut with a scalpel and embedded in fresh 10% gelatin which was then frozen rapidly with IEC Cryokwik spray. Frozen sections of 8–10 μ were cut in Models CTD and CTF International-Harris Microtome Cryostats at a temperature of –20 to –28°C.

Selected sections were transferred in the cryostat to chilled slides previously coated lightly with Haupt's gelatine adhesive and flattened gently with a small camel hair brush. Slides with sections affixed were removed from the cryostat, thawed rapidly, and placed on a rack in a covered dish containing a small amount of 37% formalin. This dish then was placed in an oven maintained at 37–40°C for 10–15 minutes. The slides were removed to running water for 5–10 minutes, stained 6–8 minutes in fresh Weigert's hematoxylin, differentiated rapidly in 2% hydrochloric acid, washed 10–15 minutes in running water, and counterstained 2–5 minutes in aqueous Eosin Y.

During early stages of developing techniques needed for this work, we discovered that sections of decalcified spines were extremely sensitive to dehydration. Even 50% alcohol produced severe and irreversible shrinking of the decalcified spine proper, although the investing integument and the venom gland appeared unaffected. After numerous futile attempts to reduce or eliminate this shrinkage with its accompanying distortion, dehydration was abandoned. Stained sections were transferred directly to warm glycerine jelly. A coverglass was added immediately, and the mounting medium allowed to solidify at room temperature. Slides were made semipermanent by sealing the edges of the coverglass with plastic cement. Sections prepared in this way show slight fading of the counterstain after more than a year of storage. In staining reaction and histological detail, they equal those prepared by any other commonly used technique.

Fourteen species of *Sebastes* were examined for presence of venom tissue. Of these the chilipepper, *Sebastes goodei* (Eigenmann and Eigenmann); vermilion rockfish, *Sebastes miniatus* (Jordan and Gilbert); calico rockfish, *Sebastes dalli* (Eigenmann and Beeson); rosethorn rockfish, *Sebastes helvomaculatus* Ayres; starry rockfish, *Sebastes constellatus* (Jordan and Gilbert); china rockfish, *Sebastes nebulosus* Ayres; treefish, *Sebastes serriceps* (Jordan and Gilbert); and cow rockfish, *Sebastes levis* (Eigenmann and Eigenmann), had only one dorsal spine examined initially for the presence of venom tissue. The six remaining species, pink rockfish, *Sebastes eos* (Eigenmann and Eigenmann); bocaccio, *Sebastes paucispinis* Ayres; brown rockfish, *Sebastes auriculatus* Girard; quillback rockfish, *Sebastes maliger* (Jordan and Gilbert); greenstriped rockfish, *Sebastes elongatus* Ayres; and half-banded rockfish, *Sebastes semicinctus* (Gilbert), were examined more critically.

Each of the 13 dorsal spines, the left pelvic spine, and the three anal spines were examined histologically. The relative amount and linear extent of any venom tissue was noted, and in each case the standard length of the fish and the length of all spines were recorded (Table I).

GROSS ANATOMY

The gross anatomy of the venom apparatus of the brown rockfish, *S. auriculatus* (Figure 1), is described. This species and the quillback rockfish, *S. maliger*, were the only ones, of the six species examined critically, found to possess venom glands in all spines. The brown rockfish was considered to be representative of the genus *Sebastes* in terms of venom organ gross morphology.

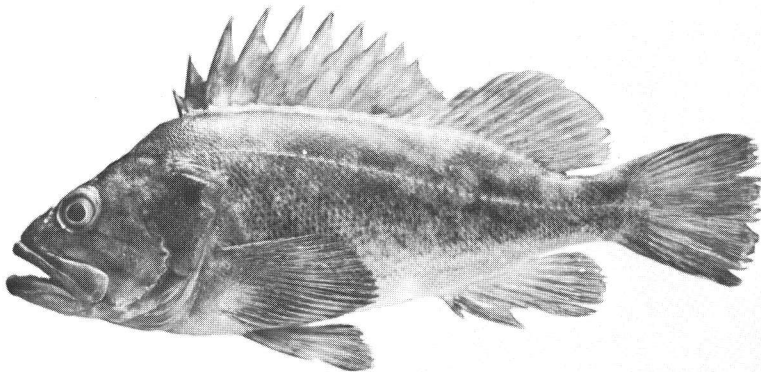


Figure 1. Brown rockfish, *Sebastes auriculatus* Girard.

The venom apparatus of *Sebastes* consists of 13 dorsal spines, 3 anal spines, 2 pelvic spines, their associated musculature, venom glands, and integumentary sheaths. The dorsal and anal spines within their respective fins are connected with each other by the deeply incised interspinous fin membranes. When the integumentary sheath is removed from the spine proper, slender strands of whitish glandular tissue may be seen in the glandular grooves of most spines. This is the venom producing tissue of the sting.

Dorsal Spines

This description is based on dorsal spine IV which is usually the longest dorsal spine. The spine is described in the upright position. From the lateral aspect (Figure 2a) the spine is elongate, slender, slightly curved with a cranial convexity, and tapered distally to a very sharp point. The acute tip of the spine is trigonal in outline. The proximal $\frac{1}{5}$ of the spine also tapers gently, so that the widest point is approximately in the middle. Anterolateral-glandular grooves originate close to this point as shallow depressions which become somewhat deeper and wider as they approach the distal tip of the spine. These grooves terminate 2 mm from the distal tip. An anteromedian ridge extends throughout the length of the spine, and the proximal $\frac{1}{3}$ of this ridge exhibits a shallow but distinct anteromedian groove. A posteromedian groove separates the posterolateral ridges. This groove is narrow and deep near the base, becomes abruptly wider and shallower in the distal $\frac{1}{3}$ of the spine, and disappears approximately 2 mm from the distal tip.

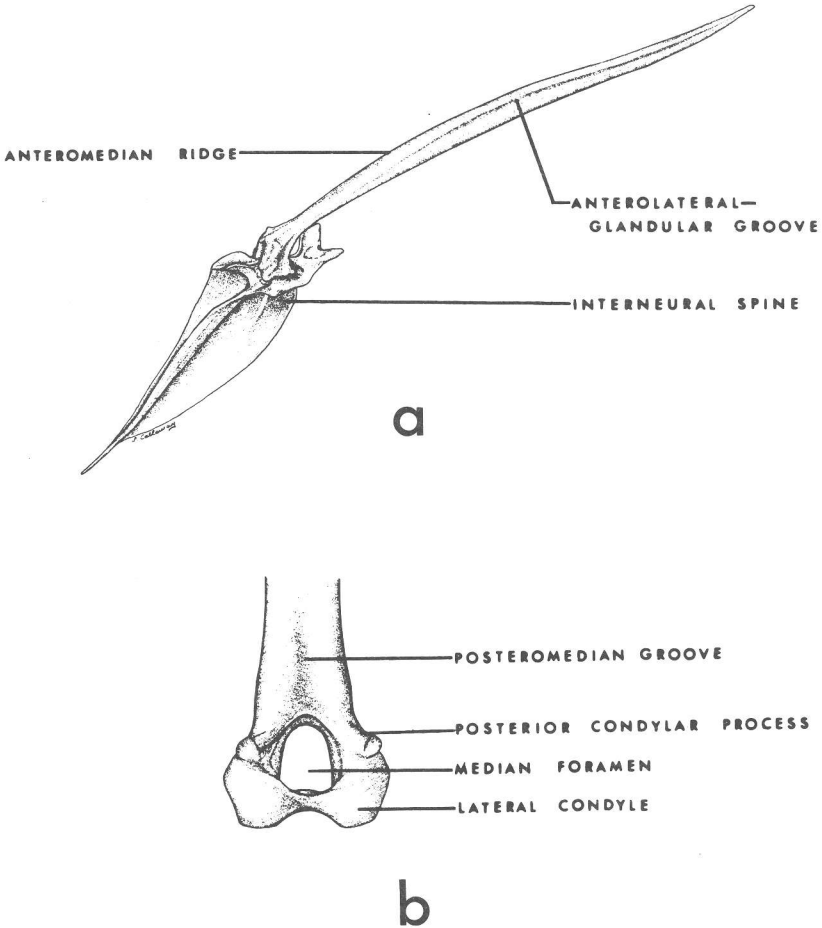


Figure 2. Brown rockfish, *Sebastes auriculatus*, dorsal spine IV. a) Lateral view of spine in articulation with its interneural spine. b) Posterior view of proximal portion.

In life this groove contains a tough membrane of collagenous fibers strongly attached to the spine and contributing to the central portion of the interspinous membrane. The base of the spine is composed of two symmetrical lateral condyles separated by a median foramen which serves as the passage of the annular process of the associated interneural spine (Figure 2B). Projecting posteriorly from the upper portion of each lateral condyle is a small spurlike process, the posterior condylar process. This process serves as the point of insertion for the depressor dorsalis muscle.

Interneural Spines

Each dorsal spine rests on and articulates with an interneural spine (Figure 2A). This is a description of the interneural spine of dorsal IV which is more or less representative of the others (Figure 3). The interneural is generally Γ -shaped. The dorsal or horizontal limb of the interneural is expanded into a flattened, platelike structure called the dorsal plate. The relative size and shape of the dorsal plate in *Sebastes*

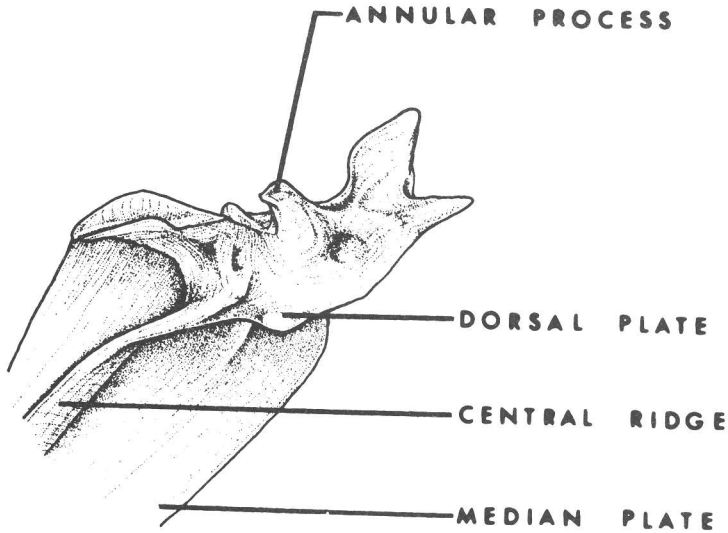


Figure 3. Brown rockfish, *Sebastes auriculatus*, interneural spine IV.

varies somewhat from species to species and spine to spine. The dorsal plate's upper surface is modified to receive the lateral condyles of the adjoining dorsal spine and provides passageways for the depressor dorsalis muscles. The posterior half of the upper surface of the dorsal plate may be flattened or depressed. The anterior half of the dorsal plate's upper surface supports three articular surfaces. There is a median articular process which appears as a spurlike bone, the annular process, that extends into the foramen at the base of the dorsal spine with which it articulates. In most instances, the annular process does not form a complete bony ring, as the anterior portion of the ring usually is composed of cartilage. Anterior to and on either side of the annular process is a small articular concavity. These concavities receive the lateral articular condyles of the dorsal spine. The vertical limb of the interneural spine extends below and anteriorly from the dorsal plate. The dorsal plate is strengthened by a central ridge of bone which appears as a flange extending out from the flattened sheet of median bone and separating the median bone into an anterior and posterior portion. Usually the posterior portion is the larger of the two and is referred to as the median plate of the interneural spine. The median plate in *Sebastes* is usually triangular and provides surfaces for the

origin of the depressor dorsalis and part of the erector dorsalis muscles of the dorsal spine.

Dorsal Spine Musculature

Erection and depression of the individual dorsal spine are controlled largely by two sets of well developed muscles (Figure 4). Removal of the epaxial muscle mass and the thin layer of fascia covering interneural spines permits examination of erector and depressor dorsalis muscles. A set of these muscles is situated on either side of each dorsal

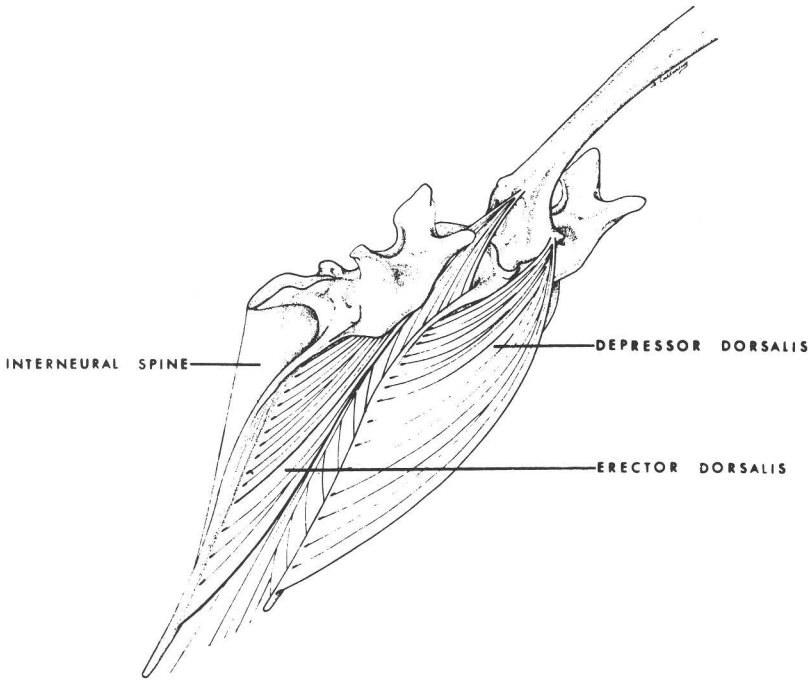


Figure 4. Brown rockfish, *Sebastes auriculatus*, dorsal spine musculature.

spine. The origin and distribution of these muscles become apparent when two adjacent dorsal spines and their associated interneurals are examined, e.g., dorsal spines V and VI. The erector dorsalis muscle of dorsal spine VI originates from the lateroposterior aspect of the median plate of interneural spine V and the anterior aspect of the vertical limb of interneural spine VI. The erector dorsalis muscle then passes between the posterior margin of the dorsal plate of interneural spine V and the anterior margin of the dorsal plate of interneural VI. The erector dorsalis muscle then inserts on the anterior aspect of the base of dorsal spine VI. The depressor dorsalis originates from the lateroanterior aspect of the median plate and the posterior aspect of the vertical limb of the interneural. The anterior portion of the interneural dorsal plate is interrupted or notched so as to provide an opening through which

the depressor dorsalis passes. The depressor dorsalis inserts on the spur-like posterior condylar process at the base of the dorsal spine.

A similar set of muscles is found on both sides of each dorsal spine. The protractor dorsalis and the retractor dorsalis muscles are not as well developed in *Sebastes* as they are in some groups of fishes, and it is doubtful that they play a very significant role in the erection and depression of the dorsal spines. No attempt has been made to describe the superficial inclinator dorsalis muscles which bend or incline the spines to the side.

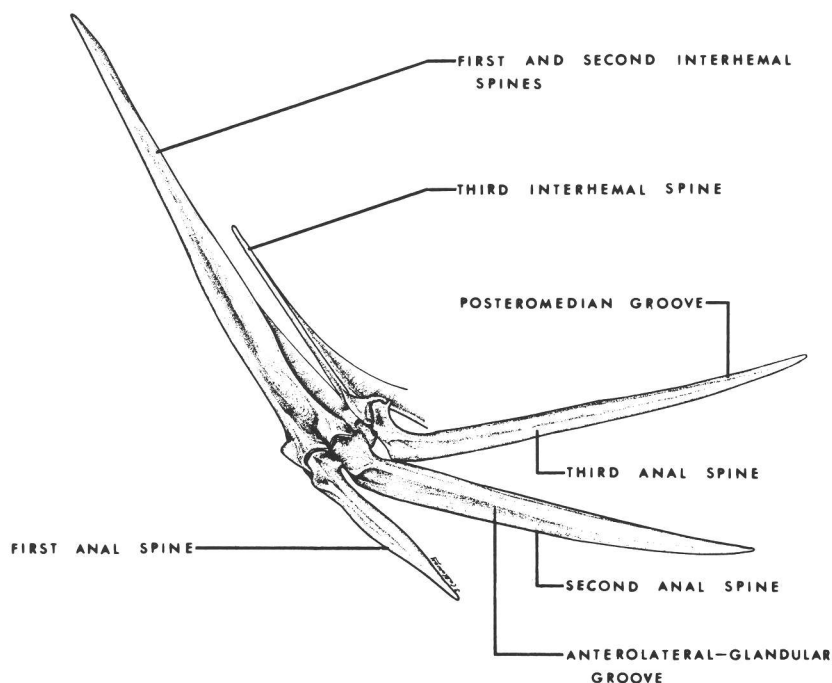


Figure 5. Brown rockfish, *Sebastes auriculatus*, anal spines.

Anal Spines

This description is based on anal spine II which is described in the upright position (Figure 5). The structure of this spine is very similar to that of dorsal spine IV and differs only in these details. The antero-medial groove extends throughout the distal $\frac{2}{3}$ of the spine. The anterolateral-glandular grooves are somewhat shallower and originate distal to the middle of the spine. The posteromedian groove extends to the extreme distal tip of the spine. The median foramen, between the two lateral condyles composing the base of the spine, is somewhat longer and wider, and the entire shaft of the spine is more curved, with a greater craniad convexity.

Interhemal Spines

The three anal spines are supported by and articulate with corresponding interhemal spines (Figure 5). However, the first and second interhemal spines are greatly enlarged in comparison with the other interhemal spines of anal spine III and the anal rays. The first and second interhemals are fused together to form a massive trigonal shaped spine which supports both anal spines I and II. This fused spine is about 1.2 times the length of anal spine II. The first interhemal is somewhat rounded and fused to the second interhemal along the midline. The shaft of the second is expanded laterally throughout its length. The fusion of these two interhemals thus forms a large angular bony structure which provides a fairly deep receptacle for the origin of the erector analis muscles for anal spines I and II, and the depressor analis muscle of anal spine I. The posterior side of the second interhemal spine is deeply grooved and provides attachment for the origin of the depressor analis muscle of anal spine II. The posterior side of the second interhemal spine is flattened. Other interhemals are similar in appearance to the third, but progressively decrease in size toward the last anal ray.

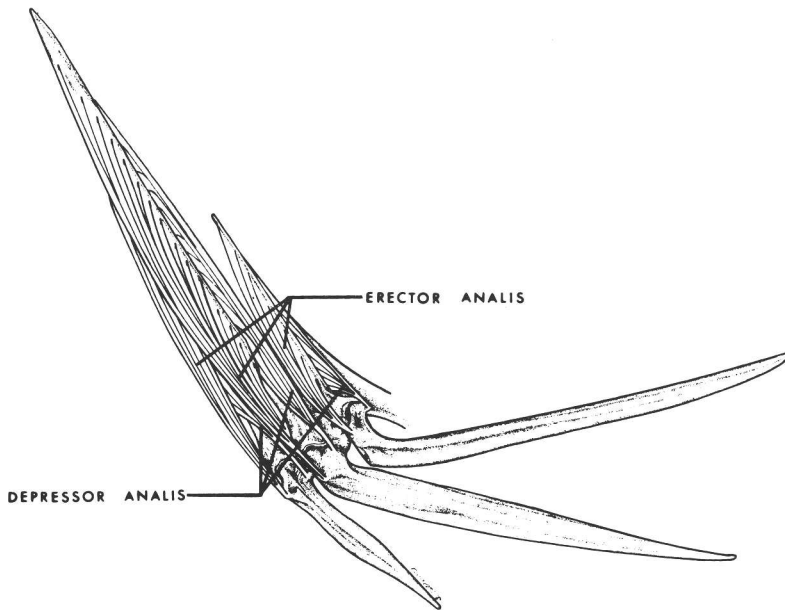


Figure 6. Brown rockfish, *Sebastes auriculatus*, anal spine musculature.

Anal Spine Musculature

Although erection and depression of *Sebastes* anal spines are affected to some extent by the protractor and retractor analis muscles, the principal muscles controlling this function comprise the erector-depressor muscle complex (Figure 6). The inclinitor analis is primarily con-

cerned with lateral movements of the anal fin. The erector-depressor muscles become apparent when the great lateral muscles are removed from the region of the anal fin. The erector-depressor muscles, like those of the dorsal fin, are covered with a fibrous connective tissue sheath. This sheath is continuous with that between the interhemal spines. The erector and depressor muscles consist of alternate slips of muscles. There is a set of erector muscle slips for each fin spine and ray, except for anal spines I and II which share a common origin. The erector muscles for anal spines I and II arise from the anterolateral aspect of the first and second interhemal spines and insert on the anterior aspect of the bases of these anal spines. The erector analis is a very large muscle and divides into two muscle bundles or heads, so as to provide for both the first and second anal spines. A similar muscle arrangement is found on each side of the fin. A comparable muscle arrangement serves the remainder of the anal fin rays. The first depressor muscle lies between and deep to the two heads of the first erector muscle. It has its origin along the lower shaft of the first interhemal and inserts on the spurlike posterior condylar process at the base of anal spine I. The second depressor analis muscle originates on the lateroposterior aspect of the shaft of the second interhemal spine and inserts on the posterior condylar process of the lateral condyle of the base of anal spine II. The third erector analis muscle originates on the anterolateral aspect of the shaft of the third interhemal spine and inserts on the anterior aspect of the lateral condyle of the base of anal spine III.

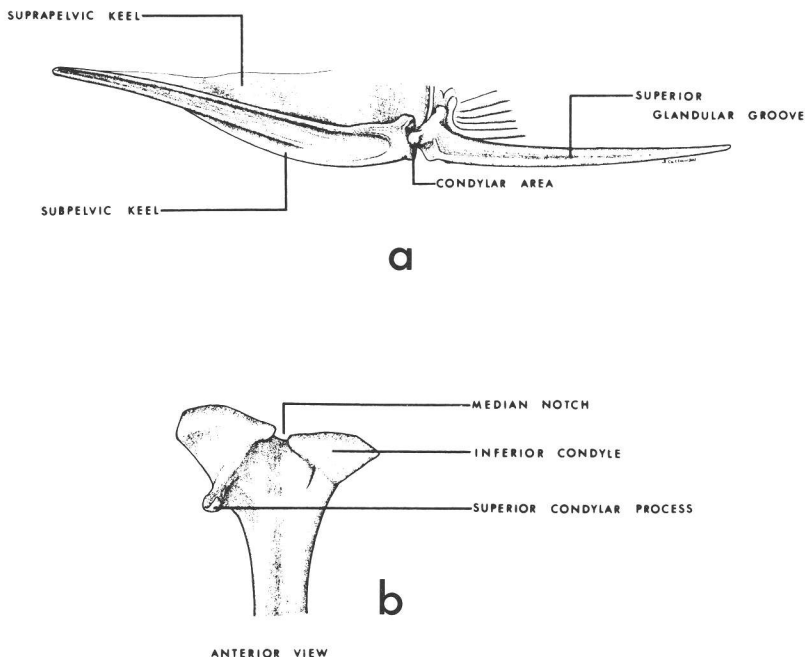


Figure 7. Brown rockfish, *Sebastes auriculatus*. a) Lateral view of left pelvic spine in articulation with the pelvic girdle. b) Anterior view of the proximal portion of the left pelvic spine.

The third depressor analis muscle originates on the posterolateral aspect of the shaft of the third interhemal spine and inserts on the posterior condylar process of the lateral condyles at the base of anal spine III. A similar arrangement is to be found for each of the anal rays on both sides of the fin.

Pelvic Spines

This description is based on the left pelvic spine in the extended anatomical position (Figure 7A). The structure of this spine differs markedly from the dorsal and anal spines in that the shaft of the spine is very stout and strongly trigonal in outline for its entire length. The superior and inferior glandular grooves (the equivalent of the anterolateral-glandular grooves of the dorsal and anal spines) are deep and run the entire length of the shaft. The lateral condyles composing the base of the spine are quite asymmetrical and somewhat flattened (Figure 7B). The superior condyle terminates posteriorly in a hook-like process which extends medially for approximately 2 mm. This structure is in a comparable position to the right posterior condylar process described for dorsal and anal spines. No comparable posterior condylar process is found on the inferior condyle. The median foramen, which exists in dorsal and anal spines between the lateral condyles, is represented in the pelvic spine by a deep notch opening medially between the basal articulating surfaces of the condyles. The postero-medial groove, originating close to the base of the spine, is shallow for the proximal third of the shaft, narrow and deeper in the middle third, and becomes shallower again in the distal portion, disappearing approximately 5 mm from the distal tip.

Pelvic Girdle

In the family Scorpaenidae, the pelvic girdle is thoracic in position. The pelvic girdle of *Sebastes* is comprised of two bones, the basipterygii, which fuse together along the midline and provide support for the two pelvic spines and the pelvic rays. The pelvic girdle is in the shape of an elongate isosceles triangle with the apex directed anteriorly (Figure 7A). The length of the pelvic girdle is about 1.3 times that of the pelvic spine. The greatest posterior width of the girdle is about half the length of the pelvic spine. The lateral sides of the pelvic girdle are stiffened by longitudinal keels which extend along the dorsal and ventral margins and are termed the suprapelvic and subpelvic keels respectively (Matsubara, 1943). On the posterior end of the pelvic girdle along the median line, a small spine projects from each basipterygium. These fuse together to form the postpelvic process. On the underside of the pelvic girdle near the base of the postpelvic process, each basipterygium sends forward a flexible bony process. These fuse and extend forward for half the length of the pelvic girdle. This process is the subpelvic process. The apex of the pelvic girdle is notched. The latero-posterior angle of each basipterygium is equipped with a specialized condylar area having an annular ring which passes through and articulates with the median notch of the pelvic spine. The remainder of the posterior surface of the pelvic girdle provides a condylar surface which articulates with the pelvic rays.

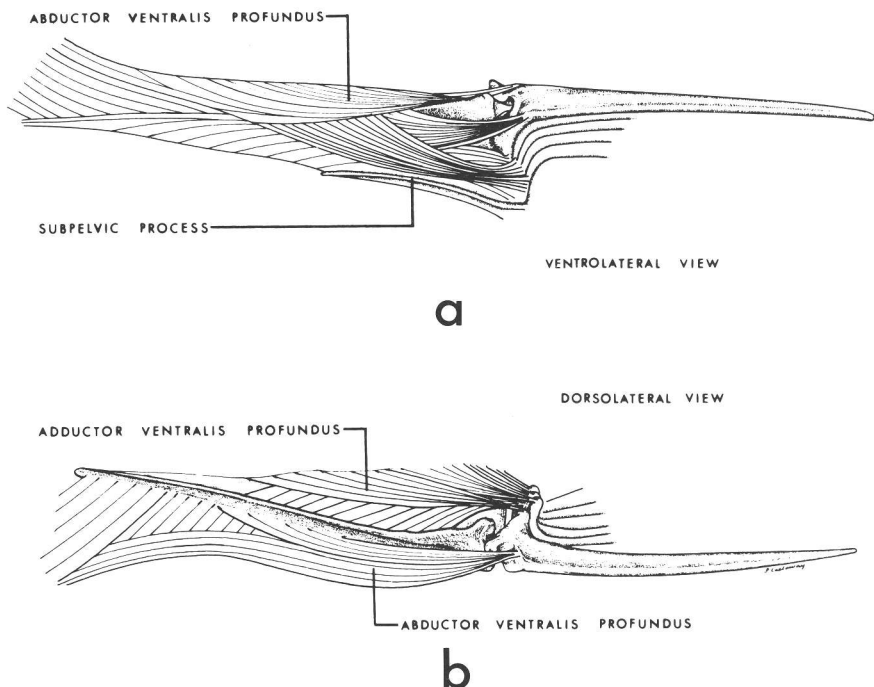


Figure 8. Brown rockfish, *Sebastes auriculatus*. a) Ventrolateral view of pelvic fin musculature. b) Dorsolateral view of pelvic fin musculature.

Pelvic Spine Musculature

Abduction of the pelvic spine is controlled by two sets of muscles, the abductor ventralis superficialis and the abductor ventralis profundus (Figures 8A,B)¹. The abductor ventralis superficialis is a V-shaped muscle arising from the median longitudinal septum of the pelvis and the median ventral aspect of the basipterygium. The superficialis inserts on the ventral aspect of the base of the pelvic spine and the ventral rays. The abductor ventralis profundus is a large and somewhat fusiform muscle. It arises from the anterior portion of the longitudinal septum of the pelvis, from the ventroposterior aspect of the lower portion of the cleithrum, and from the outer ventral aspect of the basipterygium. It inserts on the ventral aspect of the base of the pelvic spine. The posterior half of the abductor ventralis profundus is adjacent and lateral to the abductor ventralis superficialis. Adduction of the pelvic spine is accomplished by the adductor ventralis profundus and the adductor ventralis superficialis. The adductor ventralis profundus, which is the larger of the two muscles, arises from the entire length of the dorsal surface of the basipterygium. The muscle inserts on the dorsal aspect of the base of the pelvic spine. The adductor ventralis superficialis is the most dorsal portion of the pelvic musculature.

¹ The terms a.v. superficialis and a.v. profundus are used in reference to the pelvic abductor muscles of *Sebastes* with some reservation, because the relationship of superficial and deep are somewhat inaccurate when dealing with this group of fishes. However, the designation has been retained since these terms are firmly entrenched in piscine anatomical literature. More proper terms for these two muscles might be a.v. internus and a.v. externus.

TABLE I
Comparison of Venom Gland Length and Spine Length in Six Species of *Sebastes*

| Species of <i>Sebastes</i> | Structure | Spine number and length of structure mm. | | | | | | | | | | | | | | Average length | | |
|---|-------------|--|------|-------|------|-----|------|-------|--------|------|-----|------|-------|--------|-----|----------------|-----|-------|
| | | D I | D II | D III | D IV | D V | D VI | D VII | D VIII | D IX | D X | D XI | D XII | D XIII | P | | A I | A II |
| Brown rockfish, <i>S. auriculatus</i> (230 mm SL) | Spine | 9 | 19 | 30 | 39 | 40 | 40 | 34 | 32 | 30 | 21 | 19 | 23 | 32 | 8 | 30 | 31 | 28 |
| | Venom gland | 3 | 3.5 | 8 | 6.5 | 6 | 5 | 10 | 8 | 7.5 | 7.5 | 3 | 1.5 | 4 | 8 | 8 | 8.5 | 5.5* |
| Greenstriped rockfish <i>S. elongatus</i> (220 mm SL) | Spine | 13 | 22 | 31 | 33 | 32 | 29 | 29 | 28 | 27 | 24 | 20 | 24 | 30 | 18 | 34 | 28 | 26 |
| | Venom gland | 1.5 | --- | 4.5 | 3 | 2.5 | 2 | 3 | 2.5 | --- | 0.5 | --- | --- | 3 | 5 | 4 | 2 | 2* |
| Pink rockfish <i>S. eos</i> (410 mm SL) | Spine | 26 | 40 | 67 | 70 | 65 | 60 | 53 | 42 | 37 | 32 | 29 | 25 | 50 | 30 | 52 | 38 | 45 |
| | Venom gland | 2 | 7 | --- | 4 | 4 | 7 | 5.5 | 6 | 5 | 6 | 5.5 | 3 | 3 | 2 | --- | --- | 3.5* |
| Quillback rockfish <i>S. maliger</i> (245 mm SL) | Spine | 13 | 22 | 32 | 34 | 39 | 41 | 34 | 38 | 33 | 32 | 31 | 30 | 37 | 16 | 32 | 34 | 31.5 |
| | Venom gland | 5.5 | 8.5 | 5 | 9 | 4.5 | 4.5 | 5 | 5.5 | 5.5 | 1 | 2 | 0.5 | 2 | 4 | 11 | 10 | 4.5* |
| Boaaccio <i>S. paucispinis</i> (310 mm SL) | Spine | 17 | 27 | 48 | 48 | 47 | 47 | 46 | 41 | 37 | 25 | 19 | 17 | 22 | 16 | 21 | 32 | 32.5 |
| | Venom gland | --- | --- | 3 | 1.5 | 6.5 | 5.5 | 3 | 1.5 | 1.5 | 1 | 0.5 | --- | 4 | --- | --- | --- | 1.5* |
| Halfbanded rockfish <i>S. semicinctus</i> (120 mm SL) | Spine | 7 | 11 | 16 | 21 | 22 | 20 | 18 | 16 | 15 | 13 | 10 | 7 | 5 | 10 | 20 | 16 | 14.5 |
| | Venom gland | --- | --- | --- | --- | --- | --- | --- | 0.5 | --- | 1.5 | 1 | --- | 0.5 | 1 | --- | 3.0 | 0.58* |

* Calculated for all spines.

It arises from the anterior end of the basipterygium and along the aponeurosis in which the median longitudinal septum, the abdominal peritoneum, and the clavicle meet. There are several tendinous insertions of the adductor ventralis superficialis, but only the most ventral one inserts on the spurlike superior condylar process at the base of the pelvic spine. A similar complex of pelvic muscles is found on each side of the fish.

Other Descriptions of Scorpaenid Spines

The only other detailed anatomical description of the bony spines of *Sebastes* is to be found in the work of Tange (1954), who also described exhaustively the spines of species of the genera *Sebastes*, *Apistus*, *Erosa*, *Hypodytes*, *Inimicus*, *Minous*, *Pterois*, *Scorpaenodes*, and *Sebastolobus*. Halstead, Chitwood, and Modglin (1955, a,b; 1956) published detailed descriptions of the spines of the zebrafish, *Pterois volitans* (Linnaeus); the stonefish, *Synanceja horrida* (Linnaeus); and sculpin, *Scorpaena guttata* Girard. The rest of the numerous publications dealing with scorpaenid venomology contain much more superficial descriptions of the spines proper or none at all.

In most important details, the anatomy of the dorsal, anal, and pelvic spines of the brown rockfish, *Sebastes auriculatus*, compares very closely with Tange's 1954 description of these structures in the Japanese stingfish, *Sebastes inermis*. We compared the total length of each of the 17 spines examined for six species of *Sebastes* with the length of the venom gland in that spine (Table 1). For each species the mean lengths of the spines and the glands were determined, as well as the ratio of venom gland length to total spine length (Table 2). Tange reported such a ratio as 1:3 to 1:7 for the dorsal fin spines of the Japanese stingfish. This compares favorably with the 1:5 ratio calculated for all brown rockfish spines in this study. The ratios of 1:3 and 1:4 for the Joyner stingfish, *Sebastes joyneri*, and redfish, *Sebastes marinus*, respectively were calculated from scale drawings (Pawlowsky, 1911). Tange commented on the complete absence of anterolateral grooves

TABLE II
Ratio of Venom Gland to Total Spine Length

| Species | Ratio* |
|--|--------|
| Brown rockfish, <i>Sebastes auriculatus</i> | 1:5 |
| Greenstriped rockfish, <i>Sebastes elongatus</i> | 1:10 |
| Pink rockfish, <i>Sebastes eos</i> | 1:9.7 |
| Quillback rockfish, <i>Sebastes maliger</i> | 1:7 |
| Bocaccio, <i>Sebastes paucispinis</i> | 1:11.6 |
| Halfbanded rockfish, <i>Sebastes semicinctus</i> | 1:10.3 |

* Calculated for spines containing venom tissue only.

and/or venom glands in some spines of his specimens. While this condition does not exist in the brown rockfish or in the quillback rockfish, *Sebastes maliger*, each of other species we analyzed had at least one spine which lacked venom tissue. In the halfbanded rockfish, *S. semicinctus*, only 5 of the 17 spines examined contained such tissue.

Tange reported a well developed posteromedian groove in Japanese stingingfish spines but did not mention the presence of an anteromedian groove or of the posterior condylar processes we found in brown rockfish spines. It is quite difficult to prove the existence of similar structures in the two fishes since Tange only occasionally distinguished the dorsal, anal, and pelvic spines in his descriptions of certain anatomical features.

MICROSCOPIC ANATOMY

The histological structures of dorsal, anal, and pelvic stings are basically similar so this description will deal primarily with the dorsal group, indicating those variations discovered in the stings of anal and pelvic fins. This description is based largely upon the anatomy of brown rockfish, *Sebastes auriculatus*.

Dorsal Stings

A typical dorsal sting has a roughly trigonal cross-sectional outline in the distal $\frac{1}{3}$ and shows indentations representing the two anterolateral-glandular grooves and the posteromedian groove (Figure 9A).

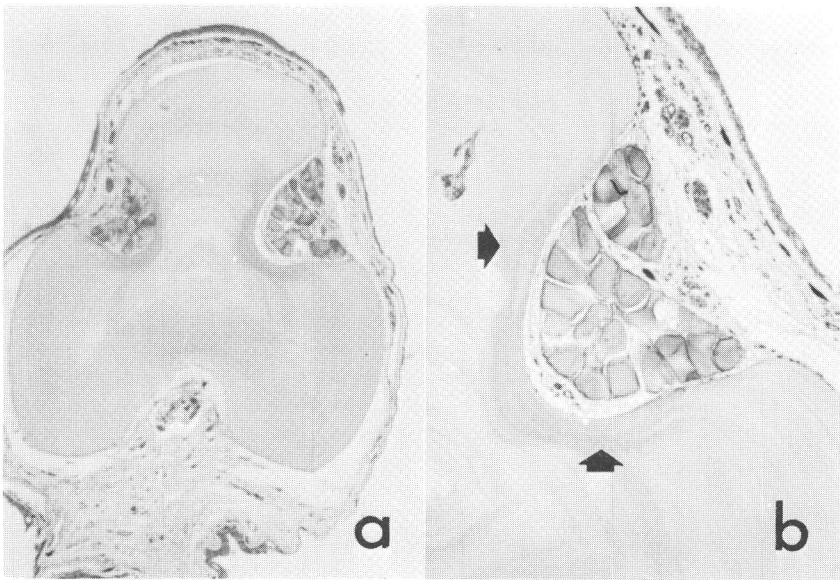


Figure 9. Brown rockfish, *Sebastes auriculatus*, dorsal sting VII. a) Cross section, distal $\frac{1}{3}$, $\times 40$. b) Glandular triangle, cross section, distal $\frac{1}{3}$, $\times 100$. Arrows indicate Sharpey's fibers.

The spine consists of dense, acellular bone exhibiting well developed concentric lamellae (Figure 9B). A thin periosteum containing numerous flattened connective tissue cells covers the bone surface. Sharpey's fibers are well developed in the areas of the anterolateral-glandular grooves and in the vicinity of the posteromedian groove at the zone of its attachment to the inner fibrous portion of the interspinous membrane (Figure 9B).

The bone is solid in the distal $\frac{1}{4}$ to $\frac{1}{3}$ of the spine, but proximal to this, "marrow spaces" occur in the central portion. In more distal areas of their occurrence, these spaces generally appear as a single large round or oval cavity surrounded by three to seven smaller satellite cavities. In the basal $\frac{1}{3}$ of the spine, these multiple cavities coalesce into a single irregularly shaped cavity partially subdivided by branching trabeculae. Numerous capillaries and venules containing blood cells can be seen within the loose connective tissue matrix filling these central cavities. Many variously sized and apparently extracellular lipid droplets are present, though no typical adipose cells are found. An endosteum of varying thickness, similar to the periosteum described previously, may be seen lining some of the larger central cavities. No evidence of hemopoietic activity was seen in any spines examined in this study. Patt and Patt (1969) stated that the term "marrow" is not applicable to fishes. Bone immediately surrounding the central cavities shows distinct differences from that in more peripheral areas of the spine. It is denser and exhibits more closely spaced lamellae. This may indicate that resorption with subsequent redeposition of bone has taken place.

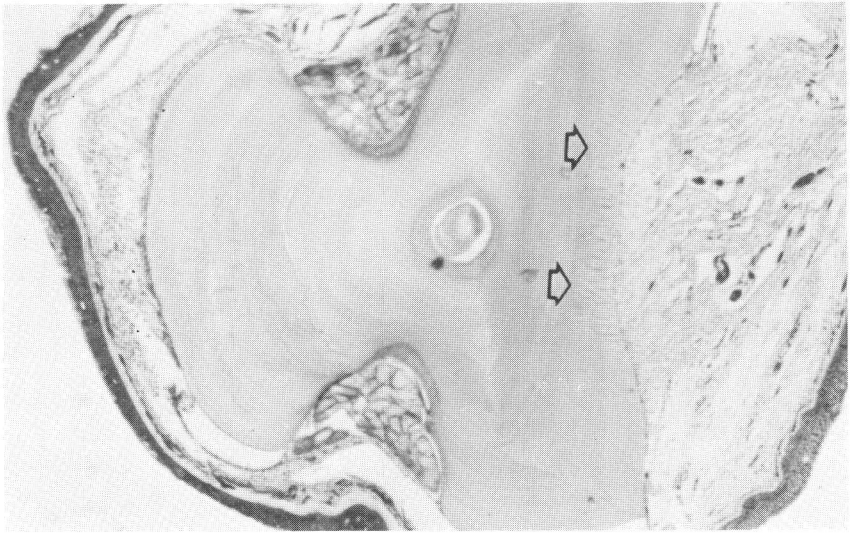


Figure 10. Brown rockfish, *Sebastes auriculatus*, anal sting III. Cross section, distal $\frac{1}{3}$, $\times 40$. Note Sharpey's fibers at the posterior surface (arrow) and the coarse fibers of the interspinous membrane.

Anal Stings

The microscopic anatomy of the anal stings is very similar to that of the dorsal stings (Figure 10). The major difference lies in the shape of the cross section. The anal spine, while basically trigonal in outline, has a broader base and a less acute apex in the distal $\frac{1}{3}$ than the corresponding cross section of a typical dorsal spine. The posteromedian groove is very wide and shallow and the fiber bundles attaching to the bone from the interspinous membrane are coarser than those of the

dorsal stings. A small central cavity is present in the anal spine, even in the distal $\frac{1}{4}$. The epidermis of the integument is somewhat thicker throughout than that covering the dorsal spines.

Pelvic Stings

As in the case of the anal spine the major difference between the cross section of the left pelvic spine and that of the dorsal spine is its shape. Again, the cross section of the pelvic spine is basically trigonal, but the distance from base to apex is relatively greater than that in either of the other spines. The glandular grooves are deep, and the posterior border of the spine is convex, displaying a posteromedian prominence rather than a groove (Figure 11a). Fiber bundles attaching to the posterior surface of the spine are coarse as in the anal sting. The pelvic spines in cross section quite closely resemble the pelvic spines of both the sculpin, *Scorpaena guttata*, and the zebrafish, *Pterois volitans* (Halstead *et al.*, 1955 a,b).

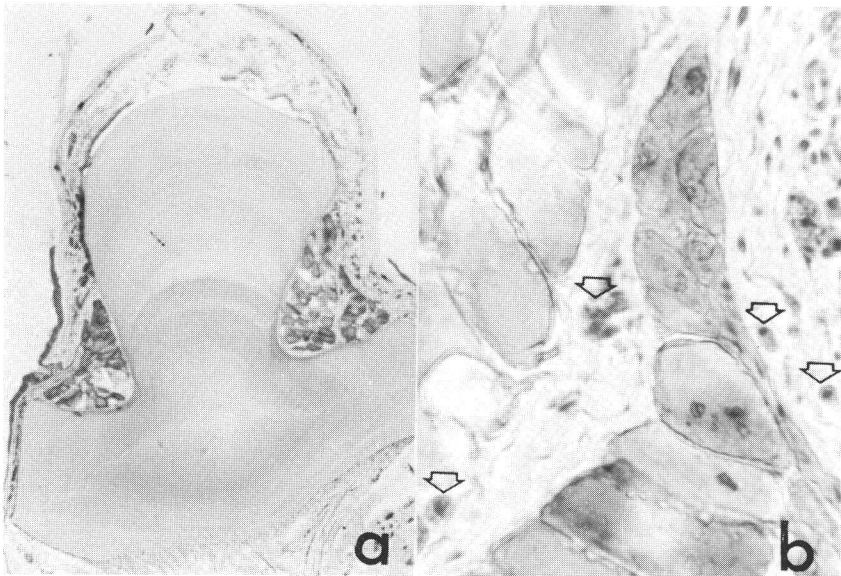


Figure 11. Brown rockfish, *Sebastes auriculatus*, left pelvic sting. a) Cross section, distal $\frac{1}{3}$, $\times 40$. Note coarse fibers of the interspinous membrane at the posterior surface. b) Cross section, distal $\frac{1}{3}$, $\times 400$. Arrows indicate supporting or undifferentiated cells closely associated with the venom gland.

Integumentary Sheath

The integumentary sheath invests the dorsal spines for at least the proximal $\frac{3}{4}$ of their length in all species of *Sebastes* studied. Anal spines are similarly invested, and pelvic spines are completely covered. This integument is discretely divided into a peripheral epidermis and an underlying dermis. The epithelium is typical stratified squamous, varying in thickness from a minimum of four layers of cells in the extreme distal portion of the sheath to more than 20 layers in the basal portion at the junction of the spine sheath and dorsal body skin. It is

noted that, even in the distal portions, the epidermis of the sheath is thinnest at the anterior surface of the sting and becomes progressively thicker as it approaches its junction with the connecting interspinous membrane. Unicellular mucus glands of the goblet cell type are present in the middle and upper layers of the epidermis. Their numbers are small in the distal portion of the spine sheath, but they increase toward the proximal end so that they are quite numerous in the basal areas. A very thick and hyaline basement membrane underlies the epithelium. Below the basement membrane is the dermis composed of loose connective tissue with many bundles of collagenous fibers, fibrocytes, and small blood vessels. A layer of melanophores forms the peripheral layer of the dermis. Most of these heavily pigmented cells are fixed in the extended position.

Scattered through the dermis, but most heavily concentrated in the vicinity of the glandular and posteromedian grooves, are structures closely resembling acini of serous glands. The modified cuboidal cells comprising these structures have round, centrally placed, strongly basophilic nuclei and weakly acidophilic cytoplasm. The cytoplasm is homogeneous and finely granular. Halstead *et al.* (1955 a,b) reported very similar structures from the dermis of the sculpin, *Scorpaena guttata*, and the zebrafish, *Pterois volitans*.

Venom Glands

Within the anterolateral-glandular grooves is a cluster of large cells comprising the venom gland. The basic shape of the cells is polygonal, but they vary widely in size. Fifteen cells from a typical glandular triangle were measured and found to range in size from a low of

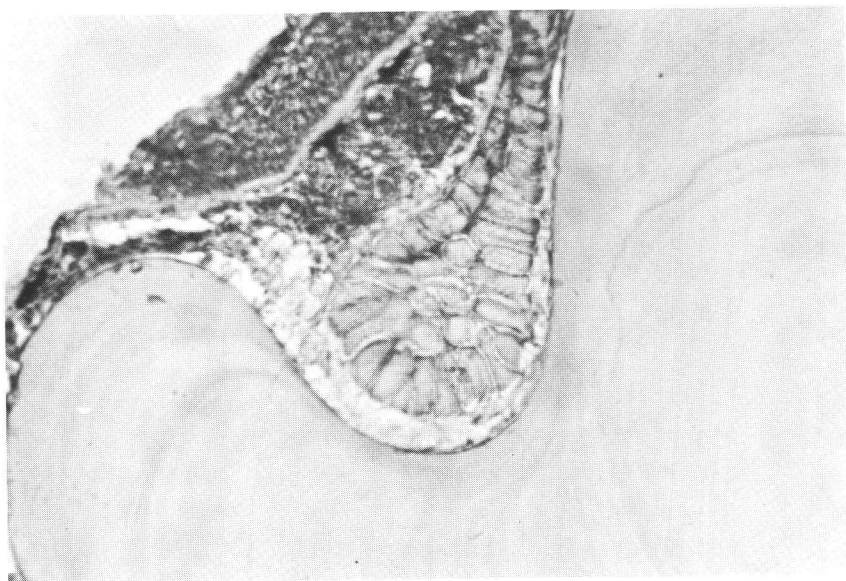


Figure 12. Vermilion rockfish, *Sebastes miniatus*, glandular triangle of dorsal sting IV. Cross section, distal $\frac{1}{3}$, $\times 100$. This specimen illustrates the most regular arrangement of venom gland cells encountered in the present study.

$26 \times 10\mu$ to a high of $64 \times 24\mu$, with a mean size of $38 \times 22\mu$. Tange (1954) recorded dimensions of $30 \times 13\mu$ up to $40 \times 33\mu$ for venom gland cells of the Japanese stingfish, *Sebastodes inermis*. The mean of these two figures is $35 \times 23\mu$ which agrees very favorably with measurements from the brown rockfish, *Sebastes auriculatus*.

The regular pinnate, or two layered arrangement, and the cardiform cross-sectional outline described for the sculpin, *Scorpaena guttata*, the zebrafish, *Pterois volitans*, (Halstead *et al.*, 1955 a,b) and the scorpionfish, *Notesthes robusta*, (Cameron and Endean, 1966) were not found in any species of *Sebastes* examined during this study. The most regular arrangement of cells observed was seen in dorsal sting IV of one specimen of vermilion rockfish, *Sebastes minatus* (Figure 12). This specimen also was found to have three glandular grooves containing venom tissue in parts of dorsal spine IV. We believe this three grooved condition in a scorpaenid sting has not been reported previously in the literature.

The irregular arrangement of venom gland cells in California *Sebastes* agrees with the findings of Pawlowsky (1909, 1911) for the redfish, *Sebastes marinus*, and the Joyner stingfish, *Sebastodes joyneri*. Tange (1954) also described and illustrated the cells in venom glands of the Japanese stingfish, *Sebastodes inermis*, as having an irregular arrangement.

The cytoplasm of the venom gland cells exhibits a staining reaction which is predominantly acidophilic in all species studied. There is some variation in intensity of the cytoplasmic stain, with disintegrating cells staining more faintly than those in which a discrete nucleus can be demonstrated (Figure 13).



Figure 13. Quillback rockfish, *Sebastes maliger*, left pelvic sting, cross section, distal $\frac{1}{3}$, $\times 400$. The middle cells are in the process of disintegrating.

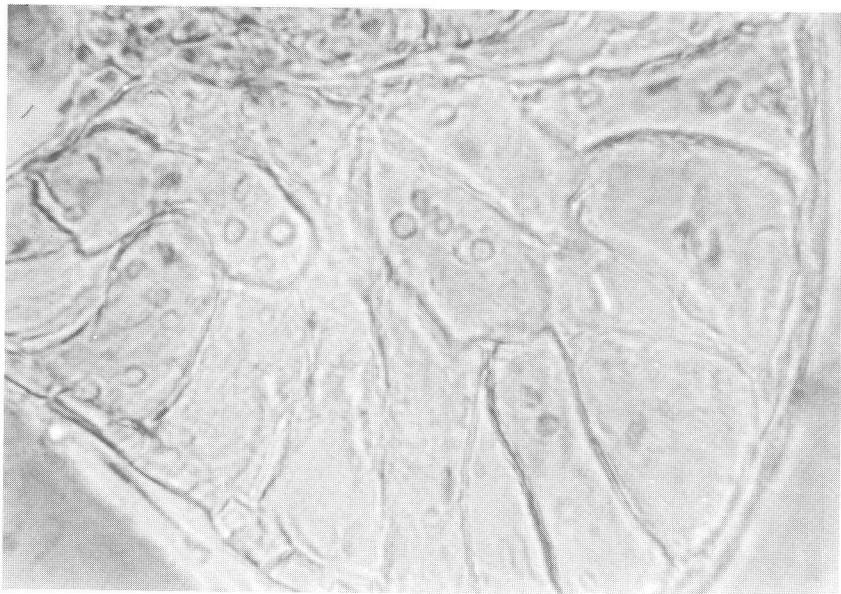


Figure 14. Greenstriped rockfish, *Sebastes elongatus*, glandular triangle of anal sting I, cross section, distal $\frac{1}{2}$, $\times 400$. Note the many small vacuoles in the venom gland cells.

Gland cell cytoplasm varies markedly in appearance, depending upon which phase of the secretory cycle is represented by the particular cell observed. Our study and work by other authors involving *Sebastes* and other genera of scorpaenids, strongly indicates gland cells produce venom by a holocrine type of secretory cycle. In this type cycle, several clearly marked phases may be demonstrated: intact cells with well defined basophilic nuclei and homogeneous granular cytoplasm (Figure 9b); vacuolated cells containing either numerous small vacuoles (Figure 14) or fewer larger vacuoles (in this stage, the cytoplasm may be more coarsely granular than in the first stage); cells obviously disintegrating, with nucleus either completely absent or in an advanced stage of karyolysis (Figure 13), and completely disintegrated cells whose contents have formed oval or circular masses within the venom gland. These masses are composed of a colloidal appearing material.

Pawlowsky (1911) referred to "pigment-like degenerated cells" which he observed in the venom glands of several scorpaenid genera. Tange (1954) alluded to Pawlowsky's meager description of these cells and stated that he could not find them in the Japanese stingfish, *Sebastes inermis*, or in any other species of venomous fish which he had examined. It seems reasonable that the degenerated cells described by Pawlowsky were actually groups of venom cells in a late stage of the secretory cycle. In Pawlowsky's 1911 publication, he presented a drawing showing a section of the venom gland of the Joyner stingfish, *Sebastes joyneri*. Included in the drawing are two large, granular, dark-staining bodies which he identified as pigment-like degenerated cells. A number of light spherical and oval bodies which might be vacuoles or disintegrating nuclei are in these cells. Cameron and

Endean (1966) presented a simple line drawing of a portion of the venom gland of the scorpionfish, *Notesthes robusta*. Several structures identified as cavities filled with extracellular venom closely resemble Pawlowsky's pigment-like "cells".

Venom cells in the early stages of secretion generally contain one nucleus, though some binucleate cells were observed in most species examined. Nuclei are usually oval in outline, stain weakly basophilic with Weigert's hematoxylin, and do not have prominent nucleoli. Fifteen nuclei from venom gland cells of six *Sebastes* species were measured and their average dimensions were calculated:

| | |
|---|-----------------|
| 1. Pink rockfish, <i>Sebastes eos</i> | 6.0 × 4.5 μ |
| 2. Quillback rockfish, <i>S. maliger</i> | 4.0 × 4.0 μ |
| 3. Brown rockfish, <i>S. auriculatus</i> | 5.5 × 4.0 μ |
| 4. Bocaccio, <i>S. paucispinis</i> | 5.0 × 5.0 μ |
| 5. Halfbanded rockfish, <i>S. semicinctus</i> | 4.5 × 4.0 μ |
| 6. Greenstriped rockfish, <i>S. elongatus</i> | 5.0 × 4.0 μ |

These nuclear characteristics and dimensions agree closely with findings of previous authors. Pawlowsky (1909) gave no measurements for gland cell nuclei of the redfish, *Sebastes marinus*, but described them as small. Tange (1954) characterized these nuclei in the Japanese stingfish, *Sebastes inermis*, as deficient in chromatin and small in contrast with the total size of the cell. He gave an average measurement of 6 × 4 μ for this species. Halstead *et al.*, (1955 a,b) described the nuclei in the sculpin, *Scorpaena guttata*, and the zebrafish, *Pterois volitans*, as large, but gave no measurements. Some of the original slides of sculpin spines used in the 1955 work were reexamined and nuclei of the venom gland cells were measured. An average of 7.5 × 6.0 μ was obtained for this species. Cameron and Endean (1966) remarked that in scorpionfish, *Notesthes robusta*, nuclei are found only in venom gland cells with homogeneous cytoplasm. They recorded an average of 5.5 μ for the weakly basophilic, spherical nuclei of this species.

Within the venom gland proper, two distinct types of closely associated cells may be seen. The first type consists of the glandular cells themselves which have been described previously in the various phases of their secretory cycle. The second type consists of small cells with round or fusiform nuclei, closely resembling those of the fibrocytes found in many types of connective tissue. These cells are found at the periphery of the venom glands as well as among the gland cells in the more central portions of the venom gland (Figure 11b). These cells were first described by Pawlowsky (1911) who named them "supporting cells". He believed that they serve as the source of new gland cell formation but was unable to trace the process in detail due to imperfection of his experimental material. Tange (1954) described the same cells from the Japanese stingfish, *Sebastes inermis*. He called them "supporting or substitute cells" but did not comment on their possible function. Cameron and Endean (1966) described these cells from the scorpionfish, *Notesthes robusta*, and called them "supporting or undifferentiated cells". They performed experiments on the regeneration of discharged venom glands, which showed that supporting cells are transformed into venom gland cells during the regeneration process.

In summary, all dorsal spines of the brown rockfish, *Sebastes auriculatus*, were found to contain venom glands in varying quantities and

in differing stages of secretion. Stings II, IV to X, and XIII contained some extracellular sacs of the colloidal appearing material which apparently represents the last stage of the holocrine secretory cycle. Most spines have venom tissue unilaterally at the distal tip.

No significant differences were noted in the venom tissue of the anal and pelvic stings. The pelvic sting and anal sting III contain some colloidal areas, while anal stings I and II contain only intact gland cells.

VENOM APPARATUS OF OTHER SEBASTES SPECIES

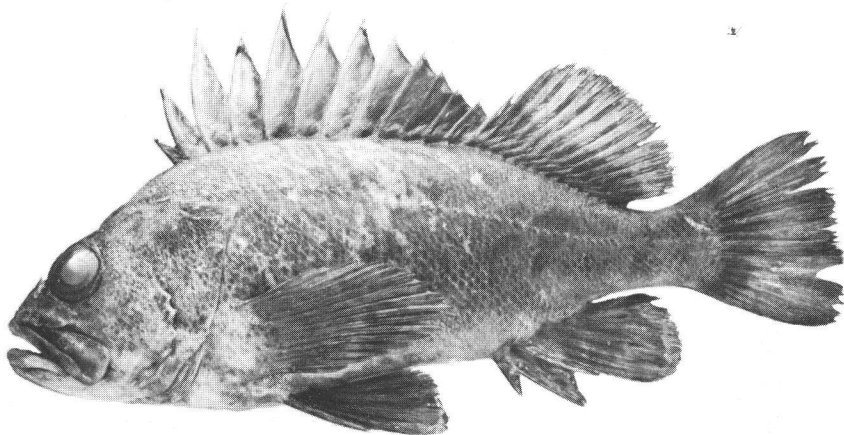


Figure 15. Quillback rockfish, *Sebastes maliger* (Jordan and Gilbert).

Quillback rockfish, *Sebastes maliger* (Jordan and Gilbert)

Dorsal Stings. All dorsal spines contain well developed bilateral venom glands except X and XII in which the gland is very small and unilateral, and II in which there is only one shallow anterolateral groove with venom tissue. This groove eventually twists around to become anterior. Dorsal stings I, II, IV, and VI to IX contain colloidal areas in addition to intact venom cells (Figures 16 a,b).

Anal Stings. All three anal spines contain well developed bilateral venom glands. In addition, sting III contains colloidal areas (Figures 17a,b).

Pelvic Stings. The left pelvic spine contains large well-developed bilateral venom glands with some scattered vacuolar areas (Figure 18).

Pink rockfish, *Sebastes eos* (Eigenmann and Eigenmann)

Dorsal Stings. All dorsal spines except III contain venom glands (Figures 20, 21a,b). In spines II, IV, V, and XIII these glands are unilateral and poorly to moderately developed. In spines IX (Figure 21a) and X there are three glandular grooves with well developed venom tissue. All the remaining dorsal spines contain bilateral venom glands moderately to well developed. No colloidal areas are present.

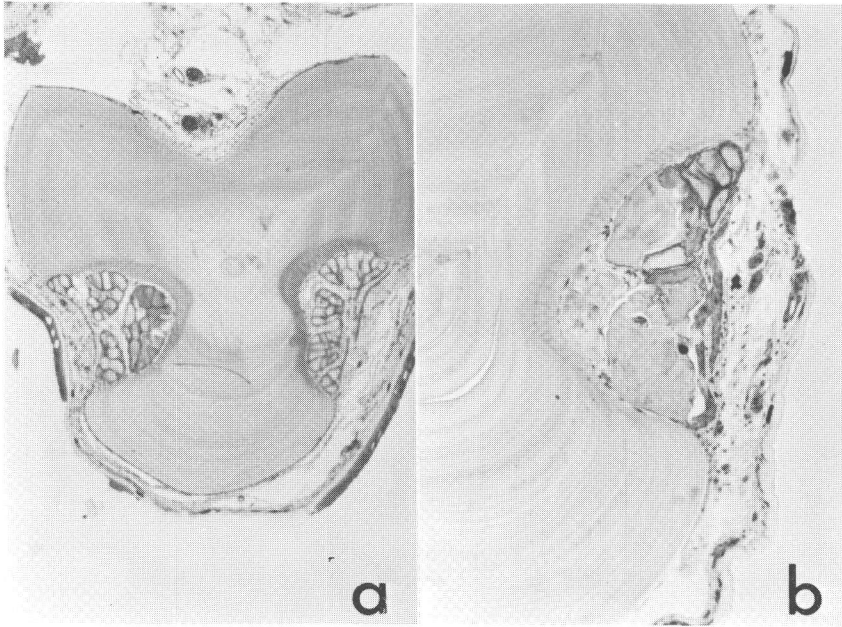


Figure 16. Quillback rockfish, *Sebastes maliger*. a) Dorsal sting V, cross section, distal $\frac{1}{3}$, $\times 40$. b) Glandular triangle of dorsal sting IX, cross section, distal $\frac{1}{3}$, $\times 100$. Almost entire glandular groove is filled with colloidal material.

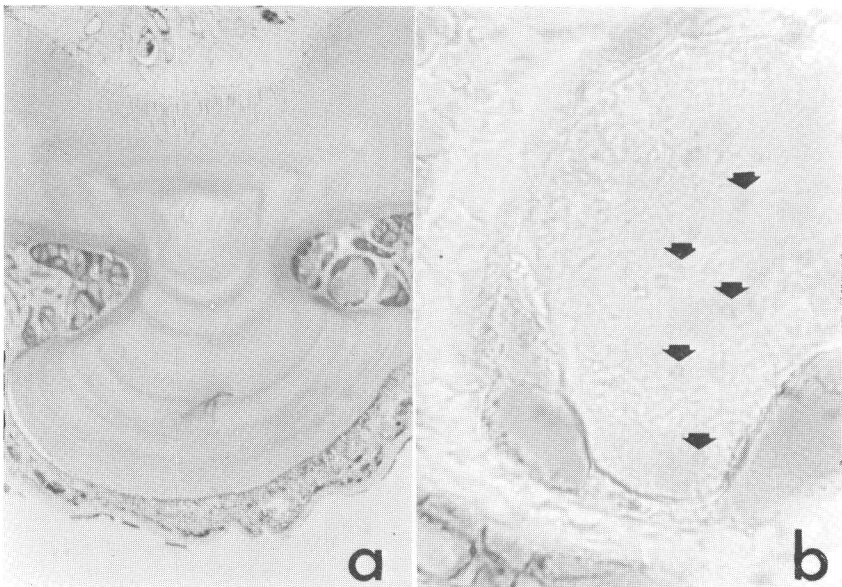


Figure 17. Quillback rockfish, *Sebastes maliger*. a) Anal sting III, cross section, distal $\frac{1}{3}$, $\times 40$. Note colloid areas. b) Glandular triangle of anal sting III. Cross section, distal $\frac{1}{3}$, $\times 400$. Arrows indicate apparent nuclear "ghosts" in colloidal material. Note discrete membrane enclosing colloidal area.

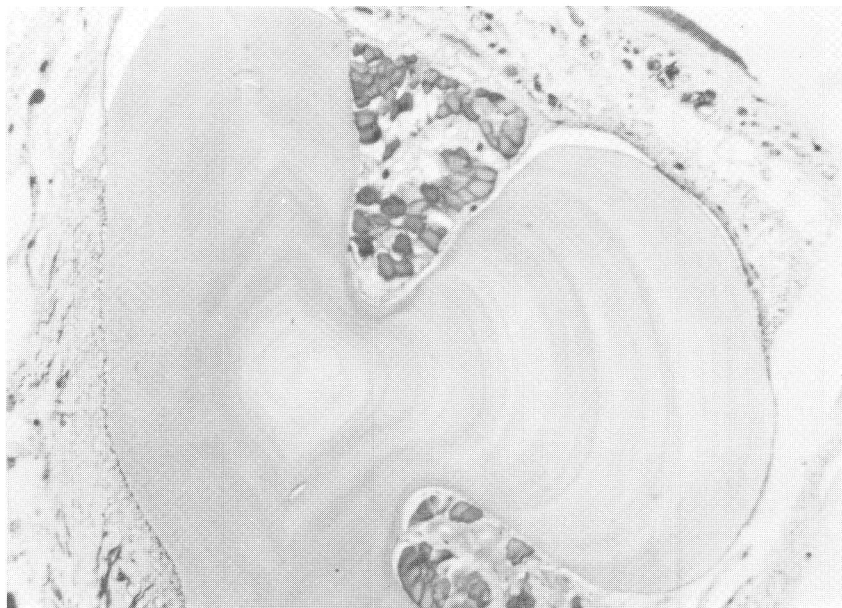


Figure 18. Quillback rockfish, *Sebastes maliger*, left pelvic sting. Cross section, distal $\frac{1}{3}$, X40. Note vacuolated areas in venom gland.

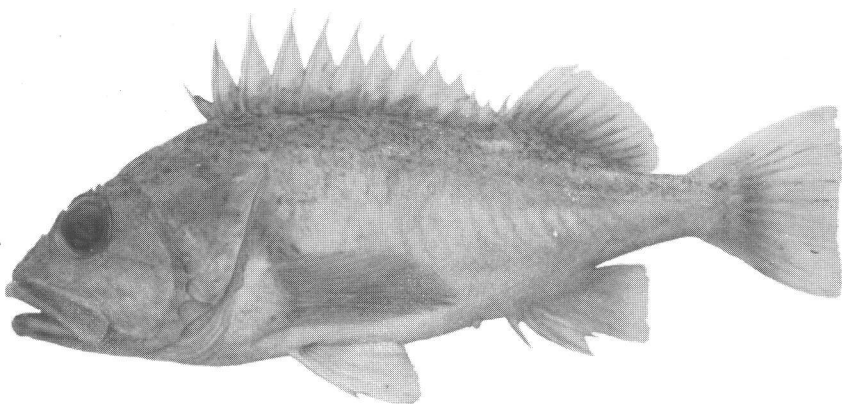


Figure 19. Pink rockfish, *Sebastes eos* (Eigenmann and Eigenmann).

Anal Stings. Anal spines II and III contain very shallow grooves, but no venom glands (Figure 22a). Anal I has a unilateral, poorly developed venom gland. No colloidal areas are present.

Pelvic Spines. No venom tissue is present in the shallow glandular grooves (Figure 22b). The posteromedian groove is extremely shallow.

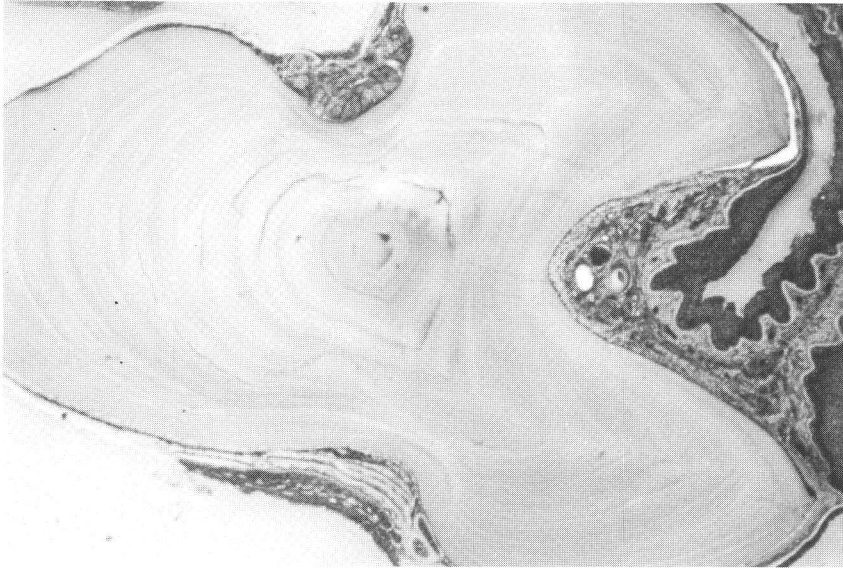


Figure 20. Pink rockfish, *Sebastes eos*, dorsal sting IX. Cross section, distal $\frac{1}{3}$, $\times 35$.

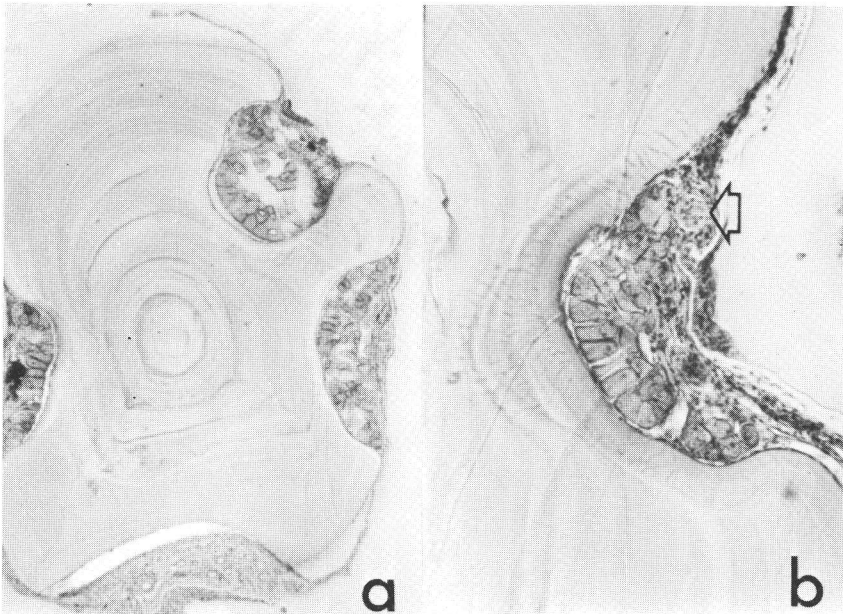


Figure 21. Pink rockfish, *Sebastes eos*. a) Dorsal sting IX. Cross section, distal $\frac{1}{3}$, $\times 60$. Note the presence of three glandular grooves containing venom glands. b) Glandular triangle of dorsal sting IX. Cross section, distal $\frac{1}{3}$, $\times 100$. Note Sharpey's fibers adjacent to the glandular groove. Arrow indicates glandular acinus.

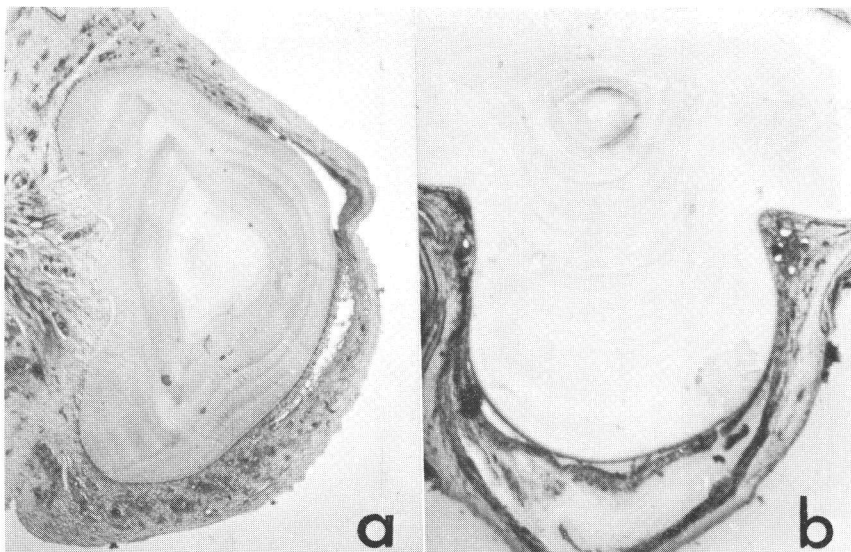


Figure 22. Pink rockfish, *Sebastes eos*. a) Anal sting II. Cross section, distal $\frac{1}{3}$, $\times 35$. Note absence of venom tissue. b) Left pelvic sting. Cross section, distal $\frac{1}{3}$, $\times 40$.

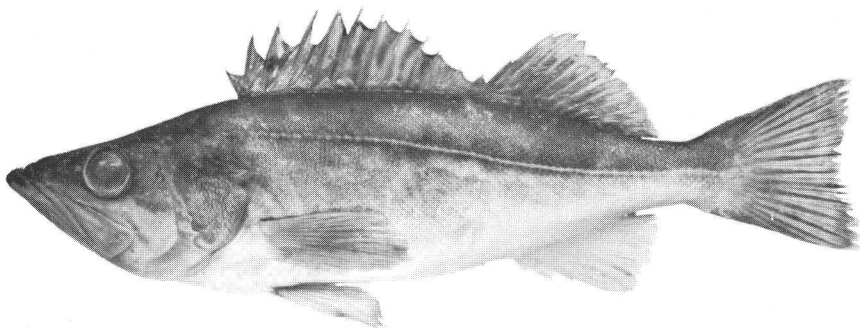


Figure 23. Bocaccio, *Sebastes paucispinis* Ayres.

Bocaccio, *Sebastes paucispinis* Ayres

Dorsal Stings. No glandular grooves or venom glands are present in spines I, II, XII, and XIII, but spines VII to XI have poorly developed unilateral venom glands. The remaining dorsal spines have moderately to well developed bilateral glands (Figures 24a,b) with the exception of IV which has a short section with three glandular grooves containing glandular tissue. No colloidal areas are present.

Anal Spines. All three anal spines lack both glandular grooves and venom tissue (Figure 25a).

Pelvic Sting. The left pelvic spine contains a short, poorly developed venom gland, unilateral for most of its length (Figure 25b). No colloidal areas are present.

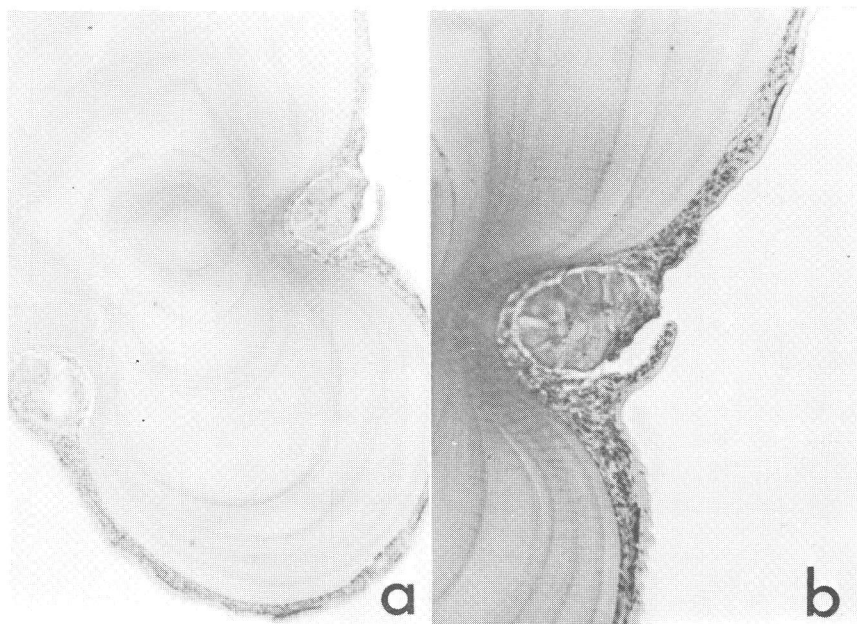


Figure 24. Bocaccio, *Sebastes paucispinis*, dorsal sting VI. a) Cross section, distal $\frac{1}{3}$, $\times 60$.
b) Glandular triangle, cross section, distal $\frac{1}{3}$, $\times 100$.

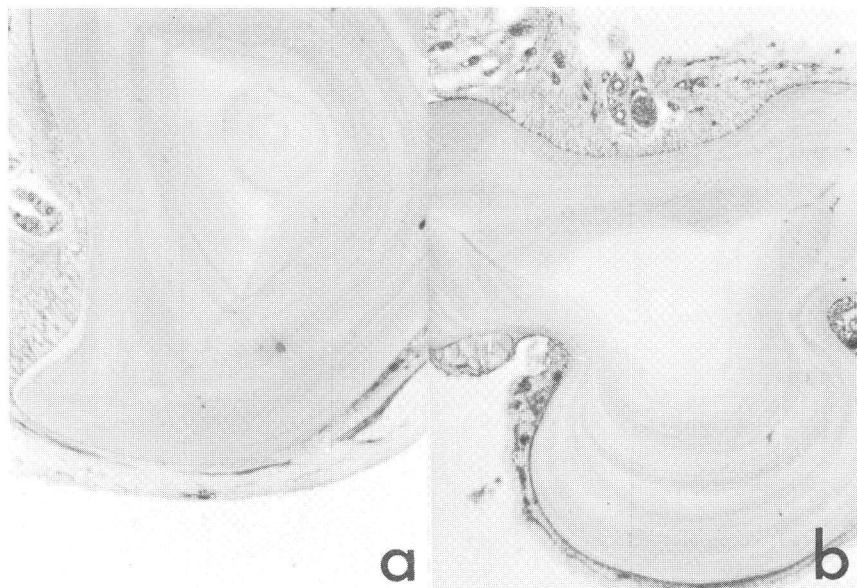


Figure 25. Bocaccio, *Sebastes paucispinis*. a) Anal sting I. Cross section, distal $\frac{1}{3}$, $\times 40$.
b) Left pelvic sting. Cross section, distal $\frac{1}{3}$, $\times 40$.

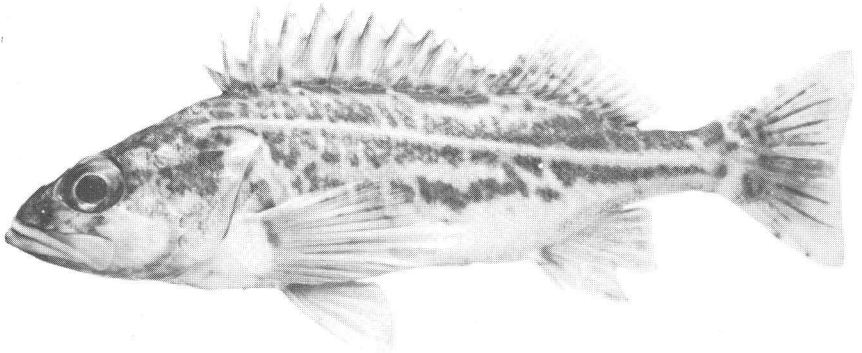


Figure 26. Greenstriped rockfish, *Sebastes elongatus* Ayres.

Greenstriped rockfish, *Sebastes elongatus* Ayres

Dorsal Stings. Spines II, IX, XII, and XIII have very shallow glandular grooves and no venom glands. Spines VI, X, and XI have poorly developed unilateral glands. The remaining dorsal spines have moderately to well developed bilateral glands (Figures 27a,b) with the exception of I which also has a short section with three grooves and glands. No colloidal areas were found.

Anal Stings. All three anal spines have bilateral, well developed venom glands (Figure 28). No colloidal areas are present.

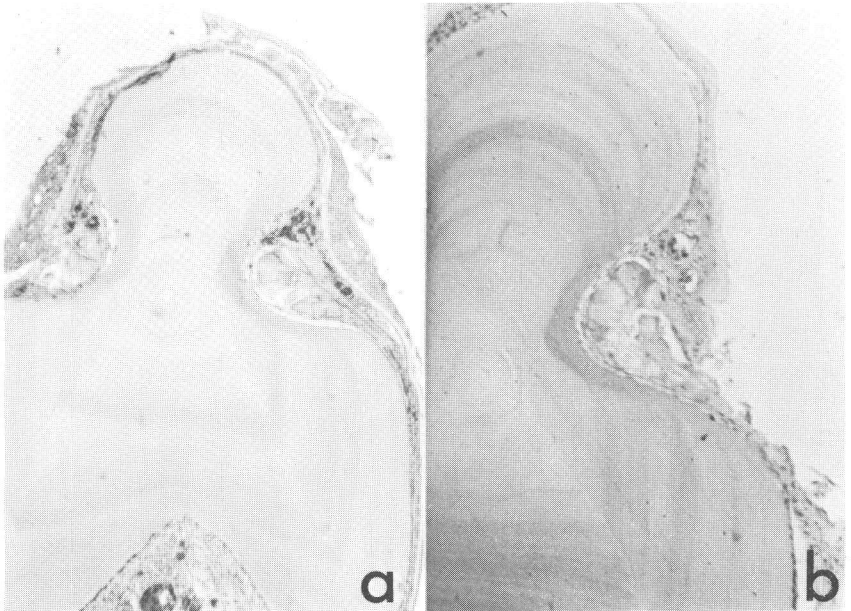


Figure 27. Greenstriped rockfish, *Sebastes elongatus*, dorsal sting V. a) Cross section, distal $\frac{1}{3}$, $\times 60$. b) Glandular triangle, cross section, distal $\frac{1}{3}$, $\times 100$.

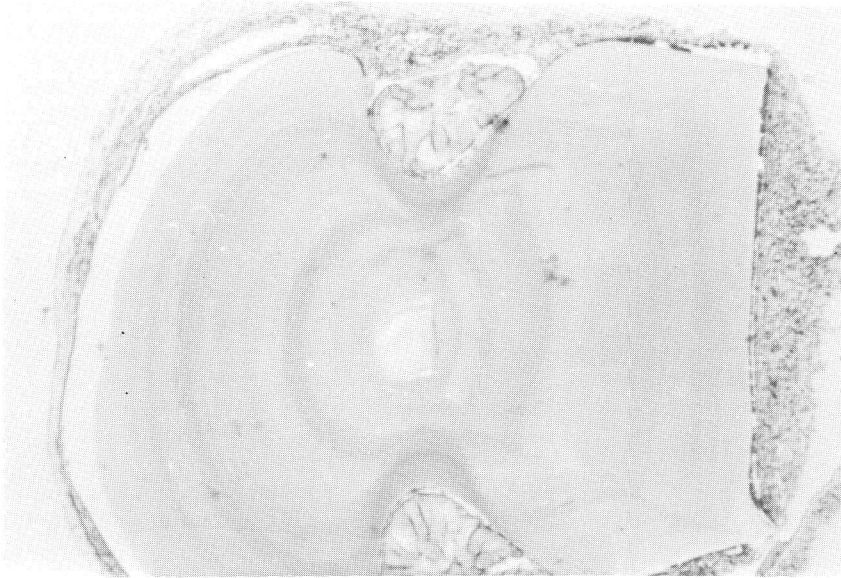


Figure 28. Greenstriped rockfish, *Sebastes elongatus*, anal sting I. Cross section, distal $\frac{1}{3}$, $\times 60$.

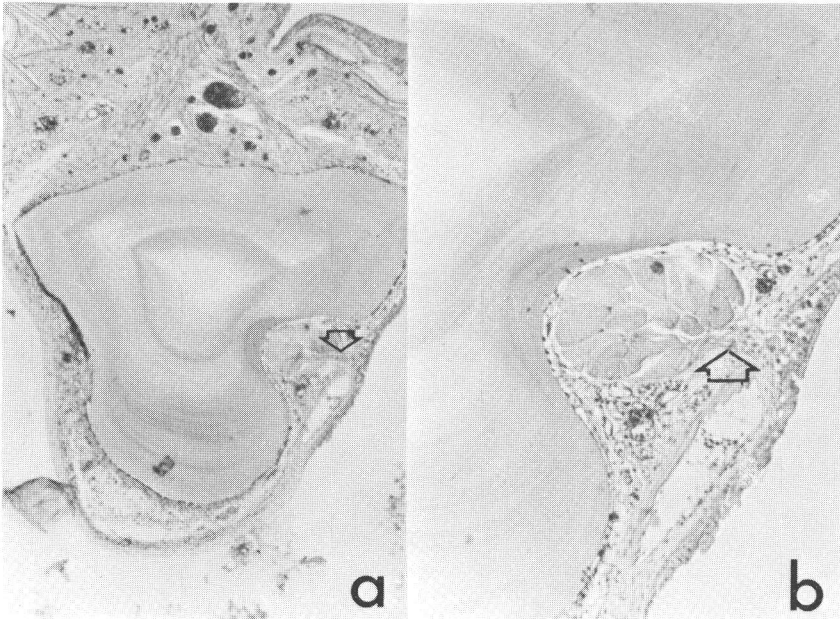


Figure 29. Greenstriped rockfish, *Sebastes elongatus*, left pelvic sting. a) Cross section distal $\frac{1}{3}$, $\times 40$. Arrow indicates a bridge of supporting cells from the epidermis to the venom gland. b) Cross section, distal $\frac{1}{3}$, $\times 100$. Higher power view of bridge of supporting cells (arrow).

Pelvic Sting. The pelvic spine has well developed unilateral venom tissue with no colloidal areas. In the distal $\frac{1}{3}$ of this sting, a short section (approximately 1.5 mm) was noted in which a bridge of supportive or undifferentiated cells link the epidermis with the venom gland (Figures 29a,b). This situation is reminiscent of the findings of Cameron and Endean (1966) in the scorpionfish, *Notesthes robusta*. It seems likely that in *Sebastes*, as well, venom gland cells develop directly from supportive cells which apparently arise from the epidermis and migrate inward toward the venom gland.

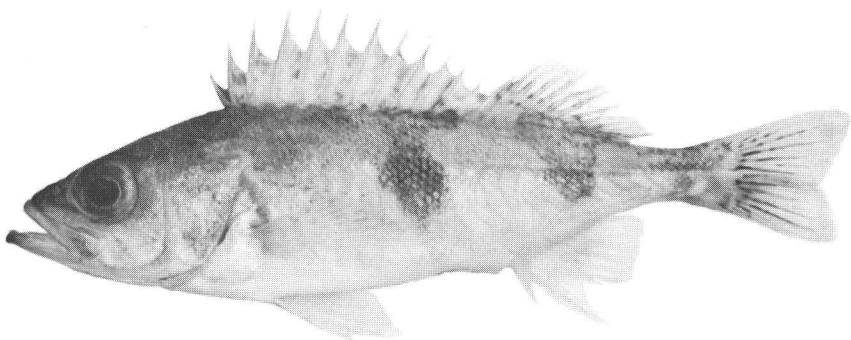


Figure 30. Halfbanded rockfish, *Sebastes semicinctus* (Gilbert).

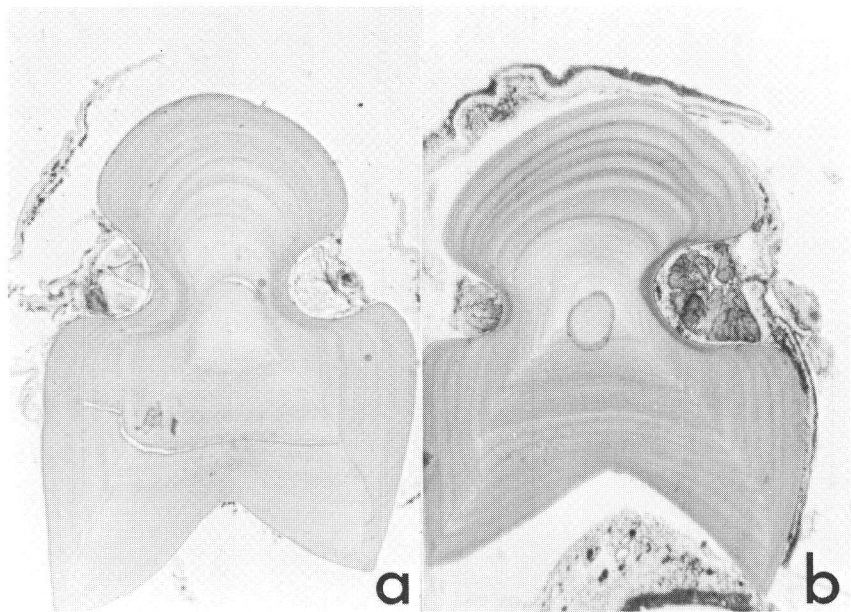


Figure 31. Halfbanded rockfish, *Sebastes semicinctus*. a) Dorsal sting X, cross section, distal $\frac{1}{3}$, $\times 100$. b) Anal sting III, cross section, distal $\frac{1}{3}$, $\times 100$.

Halfbanded rockfish, *Sebastes semicinctus* (Gilbert)

Dorsal Stings. Spines I to VII, IX, and XII contain shallow glandular grooves, but no venom glands are present. Venom glands are unilateral and poorly developed in spines VIII, XI, and XIII. In spine X the glands are bilateral with colloidal areas on one side (Figure 31a).

Anal Stings. Anal spine II has no venom gland. Anal spine I has a unilateral, poorly developed gland and anal spine III has well developed bilateral glands (Figure 31b). No colloidal areas are present.

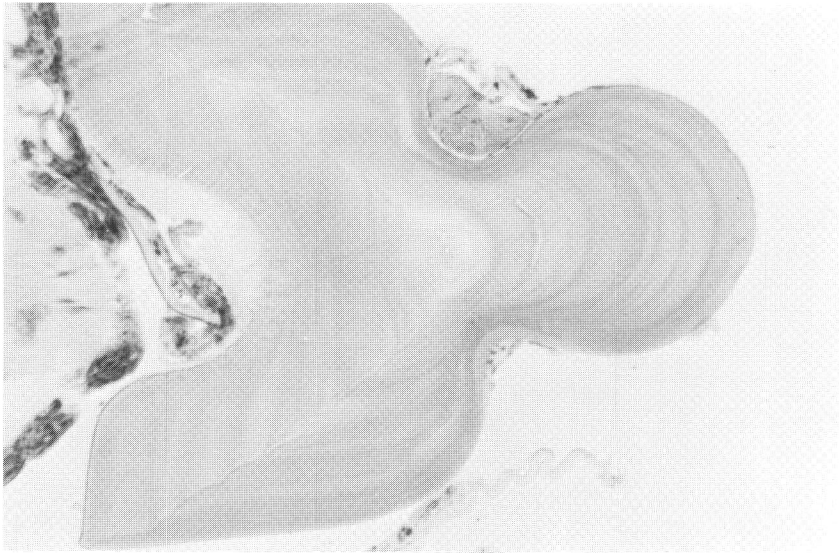


Figure 32. Halfbanded rockfish, *Sebastes semicinctus*, left pelvic sting. Cross section, distal $\frac{1}{4}$, $\times 100$.

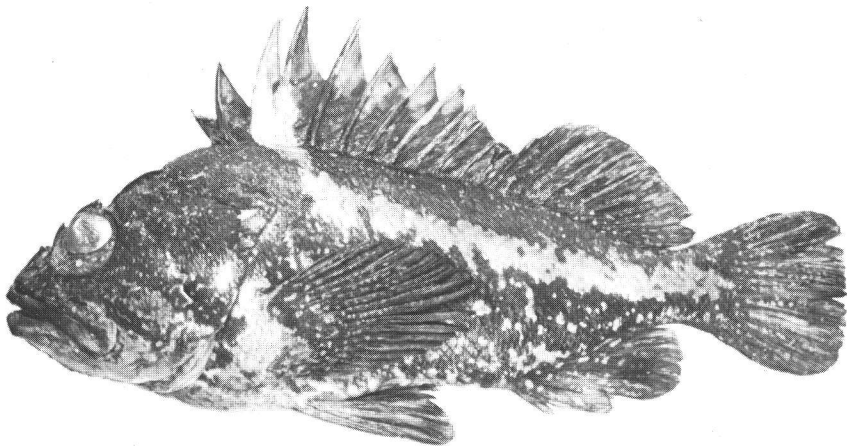


Figure 33. China rockfish, *Sebastes nebulosus* Ayres.

Pelvic Sting. The left pelvic spine has deep glandular grooves with poorly developed unilateral venom glands (Figure 32). No colloidal areas were found.

The halfbanded rockfish is the third smallest species of *Sebastes* of the 49 described by Phillips (1957); the maximum recorded size for this species is only 254 mm. The specimen which forms the basis for our description was the largest of 105 specimens measured. Even though its length was only 120 mm, it was confirmed as an adult (R. J. Lavenberg, Los Angeles County Museum of Natural History, per comm.).

Only dorsal spine IV was initially examined in the following eight species of Sebastes. If this dorsal spine failed to contain venom tissue, additional dorsal spines were examined.

China rockfish, *Sebastes nebulosus* Ayres

Dorsal Sting IV. The length of the spine examined is 31 mm. Only one glandular groove is present in the distal $\frac{1}{3}$ of the spine (Figure 34a). This groove contains a moderately developed venom gland which is present for a distance of 2 mm (from mm 3 to mm 5, measured from the distal tip). The pigmented layer forming the outer limits of the dermis is extremely well developed.

Starry rockfish, *Sebastes constellatus* (Jordan and Gilbert)

Dorsal Sting IV. The length of the spine examined is 70 mm. Two glandular grooves are present (Figure 34b), and contain moderately developed venom glands which are present for a distance of 6 mm (from mm 5 to mm 11). The glandular grooves appear wider than in most of the other species of *Sebastes* we examined.

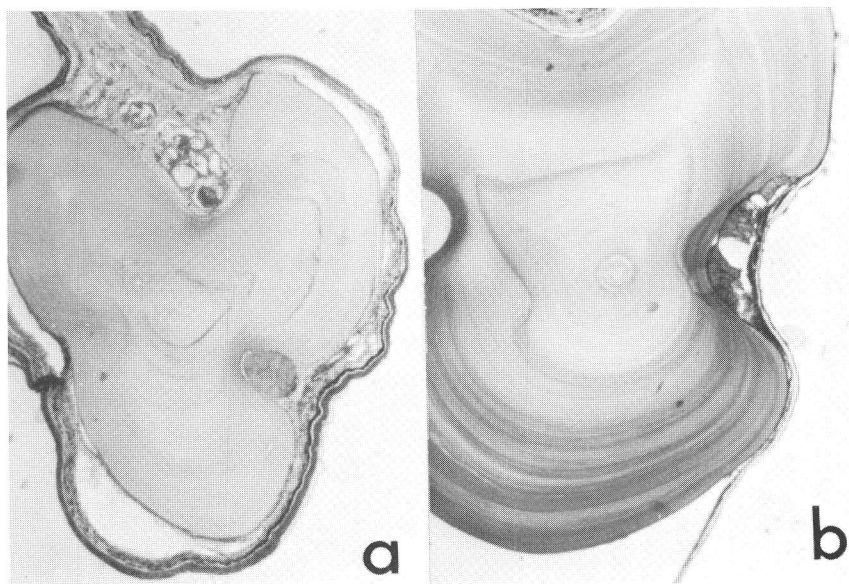


Figure 34. China rockfish, *Sebastes nebulosus*, dorsal sting IV. a) Cross section, distal $\frac{1}{3}$, $\times 35$. b) Starry rockfish, *Sebastes constellatus*, dorsal sting IV. Cross section, distal $\frac{1}{3}$, $\times 35$.

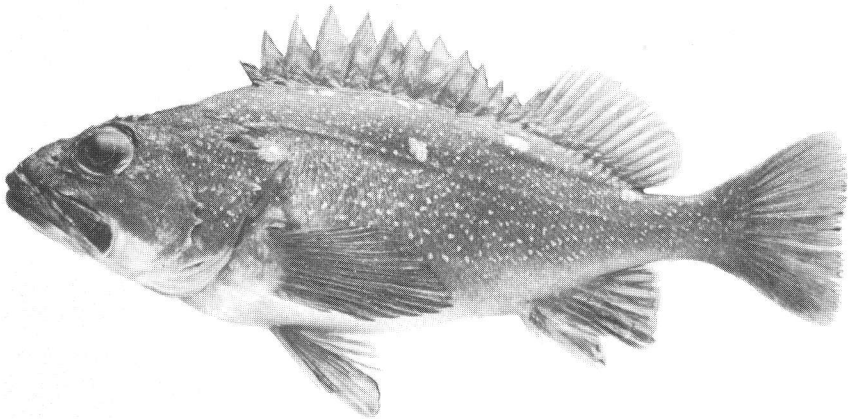


Figure 35. Starry rockfish, *Sebastes constellatus* (Jordan and Gilbert).



Figure 36. Treefish, *Sebastes serriceps* (Jordan and Gilbert).

Treefish, *Sebastes serriceps* (Jordan and Gilbert)

Dorsal Sting IV. The length of the spine examined is 35 mm. Two glandular grooves are present (Figure 37a), containing moderately to well developed venom glands which are present for a distance of 3 mm (from mm 2.5 to mm 5.5). The dermal pigment layer in this fish is well developed.

Chilipepper, *Sebastes goodei* (Eigenmann and Eigenmann)

Dorsal Sting IV. The length of the spine examined is 32 mm. The spine is extremely slim and delicate with two glandular grooves containing well developed venom glands (Figure 37b) which are present for a distance of 3 mm (from mm 1.5 to mm 4.5).

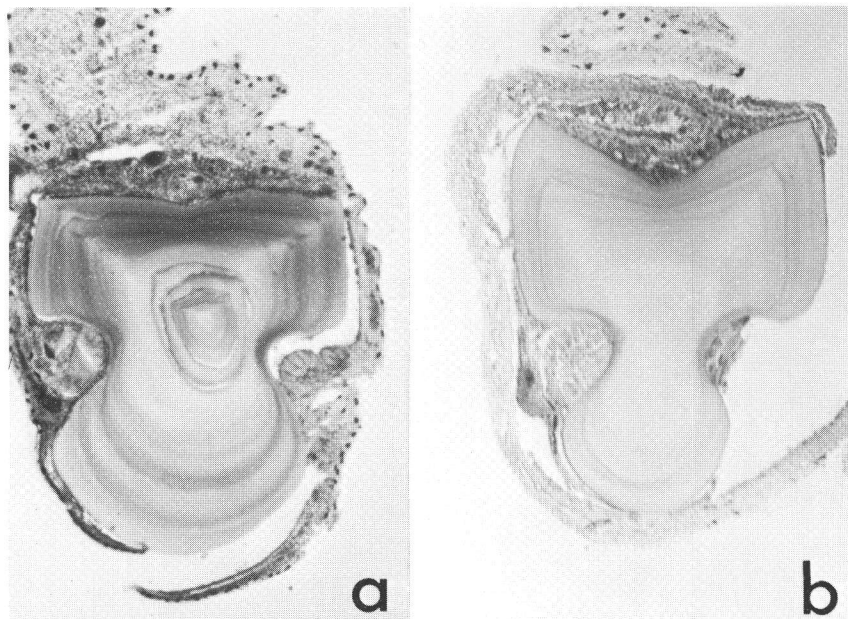


Figure 37. Treefish, *Sebastes serriceps*, dorsal sting IV. a) Cross section, distal $\frac{1}{3}$, $\times 50$. b) Chilipepper, *Sebastes goodei*, dorsal sting IV. Cross section, distal $\frac{1}{3}$, $\times 50$.

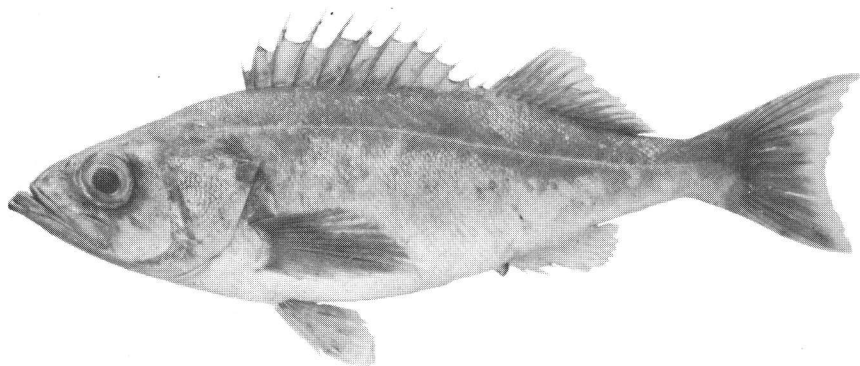


Figure 38. Chilipepper, *Sebastes goodei* (Eigenmann and Eigenmann).

Calico rockfish, *Sebastes dalli* (Eigenmann and Beeson)

Dorsal Sting IV. The length of the spine examined is 29 mm. Two glandular grooves are present. The grooves contain well developed venom glands (Figure 40a) which are present for a distance of 7.5 mm (from mm 2 to mm 9.5). The venom tissue is discontinuous on one side, with gaps of $\frac{1}{2}$ mm or more occurring several times. In these gaps the normal connective tissue of the dermis replaces the venom tissue. Several colloidal areas are seen in the venom gland, and the integumentary sheath epidermis contains many large unicellular mucus glands.

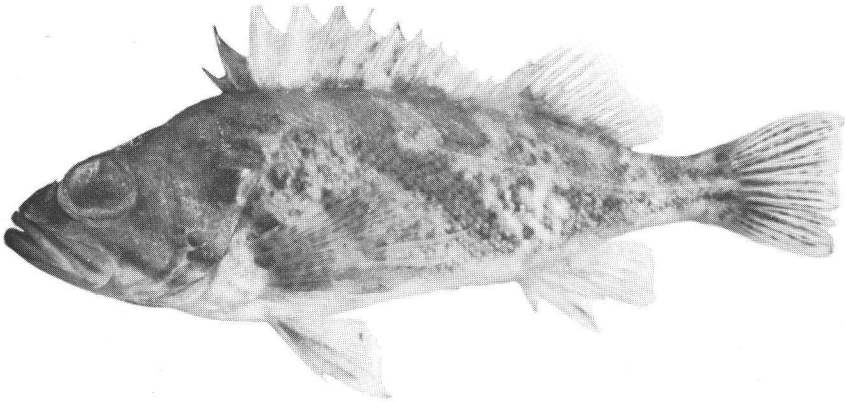


Figure 39. Calico rockfish, *Sebastes dalli* (Eigenmann and Beeson).

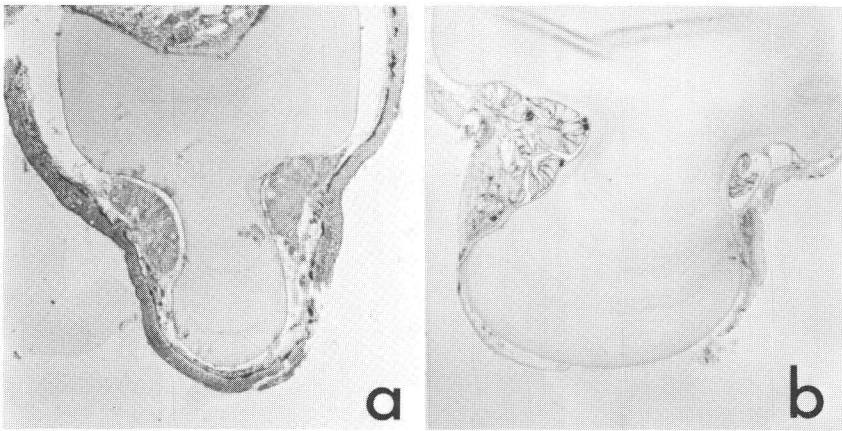


Figure 40. Calico rockfish, *Sebastes dalli*, dorsal sting IV. a) Cross section, distal $\frac{1}{3}$, $\times 50$. b) Vermilion rockfish, *Sebastes miniatus*, dorsal sting IV. Cross section, distal $\frac{1}{3}$, $\times 35$.

Vermilion rockfish, *Sebastes miniatus* (Jordan and Gilbert)

Dorsal Sting IV. The length of the spine examined is 58 mm. The spine contains two glandular grooves, one much deeper and wider than the other (Figure 40b). Venom tissue appears at mm 4 and is present until mm 11.5 for a total distance of 7.5 mm. Venom tissue is present only in a miniscule amount in the shallower groove, while a very large tripartite deposit is found in the deeper groove. Some colloidal areas are present.

Rosethorn rockfish, *Sebastes helvomaculatus* Ayres

Dorsal Sting V. Dorsal spine V is 29 mm long and contains two glandular grooves (Figure 43). Poorly developed venom glands are present bilaterally from mm 3.5 to mm 6, for a total of 2.5 mm. Dorsal spine IV has two deep glandular grooves, but contains a very small amount of venom tissue, only $\frac{1}{2}$ mm.

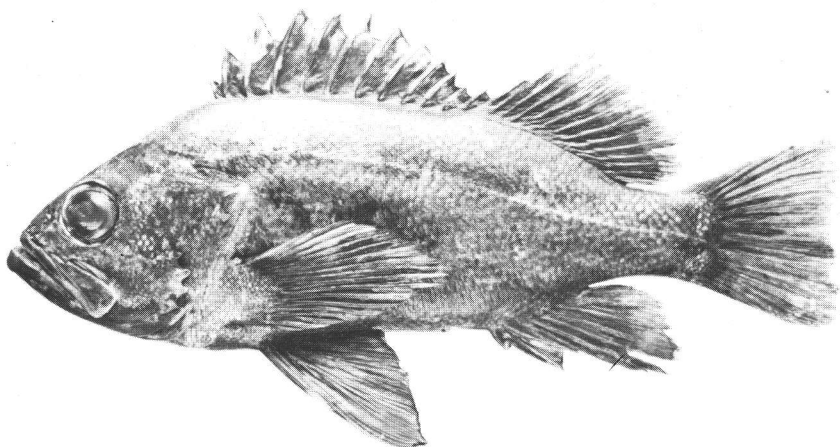


Figure 41. Vermilion rockfish, *Sebastes miniatus* (Jordan and Gilbert).

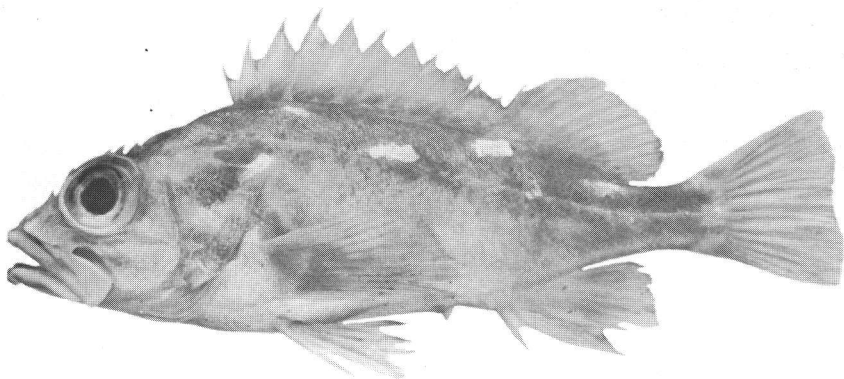


Figure 42. Rosethorn rockfish, *Sebastes helvomaculatus* Ayres.

Cow rockfish, *Sebastes levis* (Eigenmann and Eigenmann)

Dorsal Sting IV. The spine examined is 32 mm long and contains two glandular grooves with well developed venom glands beginning at mm 3.5. By mm 4, a third glandular groove with venom tissue appears (Figure 45a). Venom glands are present in all grooves until mm 8.5, for a total of 5 mm. In several places a bridge of cells joins the epidermis to the venom gland (Figure 45b). This situation was also noted in the greenstriped rockfish, *Sebastes elongatus*.



Figure 43. Rosehorn rockfish, *Sebastes helvomaculatus*, dorsal sting V. Cross section, distal $\frac{1}{3}$, X50.

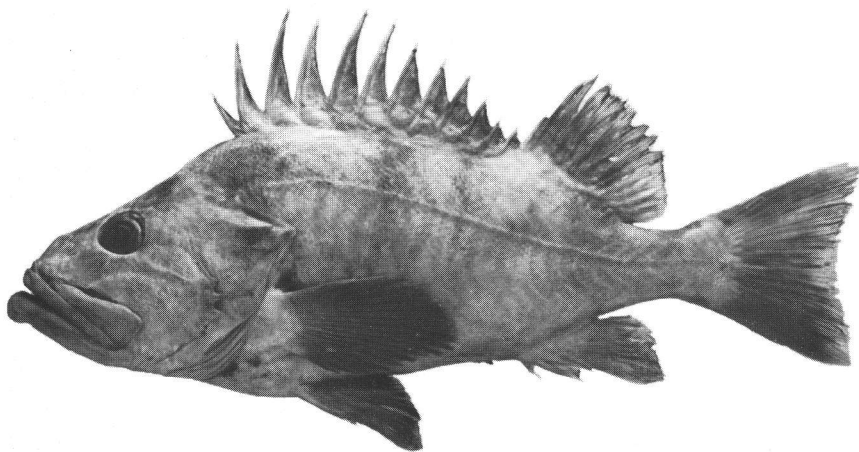


Figure 44. Cow rockfish, *Sebastes levis* (Eigenmann and Eigenmann).

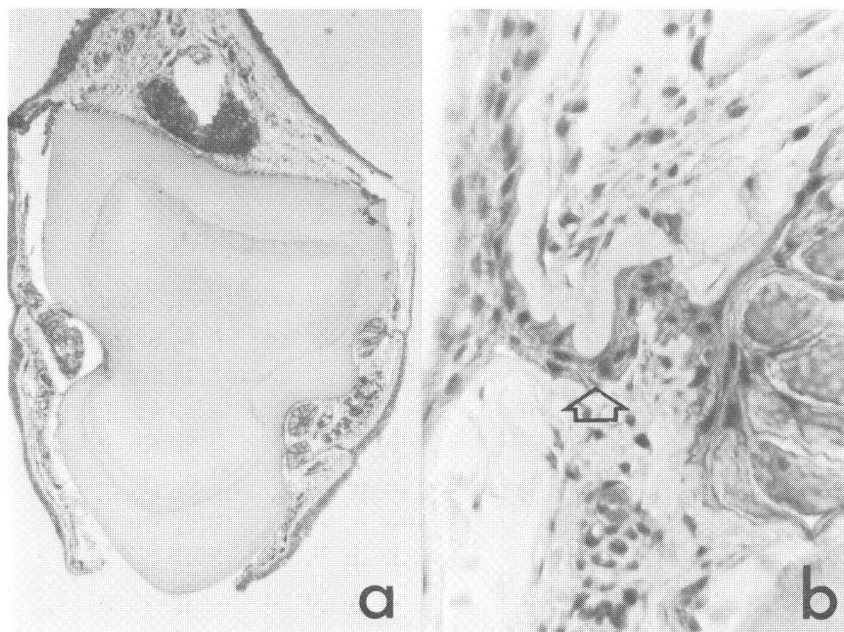


Figure 45. Cow rockfish, *Sebastes levis*, dorsal sting IV. a) Cross section, distal $\frac{1}{3}$, $\times 35$. Note the three glandular grooves containing venom glands. b) Cross section, distal $\frac{1}{3}$, $\times 430$. Arrow indicates bridge of supporting cells from the epidermis to the venom gland.

DISCUSSION

The gross anatomy of the spines of California *Sebastes* compares closely with that of the Japanese stingfish, *Sebastodes inermis*, the only closely related species which has been the subject of careful anatomical analysis (Tange, 1954). Tange noted that sometimes the venom gland is absent in the posterior dorsal spines of the Japanese stingfish as well as in the anal spines. This agrees with our findings. As stated previously, only the brown rockfish, *Sebastes auriculatus*, and the quillback rockfish, *S. maliger*, possess venom glands in all spines (Table I).

Tange described in detail a "mesentery-like" formation of the dermis associated with the venom gland in the Japanese stingfish. In his summarizing paper (1957), Tange again strongly emphasized this feature and reviewed his previous reports of its presence in the butterflyfish, *Pterois lunulata* (Temminck and Schlegel), the surgeonfish, *Xesurus scalprum* (Cuvier and Valenciennes), and the sea catfish, *Plotosus anguillaris* Lacepede. Pawlowsky (1914) reported that this mesentery-like formation, consisting of a layer of dermis reflected to form the venom gland covering, did not appear in *Sebastodes* (*Sebastes*). Most of the species of *Sebastes* we examined showed this formation in at least some spines. There appeared to be no more regularity in its occurrence than in the presence or absence of venom tissue in various spines. We found that the reflected dermal capsule was not present at all levels in even a single spine.

The venom gland cells in California *Sebastes* are very similar in size, general appearance, and staining reaction to those described by Tange (1954, 1957) for the Japanese stingfish, *Sebastodes inermis*. The irregular arrangement of cells within the Japanese stingfish venom gland capsule is very similar to that found in California rockfishes. No species we examined exhibited the regular arrangement of gland cells described for the sculpin, *Scorpaena guttata*, and the zebrafish, *Pterois volitans*, by Halstead *et al.* (1955 a,b) and in the scorpionfish, *Notesthes robusta*, by Cameron and Eudean (1966).

The presence of large and small vacuoles, varying cytoplasmic granulation, and karyolysis and cytolysis of gland cells in California rockfish venom glands, strongly suggesting holocrine venom production agrees closely with the findings of Tange for the Japanese stingfish, *Sebastodes inermis*, and Cameron and Eudean for the scorpionfish, *Notesthes robusta*.

The literature contains practically no information concerning toxicity of the venom of *Sebastes* to humans. Tange (1957) examined 14 species of venomous fishes and divided their spines into two categories. Type 1 spines are described as simple curved needles with a completely smooth surface, a sharply pointed distal end, and (usually) two moderately deep longitudinal grooves containing venom glands. Type 2 spines are complicated highly modified structures usually with sharp recurved teeth and several spine caps. Scorpaenid spines are classified as belonging to Type 1. Tange conducted a series of simple experiments designed to assess the relative toxicity of venoms from four species of fishes representing the families Scorpaenidae, Siganidae, Bagridae, and Plotosidae. A nonvenomous species of *Parasilurus* was used as a control. Mice were used as experimental animals, and venom was introduced in three ways: by thrusting a fresh spine into the thigh musculature of the mouse, by injecting 0.1 ml of an extract of the venomous spines into the thigh musculature, and by injecting 0.5 ml of the extract into the abdominal cavity. Details on the preparation of the extract were not given.

The himeokoze, *Minous adamsii*, was the scorpaenid chosen. When punctured by a fresh spine of this species, mice were lame for 2 hours. Intramuscular injection of venom gland extract produced lameness for 12 hours, and intra-abdominal injection of the extract resulted in death after 36 hours. In contrast, the control spine produced lameness for only 1 or 2 minutes when thrust into the thigh, and no symptoms resulted from injection of extract. Tange (1957) stated that the severity of the experimentally produced symptoms probably agrees with that of the clinical symptoms of natural spine punctures, but did not support this contention with additional data.

It is difficult to equate *Minous* with *Sebastes* in the hope of extrapolating the possible toxicity of the latter genus. The himeokoze, *Minous adamsii*, possesses 10 dorsal spines, 2 pelvics, and no anals; while *Sebastes* usually has 13 dorsal spines, 2 pelvics, and 3 anals. The venom gland length/total spine length ratio was calculated by Tange (1957) to be 1:2.5 for the himeokoze, and 1:3-1:10 for the Japanese stingfish, *Sebastodes inermis*. In the present study, the ratio for the brown rockfish, *Sebastes auriculatus* was found to be 1:5 (Table 2). Tange reported average dimensions of $470 \times 230\mu$ for the venom gland cells of

himeokoze, the largest discovered in any fish examined by him. In contrast, he found the average cell size for the Japanese stingfish to be $35 \times 23\mu$. Our study indicates the brown rockfish has an average venom gland cell size of $38 \times 22\mu$.

Illustrations of cross sections of the dorsal spine of the himeokoze, *Minous adamsii*, in Tange (1953) show stings closely resembling those of *Scorpaena* and *Pterois*. The glandular grooves are very deep and contain large venom glands composed of enormous gland cells. Several of these cells contain vacuoles filled with coarse granules.

Information regarding symptoms following puncture by the spines of California rockfishes was gathered by personal communication. Russell (University of Southern California, School of Medicine, per. comm.) reported having treated at least 50 cases of such injury. Bocaccio, *Sebastes paucispinis* Ayres; blue rockfish, *S. mystinus* (Jordan and Gilbert); and olive rockfish, *S. serranoides* (Eigenmann and Eigenmann), were positively identified as three of the fishes involved. Complaints bringing the patient to the hospital were usually those of pain, swelling, and fever. In all cases the spine wounds were infected, and all patients were treated successfully with antibiotics. In several cases the patients reported local pain and swelling immediately following the injury, but these disappeared before the subsequent infection occurred.

A number of sportfishermen, regular passengers on the "rock cod" partyboats leaving from Newport, have reported receiving stings from the spines of rockfishes. Usually they were unable to remember the name of the offending fish, but bocaccio and chilipepper, *S. goodei*, were definitely identified. Symptoms reported varied only in their severity: pain, usually of rapid onset, with throbbing and burning; some mild axillary pain from stings on the hands, reported by a few; swelling and redness, usually of short duration; and mild nausea in some. Those who also had been stung at some time by sculpin, *Scorpaena guttata*, reported symptoms as being much more severe and of longer duration than those from *Sebastes* stings. Russell (1965) provided a description of "sculpin poisoning" that was based on 100 case histories. All those reporting being stuck by spines agreed that rockfish stings were considerably more painful than those received from kelp bass, *Paralabrax clathratus*, or other nonvenomous fishes with spines of equal size and sharpness. A 14 year old boy, stung on the hand by dorsal spines of the chilipepper, experienced severe deep pain accompanied by nausea and chills for a period of several hours.

The senior author, while working as a deck hand on San Diego sportfishing boats during the summers of 1946-48, was wounded at one time or another by the spines of practically every species of fish taken on the boat. On several occasions, wounds from the stings of bocaccio and vermilion rockfish, *S. miniatus*, among others, produced deep pain, throbbing, swelling, and chills. When contrasted with the very severe pain accompanying stings of sculpin, it must be admitted that rockfish wounds were mild in comparison. Wounds from spines of nonvenomous fishes produced minor pain, usually proportional to the spine's diameter and the depth of its penetration. All puncture wounds from fish spines became infected very readily if not cared for promptly.

When the anatomy of the venom apparatus of the scorpionfish, *Notesthes robusta*, butterflyfish, *Pterois lunulata*, zebrafish, *P. volitans*,

sculpin, *Scorpaena guttata*, and the stonefish, *Synanceja horrida*, are compared with that of rockfish, *Sebastes spp.*, it is immediately evident that rockfishes have by far the most weakly developed mechanism for producing envenomation. Not only do rockfish have smaller venom glands, but venom tissue is often lacking in one or more spines (Table I), a condition not reported from the other four species. Upon comparing data available on symptoms resulting from stings of these other venomous scorpaenids, it appears there is a direct relationship between amount of venom tissue present in the spines and severity of symptoms produced by wounds from these spines. On this basis, while the 14 species of *Sebastes* we examined are definitely venomous fishes, they must be considered less venomous than other scorpaenids described by other authors. A sting from a rockfish, while often painful, probably should not be considered particularly dangerous unless the victim exhibits unusual sensitivity to fish venom or develops infection from secondary bacterial invaders.

SUMMARY

1. The literature dealing with the venom organs of scorpaenid fishes, especially the genus *Sebastes*, is reviewed.

2. This is the first published description of the venom apparatus of any American *Sebastes*.

3. Fourteen species of *Sebastes* were examined in the study. Of these, the starry rockfish, *S. constellatus*; calico rockfish, *S. dalli*; chilipepper, *S. goodei*; rosethorn rockfish, *S. helvomaculatus*; cow rockfish, *S. levis*; vermilion rockfish, *S. miniatus*; china rockfish, *S. nebulosus*; and the treefish, *S. serriceps*, had only one dorsal spine examined initially for the presence of venom tissue. The six remaining species, the brown rockfish, *S. auriculatus*; greenstriped rockfish, *S. elongatus*; pink rockfish, *S. eos*; quillback rockfish, *S. maliger*; bocaccio, *S. paucispinis*; and halfbanded rockfish, *S. semicinctus*, had dorsal spines, 3 anal spines, and the left pelvic spine examined for the presence of venom tissue.

4. The gross anatomy of the dorsal, anal, pelvic, interneural, and interhemal spines; the musculature of these spines; and the pelvic girdle is described for the rockfish, *Sebastes auriculatus*.

5. The microscopic anatomy of the dorsal, anal, and pelvic spines; their associated venom glands; and integumentary sheath is described for the brown rockfish, *Sebastes auriculatus*.

6. The microscopic anatomy of the dorsal, anal, and pelvic spines and their associated venom glands in greenstriped rockfish, *Sebastes elongatus*; pink rockfish, *S. eos*; quillback rockfish, *S. maliger*; bocaccio, *S. paucispinis*; and halfbanded rockfish, *S. semicinctus*, are compared to that described for the brown rockfish, *S. auriculatus*.

7. The microscopic anatomy of one dorsal sting from the starry rockfish, *Sebastes constellatus*; calico rockfish, *S. dalli*; chilipepper, *S. goodei*; rosethorn rockfish, *S. helvomaculatus*; cow rockfish, *S. levis*; vermilion rockfish, *S. miniatus*; china rockfish, *S. nebulosus*; and treefish, *S. serriceps*, is described.

8. Symptoms resulting from human envenomation by several species of California *Sebastes* are described and compared to those resulting from the stings of species of *Notesthes*, *Pterois*, *Scorpaena*, and *Synanceja*.

GLOSSARY

- ANTEROLATERAL-GLANDULAR GROOVES**—The two anterior grooves on either side of the anteromedian ridge. These grooves contain the glandular tissue.
- ANTEROMEDIAN RIDGE**—The ridge separating the anterolateral grooves.
- ENVENOMATION**—To sting or impregnate an organism with a toxin by means of a venom apparatus. Also see Stinging.
- GLANDULAR TRIANGLE**—Term used to designate a cross section of the antero-lateral-glandular groove. This term was originally used for a cross section of the ventrolateral-glandular grooves of the sting-ray's sting, but it is recommended that the term be expanded to include cross sections of the glandular grooves of other fishes regardless of the anatomical position of the groove.
- POISON**—Any substance which when ingested, injected, absorbed, or applied to the body in relatively small quantities, by its chemical action may cause damage to structure or disturbance of function.
- POSTEROLATERAL RIDGES**—The ridges, located one on either side, which comprise the posterior borders of the anterolateral-glandular grooves.
- SPINE**—The bony portion of the sting exclusive of the integumentary sheath, venom gland, and other soft tissues.
- STING**—The osseous spine, integumentary sheath, and accompanying venom glands. The integumentary sheath generally includes the venom glands which are associated with it. This particular definition is in reference to the stings of fishes only. Generally speaking, the term "sting" refers to the complete venom apparatus of the organism.
- STINGING**—The act of introducing venom into the flesh of a victim by means of a venom apparatus. Also seen *Envenomation*.
- VENOM**—The poison secreted by a venom apparatus of an animal. Venoms are usually a large molecular protein or are in association with a protein which may serve as a carrier, but it is becoming increasingly obvious that there may be many exceptions to this generality.
- VENOMOUS ANIMAL**—An animal that is equipped with a traumagenic device, i.e., a spine, tooth, nematocyst, etc., and a poison or venom gland, and associated accessory organs capable of introducing the venom into the flesh of the victim and thereby producing an envenomation.
- VENOM APPARATUS**—The traumagenic device, venom gland, and accessory organs directly concerned with the production and transmission of a venom.

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