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THE LATERAL-LINE SYSTEM OF THE CENTRARCHID
FISH, ELASSOMA ZONATUM (JORDAN)

By

BRANLEY ALLEN BRANSON

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Oklahoma Agricultural and Mechanical College

Stillwater, Oklahoma

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THE LATERAL-LINE SYSTEM OF THE CENTRARCHID
FISH, ELASSOMA ZONATUM (JORDAN)

Thesis Approved:

Geo. A. Moore

Thesis Adviser

Bryan P. Glass

Roy W. Jones

Robert Maudsley

Dean of the Graduate School

PREFACE

Most of the early anatomical work on the lateral lines of fishes consisted of simply describing the macroscopic course of the canals. Although some very excellent descriptions of the microscopical anatomy of this system in various fishes occur in the literature, many later workers have continued to follow the examples of their predecessors. Some of the cytological descriptions are misleading and vague. The present paper describes in some detail the micro-and macroscopical anatomy of the lateral-line system in Elassoma zonatum, suggests functions for some of the structures observed, and attempts to correlate the morphology of this sensory system with the habitat of the fish.

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INTRODUCTION

Since Stenonis (1664) first observed the lateral line in a skate, many morphological studies upon the course of this system in a variety of fishes and amphibians have been conducted. Although Moore (1956) studied this cutaneous sensory system in some sunfishes in the genus Lepomis and Dineen and Stokely (1956) briefly described the osteological relationships of the lateral line in Archoplites, apparently no other studies have been made in the family Centrarchidae (freshwater sunfishes). No works have come to the writer's attention concerning the possibility that the morphology of this system may be modified by an interaction of the environment with the habitat in which those fishes are found. The present work includes both the description of the lateral-line system in Elassoma zonatum, an inhabitant of paludal situations, and an attempt to correlate the observed morphology of this system with the preferred habitat of the fish.

REVIEW OF THE LITERATURE

The cutaneous sensory organs, known under such names as slime canals (Leydig, 1850; Müller, 1852), sense canals (Bodenstein, 1882), latero-sensory canals (Allis, 1904), acoustico-lateral system (Pivèteau, 1935), seismosensory canals (Tretyakov, 1938), and simply the lateral line, have been of interest to naturalists since the 17th century. According to Ewart (1895), who gave a very excellent synopsis of the literature up to that time, the first observation concerning the lateral line of fishes was made by Stenonis in 1664. Working with cartilaginous fishes, Stenonis described, in the skin of a skate, openings for the discharge of mucous, apparently not realizing the possibility of a sensory function. The view that the pores of the lateral line were openings for the secretion of mucous was accepted generally until the year 1850. At that time, Franz Leydig discovered, at regular intervals along the lateral-line canals of the head and body in young teleost fishes, discoidal bodies which he termed "Nervenhügel" (nerve hillocks). This discovery prompted later workers (Dercum, 1879; DeSède, 1884) to further study of this system. Dercum observed that two distinct types of cells existed in the sensory organ, the long cylindrical supporting cell and the

small globose or pyriform sensory cell. The organ itself he termed the maculae lateralis from its resemblance to the maculae acusticae of the ear. DeSède was more interested in obtaining insight into the function of the lateral line by experimentation on blinded fishes, or those with the lateral-line nerve excised. He concluded from his experiments that the lateral lines of fishes give them continual information on the state of the medium in which they live. A few years later Ewart (1895) expressed the opinion that only the future would elicit the function of these sensory structures. Parker's experiments (1904 a, b; 1905) were, at best, of negative value and mostly have been repudiated by the findings of later workers. He thought that the lateral-line organs might be of service to the fish in orientation but that they were of no more significance in equilibration than the general skin, and that both were distinctly inferior to the eye and ear in this function. He also contended that pressure was not a stimulus to the lateral-line organ. Freeman (1928), on the contrary, suggested that the organ is sensitive to relative pressures. This means that when a fish turns one side or the other toward the surface of the water there is a heavier column of water impinging on the organs of the lateral line on the opposite side; nerves are stimulated, and the fish makes compensating movements. A second consideration, deemed non-stimulating by Parker, was concerned with chemical changes in the water. Smith

(1930; 1933) concluded just the opposite, that the lateral-line organs furnish a device for testing physical and/or chemical changes in an aquatic environment. Since the time of Parker, many functions have been assigned to the lateral line. Among these, a mechanism for reinforcing vigorous swimming movements (Hoagland, 1933 a), photokinetic reactions in lampreys (Young, 1935), vibratory reception, detection of food and members of the same species, and maintenance of position in the water (Wunder, 1936) are the most outstanding.

During the decade in which Dercum made his observations, Beard (1884) advanced the theory that the ear was only a highly modified organ of the lateral line, basing his hypothesis upon observations of similarity in structure, innervation, and ontogeny. This hypothesis has been strengthened further by later workers. In his treatise on the embryological development of the sea bass, Wilson (1889) noted that the ear, branchial sense organ, and lateral line arise from a common anlage just behind the eye. Beckwith (1902; 1907), on the other hand, found that the cutaneous sense organs and the ear develop from separate placodes in Amia calva. The striking resemblance of the lateral-line organs of fishes to the crista ampullaris of the mammalian ear was noted by Dawson (1934), Denny (1936), and others. This interesting theory led Gregory (1920) and Kyle (1926) to the conclusion that the olfactory organ possibly may have

developed from organs similar to those of the lateral line on the heads of fishes.

The external lateral line of fishes, i.e., that portion enclosed by canals, has been used with varying degrees of success by several systematists for taxonomic purposes (Garman, 1888; Dean, 1895, 1895; Hubbs and Cannon, 1935; Lin, 1938; Gosline, 1949). Lekander (1949) and Linder (1956), however, have cast some doubt on the usefulness of this structure as a taxonomic character.

The literature concerning the general course of this system in numerous species of fishes and amphibians is voluminous. The literature reveals a paucity of information concerning the histological anatomy of the lateral-line organs. Most texts of comparative anatomy present generalized diagrams of these organs (Weidersheim, 1907; Kingsley, 1926; Neal and Rand, 1936), but few authors have offered more than cursory descriptions of them. Leydig (1850) considered the neuromasts and cutaneous organs of taste to be histologically alike but was corrected by Schultze in 1870. The latter worker differentiated the two sensory structures by comparing the lengths of the functional cells. The sensory cells of the neuromasts were found to penetrate only to the distal ends of the supporting cells; those of the "end-buds" extended all the way to the basal cells. Wilson (1889) described the branchial sense organ of the sea bass, Serranus atrarius, and stated that

histologically the lateral-line organs were essentially the same.

The presence of lateral-line canals on the sides of fishes is of such universal occurrence that its absence is especially noteworthy (Kyle, 1926). Those species in which it is lacking, the Clupeidae and Engraulidae (Berg, 1940), the genus Elassoma (Jordan, 1877; 1884), Cobitis biwae and Misgurnus decemicirrosus (Lekander, 1949), usually are placed at the top of their respective phylogenies. In Cobitis taenia and Lefua echigonia canals are entirely lacking, having been replaced by superficial neuromasts (Lekander, 1949).

If one follows the suppositions of Whitman (1884; 1889), phylogenetic standings are reversed. He not only implied that the lateral-line organs of fishes are identical with the segmental sense organs of annelids, but also that all the organs of special sense found in higher vertebrates had their inception in these annelid organs. Neal and Rand indicated that Eisig was of the same opinion. It is true that the segmental sense organs of leeches present histological pictures that are similar to lateral-line organs, but their innervation is very different. The lateral-line organs of fishes are innervated by cranial nerves which extend through many metameres; the segmental sense organs of capitellid annelids are innervated by segmental nerves (Neal and Rand, 1936: 633).

Garman (1888), Dean (1895), and others have arranged recent fishes according to the morphology of their lateral lines. At first sight these schemes of presentation seem to bear out the premises of Whitman and Eisig. Beginning with the cyclostomata and progressing upward to the osseous fishes, the following facts are noted: cyclostomes have neuromasts sunken into pits and arranged in lines on the head; sharks and rays, in generalized forms, have groove-like canals; dipnoans have canals similar to sharks but with some tubed canals and many superficial neuromasts on the head and body; chimaeroids possess a shark-like lateral line but lack superficial neuromasts; teleosts typically possess canals and scattered neuromasts.

These facts suggest an orthogenetic relationship and a gradual increase in complexity. Retzius, according to Dean (1895), denied this. According to Retzius, the Teleostomi, ganoids, and Acipenseridae have evolved along one branch and the dipnoans, chimaerans, and sharks along another. According to this theory, the forms of the lateral line in sharks and rays, on the one hand, and in teleosts on the other, are not primitive but the actual zenith reached in their respective phylogenies.

The findings of most paleontologists (Allis, 1934; Jarvik, 1944; Westoll, 1944; Stensio, 1947) are in agreement that the latero-sensory canals of archaic groups of bony fishes were of a much more complex nature than those found

in present-day forms. There is also a rather close rapport that these canals, or tubules, may phylogenetically degenerate and be replaced by lines of superficial neuromasts. The more recent works of Satô (1954; 1955 a, b), Moore and Burris (1956), and Moore (1950; 1956) have added considerably to the knowledge of both the canal organs and the so-called "pit organs," or superficial neuromasts. Moore's paper (1956) on the lateral-line system in some members of the centrarchid genus Lepomis and Dinean and Stokely's (1956) brief discussion of Archoplites are the only works concerning this sensory system in species allied to the genus Elassoma that have come to the attention of this writer.

MATERIALS AND METHODS

Collection of Fishes

Specimens of Elassoma zonatum were collected near the same locality as those first reported for the state of Oklahoma (Moore and Poole, 1948). These specimens conformed to the original description of Jordan (1877), and the same variations of eye size and pigmentation observed by Moore and Poole were noted.

About 50 specimens of this minute sunfish were collected on August 24, 1956, at Forked Lake, three miles southeast of Eagletown, McCurtain County, Oklahoma. Since the breeding season of this species begins about the middle of March, and sexually mature individuals apparently disappear after spawning (Barney and Anson, 1920), only young adults were taken in a four-foot, fine-mesh nylon seine. All were obtained by vigorously kicking over the leaves and other debris near the shore, then quickly pulling the seine through the roiled water. No specimens were found in the deeper waters.

Forked Lake was found to be similar to the habitat described for this species by Barney and Anson (1920). The surface of the water was covered with a heavy layer of organic scum presumedly derived from the deep layer of

bottom debris consisting of dead leaves, bits of wood, decaying aquatic plants, and other organic materials. This mat overlaid a bottom of deep mud. Methane, or other gas of organic decomposition, continuously bubbled up through the water. The shore was vegetated heavily with two species of Typha, several rushes and sedges, mosses, algae, and Cephalanthus and Taxodium, as well as other plants. The water was tepid and obviously low in oxygen. There was no evident current.

Other materials available for study included specimens of Elassoma from Florida, Louisiana, Missouri, North Carolina, and Texas.

Preparation of Specimens for Observation

Fixation.--During the fixation of animal tissues, there is always the possibility of forming artifacts. Therefore, the fishes used in this study were killed and fixed in three different solutions. The first of these, Helly's fluid, was suggested by Dawson (1934) for rapid fixation, a highly desirable quality in any fixative. Another desirable quality of this fixative is that Mallory's phosphotungstic acid hematoxylin stains well following its use. This stain renders the micro-structure of the lateral-line organs easily demonstrable, especially the so-called "hair cells." Denny (1937) utilized this same technique.

The second fixing agent utilized was one of Allen's modifications of Bouin's solution, P. F. A.₃ (McClung, et al., 1950). This solution preserves faithfully the cytological detail of the tissue or organ being studied. Its most desirable asset is that valuable material may be left in it for long periods of time without danger of over-fixation.

The last solution used was ten per cent formalin, a fixative widely used by ichthyologists. In addition, 11 specimens of E. zonatum were fixed in a solution of ten per cent formalin containing a small amount of thionine, a blue stain. This was suggested by Dr. George Moore to perform the double function of fixation and staining in the field.

Skins and whole mounts.---As indicated above, some specimens were killed in ten per cent formalin containing thionine. The skins of three of these were removed and mounted for study of the general morphology of the lateral line. Entire fishes also were observed through a dissecting microscope. Both stained and unstained fish were used, the former tinted lightly with methylene blue (Denny, 1936).

Decalcification.---In early preparations the process was carried out in a one per cent HNO₃ solution in 70 per cent ethanol. However, this solution proved to be highly unsatisfactory, and later specimens were treated with two per cent HCL in 70 per cent ethanol.

Dehydration.--This was accomplished by means of alcohols in increasing concentrations.

Embedding and sectioning.--The heads of several specimens were embedded in paraffin and serially sectioned at a thickness of ten microns. After the positions of organs contained in the canals were ascertained, and superficial neuromasts located, several specimens were dissected to obtain organs for sectioning in celloidin. For this purpose, Walls' (1932) hot celloidin method was followed. Transverse and parasagittal sections were cut at 50 microns. In addition, two heads of E. zonatum were double embedded (celloidin and paraffin) and serially sectioned at 20 microns.

Staining, clearing, and mounting.--Specimens fixed in Helly's fluid were stained with Mallory's phosphotungstic acid hematoxylin, as suggested by Dawson (1934). Other specimens, similarly fixed, were stained with one of the following stains: Mallory's triple connective tissue stain, Harris's hematoxylin and eosine, and borax carmine. A few specimens were prepared using Sihler's method (Williams, 1943) in an attempt to better demonstrate the innervation of the lateral-line organs, but only mediocre results were obtained. Other techniques used already have been discussed. All sections were cleared in toluene, except those in celloidin, which were cleared in beechwood creosote. All

preparations were mounted in a commercial synthetic resin, Permout.

Counts and Measurements

All specimens employed in this study were deposited in the Museum of Zoology of the Oklahoma State University.

The enumeration of superficial neuromasts and canal organs, as well as the general position of these organs on the body of the fish, was accomplished by a "mapping procedure," using a Bausch and Lomb dissecting microscope. Areas which best demonstrated the organs in surface view were selected to be sectioned. Lines of well-developed superficial neuromasts were found to occur in the infraorbital and lateralis positions. These areas were sectioned to demonstrate the micro-anatomy of these organs. To demonstrate canal organs, selected and serial sections were made of the operculomandibular, supraorbital, and cephalic-lateralis canals.

Micro-measurements were taken by means of a filar micrometer attached to a compound microscope.

Preparation of Illustrations

Illustrations were prepared, as indicated in the legends, either by free-hand methods or with the aid of a camera lucida and a compound microscope.

OBSERVATIONS

Gross Structure of the Canal System

The terminology adopted for lateral-line canals is that of Hubbs and Cannon (1935). In E. zonatum, the lateralis canal (L) is completely lacking on the trunk and is represented in the cephalic portion (Figure 10) by a very short tube. Its dorso-lateral position, just behind the orbit, indicates that it is probably contained in the intertemporal and lateral extrascapular bones. The canal opens in a single pore at its posterior extremity, just dorsal to the opercular flap.

The supratemporal canal (ST) lies just behind the level of the dorsal tip of the preopercle and extends dorsally as a branch of the lateralis (Figure 10). It is much reduced in length and is completely contained in the parietal bone. The canal is directed slightly cephalad and terminates in a rather flared pore.

The infraorbital canal (IF) is very incomplete. It is represented by a short tube in front of the eye and an even shorter one behind the eye. The tube behind the eye diverges from the junction of the supraorbital and lateralis canals (Figure 10) and extends ventrally for a short distance. It is contained partially in the frontal bone and

partially in the third infraorbital bone. The posterior portion ends in a rather large pore above the middle of the orbit. The anterior portion of this rudimentary canal, slightly smaller in diameter than the other canals, is contained wholly in the preorbital bone and possesses two openings, one at either end, directed slightly caudad. One of these pores is located at the dorsal extremity of the canal midway between the anterior nostril (Figure 10) and the orbit, and is just above the middle of the eye. The second pore is located just behind and slightly above the tip of the maxilla. The pore formula for this canal, then, is $1 + 2$. The first figure in this, and in any of the following canal formulae, indicates the most posterior pore.

The supraorbital canal (SO), just anterior to the anastomosis with the lateralis and infraorbital canals, gives off another short branch, the remnants of the supra-orbital cross-commissure (SC) [Figure 9]. After leaving a rather wide, triangular base, devoid of pores, the lumen of the cross-commissure canal narrows considerably and ends in a small pore, directed slightly posteriad. There is no indication of a coronal pore, but in the specimens studied, some variation in the length of the cross-commissure was noted. In most instances the canal lacked at least one-third the width of the cranium of being complete. In others, with seemingly no correlation between the variation and geographic distribution, the canal lacked as little as

one-eighth the width of the cranium of being complete. The cross-commissure canal is housed in the frontal bone.

From the point of divergence of the cross-commissure, the supraorbital canal continues in an anterior direction, following the curvature of the dorsal orbit, until it is terminated abruptly by a lateral bending just in front of the anterior nostril (Figure 9) where it ends in a medium-sized pore (ANP). A short interorbital branch (INT), terminated by a pore of about the same size as the previous one, diverges from the supraorbital canal just behind the posterior nostril at about the middle of the eye. The anterior portion of the supraorbital canal is of considerably smaller diameter than the posterior; the latter is contained in the frontal bone and the former in the nasal.

The lateralis canal gives off a short ventral branch, just over the dorsal tip of the preopercle (Figure 10), which shortly terminates in a small, slightly caudad-directed pore immediately above the upper end of the operculomandibular canal. The operculomandibular canal (OPM) opens near the dorsal tip of the preopercle in a caudally-directed, slit-like pore. This rather large canal then continues downward, over about the center of the preopercle, to a point where this bone bends anteriorly. Here it sends a short branch to the ventral margin of the bone where it ends in a rather large pore. The operculomandibular canal continues its forward course, following the

preopercular bone, until at the anterior extremity of the last-named structure, it gives off a second short branch to the ventral margin of the preopercle. This branch also ends in a pore, which is slightly smaller than the one behind it. The canal diameter is reduced, and the tube continues onto the angular-sphenial bone, where it usually ends a short distance behind the tip of the maxilla. However, in a few specimens the operculomandibular canal appears just to touch the dentary. There was in most specimens a very small, sub-terminal pore directed ventrally, but in a few cases this opening was lacking. The pore formula for this canal is either $1 + 4$ or $1 + 3 + 0$.

Variations in the canals.--Except for those variations alluded to above, the canals are quite uniform in their lengths and distribution.

Superficial Neuromasts.

Gross morphology.--The functional unit of the lateral-line system in fishes and amphibians is the neuromast. Some of these are enclosed in canals; others are superficial. Those of the latter category may be dispersed at random over the surface of the skin, but usually they are located in definite bands or lines. It is accepted generally that these lines represent degenerate canal loci, the canals having been replaced during phylogeny by the rows of

superficial neuromasts. This will be discussed further below.

In the following discussion, the innervation of the various organs is assumed by inference from the very excellent figures and text of Lekander (1949) and, to a lesser degree, Holmgren and Pehrson (1949).

A typical superficial neuromast of E. zonatum (Figure 4), in a surface view (invisible to the unaided eye), presents a rounded papilliform body, sunken to a greater or lesser degree in a crypt-like or moat-like pit (hence, the term "pit organ"). The average diameter of this so-called pit is about 55 microns (29-70) and that of the enclosed neuromast 46 microns (29-70). These latter measurements are somewhat misleading, since a wrinkling of the superficial epithelium around the crypt, probably peculiar to the formation of that structure, and a cupping of the terminal ends of some of the supporting cells (Figure 5) cause the neuromast to appear larger than it actually is.

In the present study it was not possible, either in sections or whole mounts, to differentiate between the sunken type of neuromast (Herrick, 1901; Satô, 1955 a) and the naked type of Herrick. However, it was noted in sections that several organs appeared to be sunken deeper into the epithelium than others. This can be explained by noting the angle that the microtome blade struck these structures during sectioning. If the cutting edge of the

knife was angled slightly away from the organ, it would tend to cut into the epithelium first, which would make the neuromast appear to be situated deeper than is actually the case. The latter type of organs graded imperceptibly into those of a more superficial nature.

The terminology of Satô (1955 c) was used in describing the well-developed lines of superficial neuromasts. In neanic (young adults) specimens of 22 to 23 mm. in standard length, these rows of sense organs number about 12. The first of these lines, which is the most extensive, is the lateralis (Figure 6). It occupies a dorso-lateral position, which corresponds to the one occupied by the lateralis canal of other fishes. This line courses caudad from the posterior terminis of the cephalic lateralis canal to the base of the caudal fin. In the specimens observed, the line begins just above the caudal pore of the lateralis canal in either a very large neuromast (69-70 microns) or as two nearly contiguous neuromasts of the usual size (45-46 microns). From this beginning, the line follows a zig-zag path caudad over the mid-portion of the epaxial musculature. At about the caudal margin of the characteristic post-opercular spot (double in Oklahoma specimens, much reduced or lacking in Missouri specimens), the series of neuromasts drops slightly ventrad, then continues posteriorly. Near the beginning of the caudal peduncle, the line seems to branch so that three rows of organs are formed: a

diagonal-dorsal branch, a medial straight portion, and a diagonal-ventral branch. The entire line is made up of 38 to 44 (average, 41) neuromasts, and it is doubtless innervated by the lateralis branch of the vagus.

The supratemporal commissural line (Figures 2, 6) is very short, consisting of only four neuromasts per side. It begins just above the dorsal pore of the rudimentary supratemporal cross-commissure canal, then extends mediad in an almost straight line. These organs also receive branches from the lateralis nerve.

There are two relatively short rows of neuromasts on the opercle: an upper and a lower one. The uppermost series consists of five or six papillae and is slightly recurved (Figure 6). This line starts just below the first ventral branch of the cephalic lateralis canal and extends onto the opercle. The lower line (Figure 6), if it may be called such, lies entirely on the opercle, just caudad to the first ventral branch of the operculomandibular canal. If this is a neuromast line (it could more aptly be called a cluster), then it is quite strongly procurved and is made up of five or six organs. The truncus hyomandibularis presumably innervates both of these short lines.

As previously stated, the infraorbital canal is incomplete. It has been replaced by a continuous line of superficial neuromasts (Figure 6) which extends from the ventral margin of the posterior remnants of the infraorbital

canal to an anterior point just below the rostral remains of the canal. From this juncture, it continues upward, overlying the degenerate canal in part to a point just above the middle of the eye. There are 27 to 29 organs in the line, 21 or 22 of which are in a linear series. Approximately eight anterior organs are arranged in two nearly parallel rows, one overlying the anterior portion of the infraorbital canal and the other lying between the canal and the eye. All of these organs are innervated by the nervus buccalis of nerve VII.

A very short line of three neuromasts (Figure 6), which Satô (1955 c) only mentioned, but which are of fairly common occurrence in teleost fishes (Lekander, 1949), lies just posteroventral to the mandible. The organs of this oral line probably are innervated by the external mandibularis.

The so-called medial extrascapular line (Figures 6, 2), which consists of eight or nine superficial neuromasts, actually begins on the frontal bone just dorsal to and behind the eye. Three or four organs are situated in a more or less straight line, directed caudad, followed by two or three medially-directed, similarly-arranged organs, which continue onto the epithelium over the parietal bone. The line then turns caudad onto the epithelial covering of the medial extrascapular bone, where it ends in two sensory papillae. This row of organs is innervated by the ophthalmicus superficialis branch of nerve VII.

The medial supraorbital line (Figure 2) is represented by only one or two neuromasts on each side of the cranial dorsum. These are placed just opposite the medial side of the supraorbital canal, near the posterior edge of the mesethmoid bone. The supraorbital line (Figure 2) is also very short, consisting of only three or four organs, all of which overlie a portion of the supraorbital canal just in front of the eye. The organs of this line, the one described above and the one discussed below, are all innervated by the ophthalmicus superficialis.

A single neuromast, ventro-lateral to the posterior nostril (Figure 2), and a second organ, similarly placed in relation to the anterior nostril, comprise the nasal line.

The horizontal line (Figure 6) lies slightly dorsal to the operculomandibular canal, beginning near the level of the first ventral branch of this canal, then following its curvature over the preopercle. It consists of four organs which receive branches of the truncus hyomandibularis, as do most of the other cheek lines.

A nearly continuous line of pit organs between the canal and the ventral edge of the preopercle runs from a point just ventral to the first branch of the operculomandibular canal to a like position on the opposite side of the head. From its initiation, it courses anteriorly onto the dentary, then is directed ventrally, from which point it follows the curvature of the jaw to the ventral midline,

where it joins the line of organs from the opposite side. In the specimens observed, this line contained 54 individual sense organs, equally disposed on each side of the head. The papillae of this preopercular line (Figures 6,3) are innervated by the truncus hyomandibularis.

Microscopical morphology.--In longitudinal section the superficial neuromasts (Figure 5) of E. zonatum appear as pear-shaped structures, contained mostly in the epithelial covering of the body. These organs tend to increase in size anteriorly. Ones near the head average 34 microns (31-39) in diameter at the base and 15 microns (11-24) at the apex and have a length of 37 microns (27-45). The smaller, posterior organs average 26 microns (21-27) at the base, 14 microns (10-24) at the apex, and 31 microns (25-38) in length.

The cellular constituents of the neuromasts, as described by Schultze (1870), Moore (1956), and others, are of two distinct types: the sensory cell and the supporting cell. Although, according to Daget (1949), Sand (1937-38) presented physiological evidence of the existence of three different kinds of sensory cells, this never has been demonstrated histologically or cytologically. The sensory cells are held at the center of a sort of retinaculum formed by the much longer supporting cells (Figure 5). These supporting cells are of two types, one distinctly rhopaloid in shape and situated mostly in the peripheral

area of the neuromast, with a few cells extending up between the sensory cells in the center of the organ and a much shorter type located below the sensory cells. Selected supporting cells from the periphery of the organ (Figure 5) average 29 microns in length (23-32) and two microns in width. The slightly ovoid nucleus is located just above the base of the cell, and since its diameter is greater than the rest of the cell, it causes the typical basal swelling which gives the supporting cell its rhopaloid appearance. The nucleus of these cells stains rather darkly with the various hematoxylin but otherwise does not exhibit any striking properties. Most of the superficial neuromasts exhibit a peculiar cupping at the distal ends of the long supporting cells which forms a chamber around the distal end of the sensory portion of the organ (Figure 5). This phenomenon is not known to have been described in any other fish. The retinaculate arrangement of the supporting cells causes the adjacent epithelium to be thrown into wrinkles and, in some instances (Figure 5), into folds over the surface of the organ. If the organs are measured only in surface views, this would cause considerable error, as is indicated by the measurements cited in the text above. The basal supporting cells (Figure 5), as indicated above, are arranged beneath the sensory cells in the center of the neuromast. Selected cells of this type average 10 microns in length and three microns in width (3-4), being somewhat wider than the

peripheral cells of the same function. The spherical or ovoid nuclei of these cells are also slightly larger (2-3 microns), take more stain than those of the longer cells, and are basal in position.

The centrally-located sensory cells usually are described as pear-shaped, but this is not very descriptive of them. They are better described as having the shape of a tenpin (Figure 5), an average length of 16 microns (15-17), and a maximum width of four microns (4-5). The large nucleus (3-4 microns) is nearly spherical and is easily demonstrated by most hematoxylin because its periphery stains very darkly and the nucleoplasm much more lightly. Extending from the distal ends of these cells into the cytoplasm for a short distance are several minute rod-shaped structures which stain with about the same intensity as the nuclear membrane (Figure 5). The typical teleostomian sensory hairs (Weidersheim, 1907; Denny, 1937; Dijkgraaf, 1952; Moore, 1956; and many others) are very small (about 2 microns in length), dark-staining, setiform bodies which extend from the surface of each sensory cell into the cup formed by the supporting cells (Figure 5). Basally, some other protoplasmic extensions from these sensory cells (demonstrable only with difficulty) extend downward between the supporting cells (Figure 5). These three structures, the sensory hairs, the rods extending from the apical cellular membrane downward into the cell, and the basal

extensions, would seem to form a mechanism by which stimuli are transferred from the end-organs (superficial neuromasts) to the various branches of the innervating acustico-lateralis system which enter the neuromasts at about their basal center, as do the blood vessels. The subnuclear granules present in canal sensory cells were not seen in the superficial neuromasts. In some preparations, the cytoplasm of sensory cells seems to be quite reticulated.

Microscopical Morphology of the Canal System

General canal interior.--The vestigial nature of the canal system of this species already has been mentioned. The canals are confined to the cephalic portion of the body and are contained mostly in bony grooves. The supraorbital canal is such a groove (Figure 7). In transverse section the bony groove is a roughly lyre-shaped structure formed in the frontal bone, which opens mesially and, except for nerve foramina, is closed laterally. The groove is lined with a layer of undifferentiated connective tissue that is about seven microns thick in most areas but which is much thickened (up to about 46 microns) under those parts of the canals which bear organs. At these loci (Figure 7), this tissue forms a support for the canal at its lateral wall, and the superficial epithelium forms a similar investment on the mesial side. The epithelium also covers the open side of the groove throughout its length. The other bony grooves

differ from that of the supraorbital structure mainly in shape; the operculomandibular canal is situated in a U-shaped groove, and the supraorbital cross-commissure follows a shallow furrow.

The canals themselves are relatively thin-walled (about 8 microns), elliptical tube-like structures of a hyaline appearance (Figures 7, 8). In straight portions of these canals, the diameter is about 52 microns, but it is greater at points where branches are given off (Figures 9, 10). Immediately over the organs, the canal lumen is much reduced in diameter by a definite stricture of the canal itself (Figures 9, 10) and a velum-like structure (Figure 8) composed of columnar epithelial lining cells. The occurrence of this latter structure was first described by Moore (1956) in sunfishes. In the early 1800's, according to Knox (1825), Treviranus recorded the presence of short septa which divided the lateral line of sharks and rays into compartments. Moreover, Brockelbank (1925), working with Ameiurus nebulosus, described a differentiation of the canal lining in the region of the sensory organ which was much thickened and completely surrounded the organ. It is evident from Figures 7 and 8 that this is practically the case in E. zonatum. The canal lumen is occluded further by the organ itself until the diameter is reduced to about 25 microns, a decrease of nearly 50 per cent. In addition, a cupula-like structure, which stains light blue with

Mallory's triple connective tissue stain, occupies the apex of many organs (Figure 8). The cupula covers a somewhat circular area about 58 microns in diameter and nine microns in depth, roughly corresponding to the sensory surface of the organ. This ensconcement, when present, further reduces the lumen of the canal, so that the pressure over a canal neuromast must be of considerably greater intensity than at any other point in the canal. As intimated above, the cupula was not seen on all organs. This probably can be attributed to disruption of the very delicate structure during fixation and handling. According to Denny (1937), the cupula was first observed by Emery in 1860. It was noted in various fishes by Dercum (1879) and Ewart and Mitchell (1895) and discussed in detail by Denny (1936; 1937). It apparently has not been described in sunfishes.

Morphology of the canal organs.---The canal neuromasts are structurally identical to those of the superficial type but are much larger. The canal neuromasts are of two nonintergrading sizes. The larger organs are located in the cephalic lateralis, supraorbital, and operculomandibular canals and are about 123 microns long and 24 to 32 microns deep. The smaller neuromasts, found in the supratemporal canals and the short preorbital portion of the infraorbital, are about 69 microns in length and 18 to 24 microns in depth. The entire canal system contains only 20 organs (occasionally only 18). In most instances, these

cushion-shaped structures are inserted upon the parietal wall of the canal, but in the cross-commissure and anterior infraorbital they are attached to the floor. The loci of these organs (Figures 9, 10) are as follows: one just caudad to the cross-commissural branch of the lateralis; one beneath the dorsal opening of the cross-commissure; one midway between the juncture of the ventral branch of the lateralis and the infraorbital branch; one on either side of the short, mesially-directed branch of the supraorbital; one midway between the posterior and anterior nasal pores of the supraorbital canal; one just under the superior pore of the anterior portion of the infraorbital; and one between each branch of the operculomandibular canal. An occasional specimen lacked either one or the other, or both, of the organs located in the cross-commissure and infraorbital canals.

Innervation of these organs is achieved by rami from the acustico-lateralis system. The nerve fibers enter a foramen through the bony groove (Figures 7, 8) described above, join the organ basally, and penetrate between the basal supporting cells to reach the sensory cells. The organs of the lateralis and cross-commissure canals are ramified by the lateralis branch of nerve X; those of the supraorbital canal by the ophthalmicus superficialis of nerve VII; the infraorbital organs by the nervus buccalis of nerve VII; and the truncus hyomandibularis of nerve VII sends branches to the operculomandibular canal.

The cells of the canal organs are nearly identical with those of the superficial neuromasts (Figures 7, 8) but differ in minor details. The sensory cells occupy a central portion of the neuromast, which is the reverse of the situation in Lepomis cyanellus but similar to that in L. humilis (Moore, 1956). As in the superficial neuromasts, the supporting cells are of two sizes: the very long, attenuated-rhopaloid, peripheral type and the smaller, basal rectilinear type (Figures 7, 8). Selected cells of the first type average 26 microns in length (23-32) and three microns (2-3) in width. The ovoid, dark-staining nuclei average two microns in diameter and are sub-basal in position. An interesting phenomenon, apparently of only recent notice (Moore, 1956), is the presence of protoplasmic plates between the long peripheral supporting cells (Figure 1). Possibly these protoplasmic plates extend the length of the organ since Moore found them in a basal position, and they are herein described in a apical position. They are about two microns wide and, obviously, the same length as the supporting cells. Gråberg (1899) has imputed the function of irrigation of tastebuds to similar structures in the tongue of man and possibly the function of increasing the intragemmal spaces. Moore (1956) thought that their main function in fish neuromasts was probably one of mechanical support and strength. It is quite possible that they also may lend increased resilience to resist deforming

pressures. A few of the attenuated supporting cells appear to be scattered throughout the neuromast, extending from the base to the apex between the sensory cells. The dimensions of the basal supporting cells are quite similar to those of the superficial neuromasts. They average 10 microns in length (10-11), four microns in width (3-4), and possess spherical, dark-staining basal nuclei, three microns (2-3) in diameter.

The sensory cells (Figures 7, 8) are, as usual, tenpin-shaped. They average 13 microns (10-16) in length and four microns (4-5) in width. They bear a minute, apical, sensory hair, two to three microns in length, which extends into the cupula described above. The large nuclei (3-4 microns in diameter), which are located slightly below the center of the cell, are of striking appearance. They nearly completely fill the space delimited by the two lateral membranes of the cell. The dark-staining nuclear membrane is granular in appearance, probably because the chromatin material is clumped in that region. There are from three to five grain-like or rod-like bodies, possibly nucleoli, dispersed in the nucleoplasm. Located in a position near the proximal end of the cell are several very dark-staining structures which appear to be much smaller than those described in Lepomis humilis (Moore, 1956). Such bodies are apparently of nearly universal occurrence in sensory cells and nerve cell bodies (Barbey-Gampert, 1943) and are possibly mitochondria. The

same filamentous fibers noted at the proximal ends of the superficial neuromast sensory cells also are present here. The more central sensory cells are larger and longer (5 microns in width, 15-16 microns in length) than the more peripheral cells (4 microns wide, 13-14 microns long). Under optimal conditions of lighting and microscopy, the cytoplasm of the sensory cells appears to be filled with very fine, longitudinally-arranged fibrils. This observation possibly is based upon simple cytoplasmic reticulations as described by Denny (1937) but could be the result of something on the order of the pericellular (or inter-cellular) network observed by Barbey-Gampert (1943) and others.

DISCUSSION

The genus Elassoma is distinctly different from all other centrarchids in its complete lack of the lateralis canal. Furthermore, it was found, in the present study, that the cephalic lateral-line system of E. zonatum is quite incomplete and that the cutaneous sensory organs are few in number. This is a very interesting adjunct to the palaeontological evidence that extinct fishes possessed many sensory canals and possibly many thousands of superficial neuromasts (Jarvik, 1944; Westoll, 1944). This last evidence is strengthened further by such studies as that of Allis (1889) on the primitive Amia calva. He found over 3,700 lateral-line pores occupying the head of the relict species and stated that the number apparently increases indefinitely with the age of the fish. If one possessed a complete developmental phylogenetic record of fishes, he might find, in any given phylogeny, a steadily decreasing number, as well as complexity, of lateral-line canals. It is well known that as lateral-line canals become degenerate in phylogeny, they are replaced by rows and lines of superficial neuromasts (Allis, 1934; Westoll, 1944; Stensio, 1947). Since the loss or gain of parts usually is considered to constitute specialization, any fish possessing

the most abridged canal system, in its own taxon, would by definition, as far as this one character is concerned, be the most advanced. In light of this knowledge, Elassoma would have to be considered as the most specialized nominal member of the Centrarchidae. One might even consider the lack of canal organs in the preorbital-infraorbital and temporal canals, in some specimens, as indicative evidence of continuing degeneration in this species (Elassoma zonatum).

However, all of the evidence does not support such a view. Lekander (1949) found that the canal system begins to develop quite early in some fishes but only reaches its final configuration in sexually mature specimens. The same was true in the case of the superficial neuromasts, and new lines of these organs continued to appear until comparatively late in the development. The situation in Amia calva was alluded to above. Moreover, in a recent study by Eaton (1956), it was suggested that E. zonatum is a nectenic sunfish, or one that reaches sexual maturity while other features are still juvenile. This statement had its basis in a study of the olfactory organ, which was found to be rudimentary in form as compared to the condition in other sunfishes, and a few other characters, such as the presence of cycloid scales instead of ctenoid, and the degenerate condition of the lateralis canal. Taking only these considerations into mind, it could be possible that one

might misinterpret the extent and morphology of the lateral line in any fish species. Nonetheless, it is not probable that the extent of the lateral line in E. zonatum, as described herein, is only an incipient stage in the development of that system. As indicated by Dantan (1906), the lateral line probably approaches its adult form while the fishes are still very young, starting to function even before hatching occurs, in most species. Furthermore, it has been shown (Garman, 1888) that it is in the embryos of fishes that the lateral line takes on its generic and specific characters, even before other characteristics, normally utilized to separate species, become apparent.

The supposition that the reduced lateral line, cycloid scales, and rudimentary organs of olfaction are manifestations of neoteny does not seem to be in concordance with the other evidence. Ctenoid scales (usually present in centrarchids) according to Creaser (1926), in all fishes possessing this type of scale, are at first cycloid, only developing ctenii at a later time. In Lepomis gibbosus and L. cyanellus the ctenoid scales may not develop until late in life, sometimes never. In addition, several fishes lack the lateralis canal, as many clupeids (Kyle, 1926), and some cobitids are completely devoid of canals (Lekander, 1949). These two rudimentary characters are probably not the result of neoteny in the species under consideration but represent the end product of phylogeny. If the olfactory

organs, as indicated by Kyle (1926), have developed from cephalic lateral-line organs in fishes, then it follows as a necessary corollary that any degenerative tendency in the cutaneous sense organs also might affect the organs of smell. Unless it can be shown that the genus Elassoma has affinities with another taxon (Jordan thought, in his original description of the genus in 1877, that its affinities possibly were with the predominantly South American cichlid family), E. zonatum must be regarded as a sunfish possessing a highly reduced lateral-line system, being thus specialized to that extent.

A more tenable line of thought is that, over a period of time, an interaction of habitat preference with definite evolutionary tendencies has produced the present configuration of the cutaneous sensory organs in E. zonatum. That is, it may be possible to correlate the structure and configuration of the lateral-line system with the habitat in which the species lives. Fishes inhabiting quiet or sluggish waters, or fishes of lethargic habits, are known to be supplied less abundantly with lateral-line canals than those which are more active swimmers or which frequent flowing water (Garman, 1888; and others). Etheostoma nigrum (family Percidae) has a complete lateral line, and the tubes of the lateralis canal seem to be augmented by one or two superficial neuromasts on each scale pocket. Drawing examples from the same family, three other species of

Etheostoma, E. microperca, E. chlorosomum, and E. proeliare, all have varying degrees of incompleteness of the lateral line. According to Linder (1956), E. nigrum is taken in streams of considerable gradient; the other three species prefer to live in swampy or quiet pools. Ictalurus nebulosus, the brown bullhead catfish, is notoriously a sluggish animal, and its lateral-line canal organs do not seem to be much more sensitive to external stimuli than other portions of the skin (Hoagland, 1933). Trout, on the other hand, which are known to be vigorous swimmers, were shown in the same set of experiments to possess very sensitive lateral-line organs. Moreover, it was shown that a predominant number of the lateral-line organs were situated in the forward part of the catfish's body, facilitating reception during progression through a darkened habitat, as contrasted to a larger number in the caudal portion of the body of the trout which might assist this fish in vigorous swimming movements. At first sight, the lateral line found in Aphredoderus sayanus, the pirate perch (Moore and Burris, 1956), seems to be contradictory to the present line of thought. This fish possesses a very extensive system of canals and superficial neuromasts and inhabits sluggish waters, but the fish itself is a very active animal. Elassoma zonatum is also an inhabitant of very sluggish waters (Jordan, 1877; Barney and Anson, 1920), which may even approach paludality (Moore and Poole, 1948). Its

habits are quite sedentary, in the wild at least, and as was shown in the description of the lateral line, the cutaneous sensory organs are most abundant in the cephalic portion of the body.

The present author does not share the opinion of Linder (1956) that, in the absence of genetic interference, the lateral line is so plastic in any one generation as to respond to environmental pressure by changing the specific extent and conformation of this system. Stone (1937) pointed out that the lateral line would develop normally under any variety of experimental conditions, and Tretiakov (1944) considered these organs to be only very slightly under the influence of the environment, being to a great extent conditioned phylogenetically.

Fishes that occupy sluggish waters, or ones that are themselves indisposed to vigorous habits, have no need for an extensively developed cutaneous sensory system, such as cave animals do not require well-developed eyes. The potential of action in a given nerve, innervating lateral-line organs, is a direct function of the number of cells excited (Daget, 1949) and increases in accordance with the intensity of the stimulation. Lateral-line nerves are in a state of constant activity in response to the repetitive discharges of neuromasts (Hoagland, 1933). The feeble excitants are perceived by the organs of the lateral line, according to Daget (1949), whereas the stronger impulses are

picked up by the ear, principally by the labyrinth. Thus, it can be seen that a fish inhabiting a running stream, or a riffle, would have much greater need for a well-developed cutaneous receptor system than one of quieter waters. The former, constantly surrounded by the noise of running water, as well as continuous stimulation of the neuromasts by this same movement, must have keen perception to be cognizant of extra-normal stimuli, such as obstacles, abnormal position of the body in the water, approach of predators, food organisms, or members of the opposite sex during periods of breeding. The latter, E. zonatum in this instance, living in a serene habitat lacking the constant stimulation of rushing water, would require only a minimum of receptors to accomplish the same end. It would seem that, if these sensory receptors were in direct contact with the medium in which an animal lived, the efficiency of seismosensory reception would be increased greatly. Consequently, through phylogeny, the canals, in some species, gradually have disappeared, leaving the cutaneous sense organs exposed on the skin. Those species with the fewest sensory organs have undergone selection fitting them to live in quiet waters. That is not to say that there has not been convergence and parallelism, or even proterogenesis, in some species, which would, of course, cloud the issue, but that most of the evidence seems to point to the above considerations.

The presence or absence of sensory hairs at the summit of the sense cells in lateral-line organs has been controversial since Beard's (1884) postulation that the ear and lateral line were only very different developments of the same structure. As early as 1825 Knox noted the similarity between the innervation of the ear and the lateral line and considered the latter to be intermediate between the sense organs of touch and hearing. The resemblance of the cutaneous sense organs to the sensory cells of the mammalian and other vertebrate ears has been noted by many authors. But, considering the evidence that the ear and lateral-line organs develop from a common anlage (Wilson, 1889; Stone, 1931; and others), this should not be surprising. In the ear, the sensory cells of the maculae acusticae, recessus utriculi, and sacculus (Lee, 1894) bear at their distal ends sensory hairs which extend into the endolymph. The normal stimulation of any crista acustica (Lee, 1895) is effected when the canal is rotated in any direction and the hairs dragged through the inert endolymph. These same hairs, or ones very similar to them, have been described in lateral-line organs of several fishes and sharks (Ewart and Mitchell, 1895; Hoagland, 1933; Denny, 1937; Moore, 1950; Moore and Burris, 1956; and many others) and, herein, in the pigmy sunfish, Elassoma zonatum. The bulbous sensory device described at the distal ends of the sensory cells of Lepomis humilis by Moore (1956) may be assumed to be a

specialization of these minute sensory bristles. These hairs, when present, doubtless perform the same function as those of the ear. In light of the mass of recorded evidence, the absence of sensory hairs, or some modification of them, in lateral-line organs would seem to be the exception rather than the rule.

The function of the lateral line in Elassoma is probably the same as in other species. It is an organ for the perception of disturbances in the water which Bonnier (1896) preferred to call "seisesthésie" to distinguish it from audition. This structure also may be of assistance in obtaining food (Scharrer, 1932), for testing the physico-chemical composition of the medium (Smith, 1933), or any of the other functions alluded to above. From studies such as Young (1935) made on lamprey ammocoetes, in which he found the lateral line to be sensitive to light, it becomes more and more apparent that there is a great deal that is not understood about the function of this structure. It is not impossible, in the estimation of Daget (1949) that the latter furnishes sensations for the brain of fishes and amphibians of a nature unknown to physiologists and anatomists, who are essentially adapted to live on land.

The lateral line of Elassoma, as described above, is essentially similar to that of other fishes, but it is strikingly different from all other sunfishes in being quite degenerate in length. However degenerate the canals may be,

the superficial neuromasts should not be considered functionally different from the organs in the canals, but only as specialized receptors of the same system which have been modified in response to the combined pressures of environment and evolution. Moreover, inasmuch as the lateral line and ear are members of the same sensory system (acustico-lateralis), it would seem impossible to consider the function of one without the other.

SUMMARY

The lateral-line canal system of Elassoma zonatum has been replaced extensively by rows of superficial neuromasts. These lines of sensory papillae coincide nearly exactly with the positions that would be occupied by canals if these were present. This sensory system, described for the first time herein, is discussed at some length from gross and micro-anatomical aspects. Several structures observed were described for the first time in sunfishes: sensory hairs, cytoplasmic reticulations or networks, and subapical, dark-staining rods in the sensory cells. All of these structures probably are concerned with the conduction of nervous impulses. The presence of other structures, protoplasmic bridges between the supporting cells, extensions from the basal portion of the sensory cells, and subnuclear granules, were for a second time observed in a sunfish.

A correlation between the vestigial nature of this species' lateral-line system and its paludal, or subpaludal, habitat is postulated.

SUGGESTIONS FOR FURTHER STUDY

1. The lateral-line systems of other centrarchids should be investigated fully, and an attempt should be made to establish phylogenetic lines more satisfactorily.
2. Embryological studies of sunfishes with emphasis on the lateral-line system could be expected to cast light on centrarchid phylogeny.
3. Further work also is needed to correlate the extent and morphology of the lateral line with the habitats of fishes. Species should be chosen from extreme ecological conditions, such as subterranean situations or torrential streams, as well as the more common types of habitat.
4. The innervation of these sense organs should be intensively studied with the aim of discovering better selective stains for nervous tissue.

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APPENDIX

PLATE I

Camera lucida and freehand representations
of the lateral line in Elassoma zonatum

Figure 1. Dorsal section of some supporting cells from the supratemporal cross-commissure.

Figure 2. Distribution of dorsal superficial neuromasts.

Figure 3. Distribution of ventral superficial neuromasts.

Figure 4. Surface view of a superficial neuromast from the infraorbital neuromast line.

Figure 5. Longitudinal section of a superficial neuromast from the horizontal neuromast line.

Figure 6. Distribution of lateral superficial neuromasts.

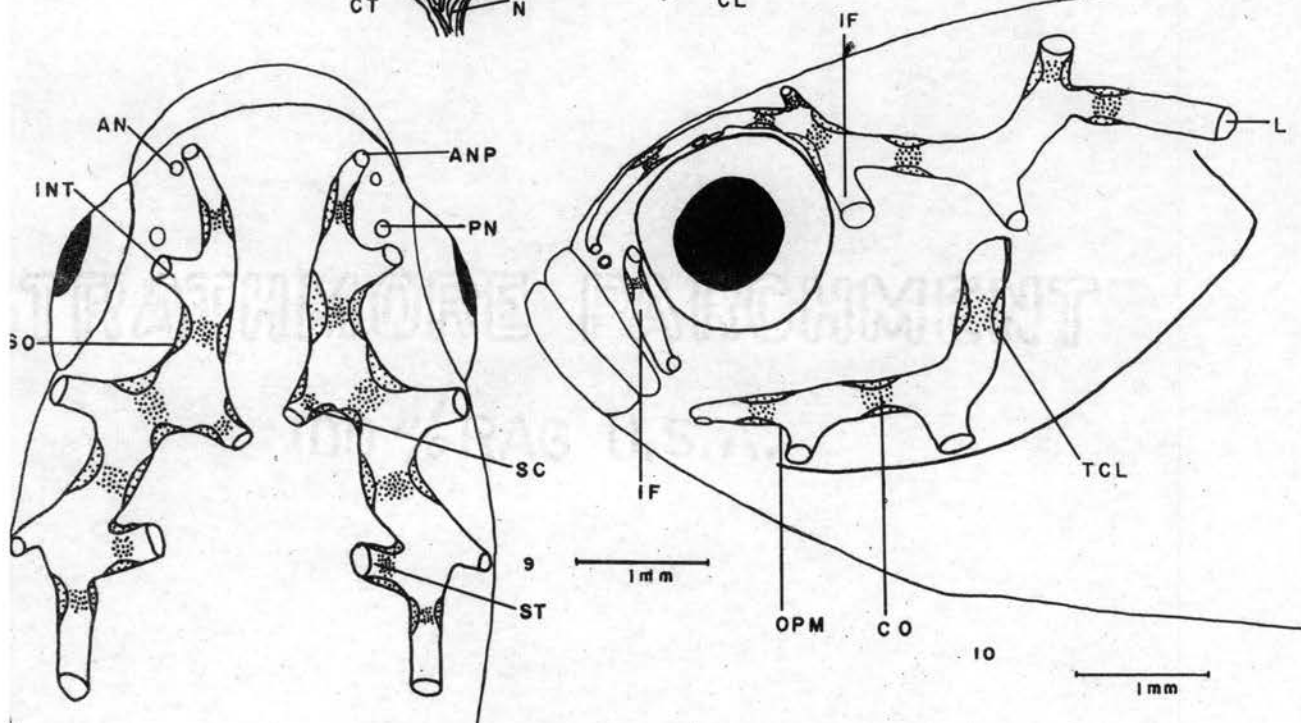
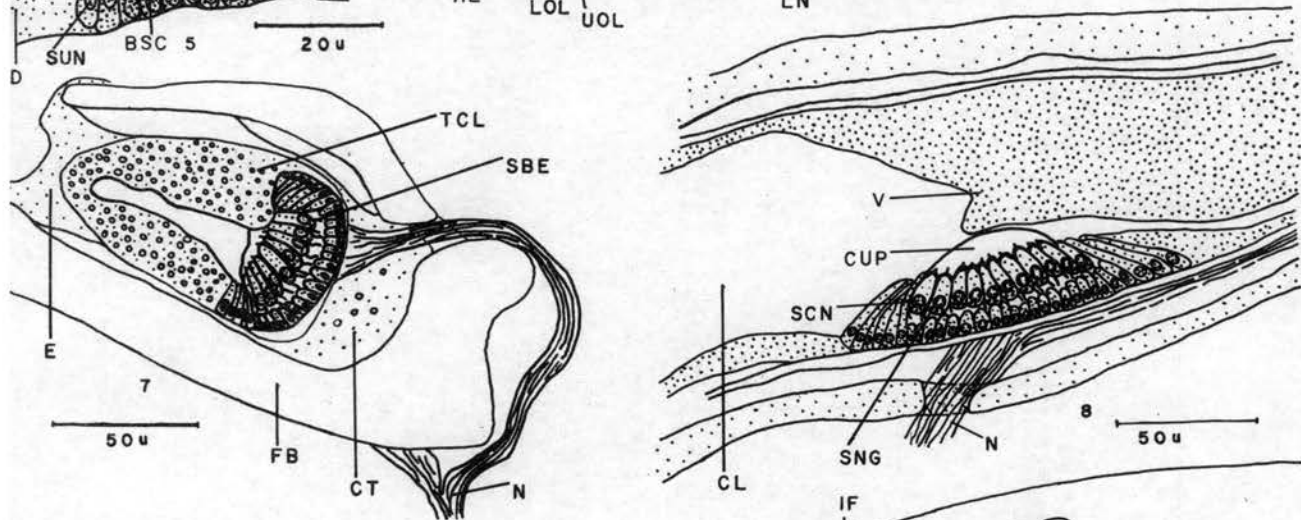
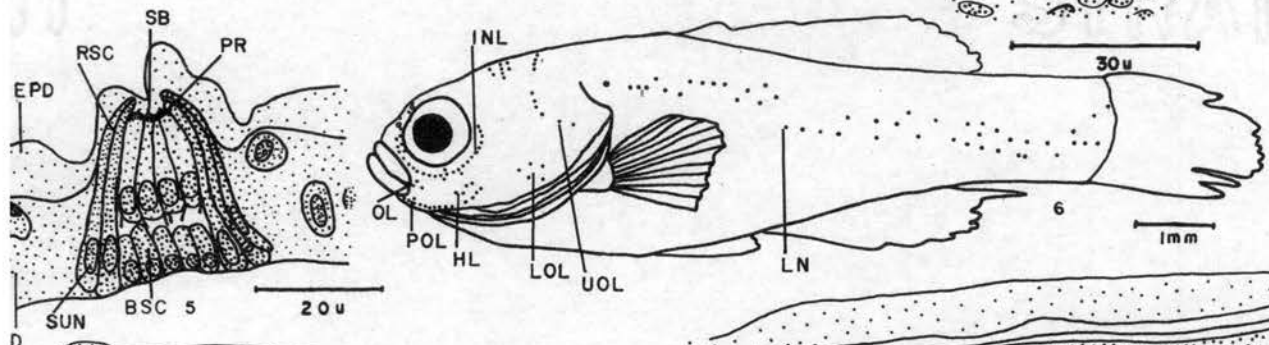
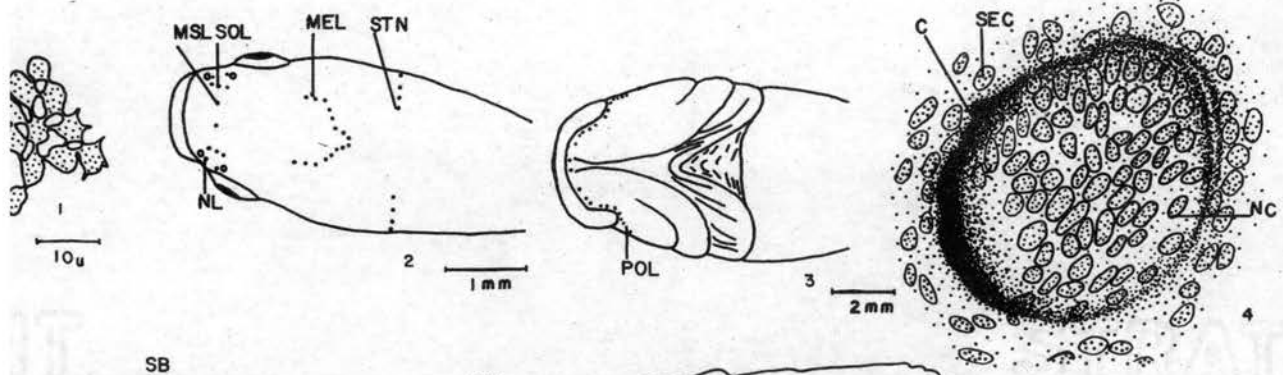
Figure 7. Cross-section of supraorbital canal and canal organ.

Figure 8. Longitudinal section of a portion of the lateralis canal and canal organ.

Figure 9. Position of dorsal canals and canal organs.

Figure 10. Position of lateral canals and canal organs.

Abbreviations: AN, Anterior Nostril; ANP, Anterior Nasal Pore; BSC, Basal Supporting Cell; C, Crypt; CL, Canal Lumen; CO, Canal Organ; CT, Connective Tissue; CUP, Cupula; D, Dermis; EPD, Epidermis; FB, Frontal Bone; HL, Horizontal Neuromast Line; IF, Infraorbital Canal; INL, Infraorbital Neuromast Line; INT, Interorbital Branch; L, Lateralis Canal; LN, Lateralis Neuromast Line; LOL, Lower Opercular Neuromast Line; MEL, Median Extrascapular Neuromast Line; N, Nerve; NC, Neuromast Cell; NL, Nasal Neuromast Line; OL, Oral Neuromast Line; OPM, Operculomandibular Canal; PN, Posterior Nostril; POL, Preopercular Neuromast Line; PR, Protoplasmic Rods; RSC, Rhopoid Supporting Cell; SB, Sensory Bristle; SBE, Basal Extension of Sense Cell; SC, Supraorbital Cross-commissure; SCN, Sensory Cell Nucleus; SEC, Superficial Epithelial Cell; SNG, Subnuclear Granules; SO, Supraorbital Canal; SOL, Supraorbital Neuromast Line; ST, Supratemporal Canal; STN, Supratemporal Neuromast Line; SUN, Supporting Cell Nucleus; TCL, Thickened Canal Lining; UOL, Upper Opercular Neuromast Line; V, Vellum-like Structure.



VITA

Branley Allen Branson

Candidate for the Degree of

Master of Science

Thesis: THE LATERAL-LINE SYSTEM OF THE CENTRARCHID FISH,
ELASSOMA ZONATUM (JORDAN)

Major Field: Zoology

Biographical:

Personal data: Born at San Angelo, Texas, February 11, 1929, the son of B. Allen and Era Branson.

Education: Attended grade school at Gladewater, Texas, Salem, Illinois, and Afton and Lawton, Oklahoma; highschool at Lawton, Pryor, and Afton, Oklahoma, graduating from the latter in 1948. Attended U. S. Naval Hospital Corps School in 1948, electrocardiographic technician school in 1949, and field technician school in 1950. Graduated from North-eastern Oklahoma Agricultural and Mechanical Junior College with a major in Zoology in 1954; received the Bachelor of Science Degree from Oklahoma Agricultural and Mechanical College with a major in Zoology in 1956; completed requirements for the Master of Science Degree in August, 1957.

Professional experience: Served in the United States Naval Reserve from 1945 to 1946; regular navy from 1948 to 1952; served as research assistant in 1955, and as graduate teaching assistant at Oklahoma Agricultural and Mechanical College in 1956 and 1957.