THE LATERALIS COMPONENTS OF THE ACOUSTICO-LATERALIS SYSTEM IN THE SUNFISH FAMILY CENTRARCHIDAE

By

BRANLEY ALLEN BRANSON

Bachelor of Science
Oklahoma State University
Stillwater, Oklahoma
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Master of Science
Oklahoma State University
Stillwater, Oklahoma
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Thesis Approved:

Geo. A. Moore

Thesis Adviser

Roy W. Jones

L. Herbert Bruneau.

Bryan P. Glass

D E Bryan

Dean of the Graduate School

PREFACE

With the exception of Archoplites interruptus (Girard), which is a relict species of the Pacific Coast, all of the extant species of the family Centrarchidae range east of the major uplift in the Rocky Mountain System. However, during the Pliocene and Pleistocene geological periods the range of this family extended over a much more extensive area (Miller, 1946, 1959). Notwithstanding a single genus from the Eocene of Europe (Romer, 1945), which is probably a member of some other taxon, the family has always been endemic to North America. The centrarchids are primarily adapted to live in warm waters and form a conspicuous element in most of the waters east of the Rocky Mountains and south of the colder latitudes.

The Centrarchidae is a relatively large family consisting of eleven genera and 30 described species (Moore, 1957; Böhlke, 1956). Although a considerable amount of information is available in the literature, most of the investigations concerning various members of this family are of a pragmatic or systematic nature. Very little is actually known concerning the anatomy of the sensory systems and allied structures of sunfishes. Furthermore, no one has proposed (in print) a tentative phylogeny for the whole family.

The primary aim of this project has been to study and describe the gross soft, osteological and lepidological anatomy of the lateralis components of the acoustico-lateralis system and the histological structure of the organs contained therein. Where applicable, comparison has been made with other taxa. Secondary considerations have dealt with the reconciliation of the findings adduced from the above studies to the ecological affinities of the fishes involved. Finally, the conclusions derived have been utilized in an attempt to synthesize a suggested phylogeny in order to show relationships in this important family of freshwater fishes.

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CHAPTER I

SURVEY OF THE LITERATURE

All vertebrate animals which have lived continuously in an aquatic habitat, excluding those which have secondarily taken to the seas or fresh bodies of water, possess a lateral-line system. Even the larvae of xerically adapted amphibia, with some exceptions, which only return to water for spawning purposes possess this system. It is thus seen that the lateral-line system has a very respectable antiquity, the very first vertebrates bearing such structures (Stensiö, 1947; Sarasin and Sarasin, 1890; Piveteau, 1935; Allis, 1936; and many others). In primitive fishes and fish-like animals the lateral line sometimes attained an amazing degree of complexity. This complexity may be seen in several forms which have persisted to the present. Allis (1889), for example, counted as many as 3700 pores on the head of one large _Amia_ and the same system is tremendously complex in the gar _Lepisosteus_ _osseus_ (Collinge, 1893). In general, it is concluded from such works that the more primitive the group of fishes the more complex will be its lateral-line system, and progressive degeneration in canal complexity seems to be the rule as various taxa become more and more specialized. The cephalic canals are still very complex in the Clupeidae (Tretyakov, 1938; 1950), less so in the Catostomidae (personal observation) and still less so in the Cyprinidae, though quite complex when compared with more advanced fishes (Illick, 1956). As the ichthyine phylogenetic tree is ascended this reduction continues until the system is very simple, comparatively speaking, in perciform fishes such as the Centrarchidae (Moore, 1956) and the Cichlidae (Branson, in press).

The amount of reduction varies from group to group and is of phylogenetic significance since it is fairly constant within a species (Tretyakov, 1944). Reduction may take several forms. There may be a loss of the numerous side branches and the complete disappearance of the trunk canals (Tretyakov, 1950) or there may be gaps in canals (incomplete) (Hubbs and Cannon, 1935). The most commonly observed phenomenon in the process of specialization is the replacement of canals by simple or compound lines of external neuromasts. This has been observed many times in different groups of fishes: Pehrson (1945) in Gymnarchus; in some Palestinian fishes (Steinitz, 1954); generalization for several fishes (Stensiö, 1947); Allis (1934); and many others. With the exception of the canal on the trunk, such reduction usually involves a decrease either in the size of or number of bones associated with the lateral-line tubes. Such a statement, perhaps, requires amplification.

There are several theories as to the origin of the vertebrate lateral-line system. All of these have one thing in common, they assume the system to be derivable from a precursor system in some group of higher invertebrates. One of these theories (Whitman, 1884; 1889), based upon the similarity between the segmental sense organs of certain annelids and the neuromasts of vertebrates, would derive the lateral line from preexisting organs in the segmented worms. Although there are some good reasons for doubting the origin of chordates from the segmented worms, the reasoning behind the hypothesis is sound. The piscine lateral-line system doubtless did not suddenly come into being without having passed through some sort of evolutionary sequence and, since the first chordates probably did not have skeletons, the system would most likely have been represented by neuromast lines (Allis, 1936). This is more than an assumption as any one can easily verify by studying the ontogenetical development of any number of fishes. The neuromasts form first and are later enclosed in canals and bone (Moodie, 1922). All of the bones associated with the lateral line are dermal in origin and are aptly termed "lateral-line bones;" the other dermal bones of the head have been termed "anasmestic" (Moy-Thomas, 1939; Westoll, 1937; 1943; Stensiö, 1947). The lateral-line bones often become fused to the anasmestic ones and become a compound unit.

There has been a great deal of discussion as to whether the neuromasts act as evocators of the lateral-line bones or whether these organs are passively enclosed by the bones. Allis (1936) thought that the lateral-line canals and/or the organs exerted some sort of force in causing lateral-line bones to be formed. On the other hand, Moodie (1922) and others considered the lateral-line to lack any tropic abilities in the formation of these ossicles. A third line of thought (Stensiö, 1947) would have the bones of composite origin, i. e., partially as the result of tropic activity on the part of the neuromasts and partially from anasmestic activity. Whatever the case, it can be shown that when lateral-line canals degenerate and disappear the bones with which they were associated often vanish. There is, then, such a constant association of the lateral-line system with the same bones from taxon to taxon that these bones can be homolgized by the neuromast lines alone when the canals are absent (Jarvick, 1948).

According to several authors, among them Ewart (1895), the first observations recorded on the lateral line were made by Stenonis in 1664 and 1669 on skates and sharks. The tubular structures were assumed by him and later workers to be slime canals (Schleimkanalës) and the term is still occasionally seen in the literature. Although Leydig (1850) is usually accredited with the discovery of the sense organs associated with the lateral line and subsequently disproving the idea that these tubes were responsible for secreting mucous, Knox (1825) had noted the great similarity between the ear and the lateral-line organ 25 years before him. The latter worker even suggested that the organ held a place intermediate between the sense of hearing and touch. Two years later Weber (1827) correctly identified taste buds in the mouth of the carp and Leydig (1851) the same kind of organs on the general skin. Leydig (1851), as well as some of his contemporaries, regarded all of the cutaneous organs to be of the same function. Later workers (Herrick, 1903) discovered still a third class of sensory receptors in the skin, the ordinary cutaneous nervous terminals. Schultz (1870) and Merkel (1880), according to Herrick (1903), were the first to actually demonstrate differences between the end buds (taste buds) and neuromasts. The sense cells of lateral-line organs bear "hairs" at their apices and do not sit on a basement membrane whereas the gustatory cells of the taste buds lack sensory hairs and extend, with their sustentacular cells to the basement membrane. The sense organs of the lateral-line system supposedly have been derived phylogenetically from the general cutaneous organs (Herrick, 1903) since they are in every sense of the word a part of the cutaneous-sensory system (Hyman, 1956).

In 1884 and 1885 Beard showed that the organ of hearing was a modification of the lateral line. It is from this knowledge that the term "acoustico-lateralis system" has evolved. Beard's premises laid the groundwork for Ayer's (1892) larger exposition in support of this idea.

Wilson (1889) and Wilson and Mattocks (1897) are often cited as being the first to actually observe the ontological development from a common anlage of the ear and lateral line (in the sea bass Serranus atrarius and a salmon). However, according to Wilson and Mattocks, Mitrophanow (1893) made a similar discovery in selachian embryos. These discoveries set off another series of debates, which were temporarily kept in the background by Lee (1898) and Johnston (1905), who marshalled most of the existing evidence in support of the Wilson-Beard school. A few years later, however, Beckwith (1902, 1907) discovered that a common anlage did not form in Amia calva, but that the ear placode formed first. This was not much of a blow to the theory, which had by this time assumed the status of a biological law, for as Ayers had stated 15 years before, the two anlages do not necessarily maintain this connection in all species. Lee (1931) gave further support for the theory when he observed the lateral line and ear to develop from a common placode. He termed this anlage an "acousticolateralis placode."

According to Allis (1904) the nasal organ may also be derived from the lateral line. The olfactory organ may have originally been innervated by lateral-line fibers but during its evolution pre-existing fibers were usurped so that the present-day configuration resulted. Allis received some support for his thesis from Watson (Gregory, 1920) who suggested that the lachrymal portion of the suborbital ossicles may have given rise to the naso-lachrymal duct in higher forms, and from Kyle (1926) who, possibly quoting another author, stated that the olfactory organ developed from "similar pits" (lateral-line pits) on the head.

There is considerable evidence that the neuromasts originally were arranged in a metameric fashion (Neal and Rand, 1936) but as the original (primary) neruomasts divided (to form secondary and tertiary neuromasts) and migrated (Neave, 1946; and others) this arrangement became obliterated. The first neuromasts arise from a placode behind the eye (Wilson, 1889), or from a primordium near the ventral half of the mandibular cleft (Stensiö, 1947) or as a separate placode (Beckwith, 1902, 1907). The neuromasts thus formed undergo multiplication and migration to form several primitive neuromast or pit lines. When the neuromasts become enclosed in canals, division ceases (Bamford, 1941), whereas those which remain on the exterior may continue to form new sense organs for some time. The primary neuromasts, during migration, move in definite directions (Stone, 1933). The cephalic lines precede, both ontogenetically and phylogenetically, the development of the trunk lines (Miyadi, 1929). Sâto (1955a) has given the distribution of the pit lines on the top of the head in several adult fishes; his terminology follows. The <u>supratemporal commissure</u> is directed medially in the region of the posttemporal bone and apparently sends a ventral branch onto the opercle in some species. This ventrally directed line represents the <u>upper opercular line</u> and is without homologue in many species. A <u>medial extrascapular line</u> (parietal line) represents the <u>supraorbital commissure</u>. The <u>supraorbital line</u>, above the eye, is continued anteriorly as the <u>nasal line</u>, in front of which, and at right angles to, there develops, in a few modern fishes and in many ancient ones, the <u>rostral commissure</u>. All of these lines, except the last-named, which is apparently a continuation of the infraorbital series, discussed below, are derivatives of the main lateral line and supraorbital line.

In most fishes and in many amphibians six primitive neuromast lines develop on the cheeks (Stensiö, 1947). These are as follows: (1) the <u>infraorbital line</u>, with its two divisions, the <u>postorbital</u> and <u>suborbital</u>;

(2) the <u>preopercular line</u>; (3) the <u>mandibular line</u>, which is the ventral continuation of the preopercular; (4) the <u>supramaxillary line</u>, a line composed of three components, <u>anterior</u>, <u>posterior</u> and <u>middle</u>, which connect the infraorbital with the preopercular; (5) the <u>postmaxillary line</u>, a short, oblique line connecting the anterior and middle supramaxillary lines; and (6) the <u>oral line</u>, actually only a ventral continuation of the postmaxillary which is directed onto the dorsal parts of the lower jaw. This last line is single in teleosts but becomes double in dipnoans. For the most part, these lines are homologous from one group to the next (Stensiö, 1947) but after embryonic stages their homologization becomes difficult because of a variety of factors. Stensiö (1947) listed a few of these factors as being: changes in position, lengthening of the head, outgrowths and longitudinal subdivisions of the neuromast lines, formation of new connections and disappearance of embryonic connections and partial or complete obliteration of certain lines. This may also happen in the embryos of advanced fishes. For example, Pehrson's (1944) vertical pit line is only the residual part of a reduced supramaxillary line; and the ventral opercular line of Pehrson (1945) and Herrick (1899) is probably only a posterior continuation of the supramaxillary branch, and in general the postmaxillary line is represented in teleosts only by its ventral part (Stensiö, 1947). In fishes with well-developed canals (Sâto, 1955a) most of the pit lines may disappear but remain strongly developed in those species with poorly developed canals. In the latter group the primitive pit lines may become highly compounded by further division so that "pit fields" (Sâto, 1955a) or many accessory pit lines are formed. This may also occur in fishes with a moderately-developed canal system such as <u>Aphredoderus</u>, in which superficial neuromasts are aggregated

extensively in bands and patches (Moore and Burris, 1956). The canal neuromasts are developed from external neuromasts and the main lateral line of the trunk is formed in the same manner as those of the head, i. e., by a linear budding and migration of neuromasts (Neave, 1946).

Once the embryonic, primitive pit lines are formed, metamorphoses of the canal system begins. The first process to occur is a sinking into the skin of the external neuromasts (Dijkgraaf, 1952; and others), which become covered over by these tissues. Fundamentally, although there is not general agreement, each canal neuromast is enclosed by one bone primordium (Stensiö, 1947) which may become fused to some anasmestic element. There are thus formed chains of embryonic lateral-line bones which may remain more or less separate, but which, as a rule, fuse together to form composite bones. Furthermore, there may be some osseous accretion by the lateral-line bones for some time after they are formed (Parrington, 1948). Thus it may be seen that the preoperculum is of composite origin, the ventral portion developing from the preopercular neuromast line, the dorsal portion consisting of the supramaxillary line; the mandible (dentary, articular, and, in some, the angular) develops from the mandibular line and either annexes the oral line or that line fails to develop altogether. The infraorbital neuromast line gives rise to the canal of the same name; the supraorbital and nasal lines, respectively, become a part of the supraorbital and nasal canals; the medial extrascapular line forms the supraorbital commissural canal as a branch from the supraorbital; the supratemporal forms the supratemporal commissural canal; and the main lateral-line series gives rise to the canals in the skin or in the scales along the trunk.

As noted above, there are, according to their placement, two kinds of neuromasts, those enclosed within canals and the external type. Herrick (1901) further distinguished two types of external neuromasts, the pit organ (sunken into a crypt which opens to the exterior by a tube or pore) and the naked type (free on the skin). His observations were extended to some Japanese fishes by Sâto (1955b). Regardless of these differences, it has been pointed out by several competent observers (Daget, 1949; Holmgren, 1942) that all of the components mentioned above are parts of the same morphological system. The neuromasts, except for size and placement differences, cannot be histologically or embryologically differentiated.

There have been many attempts to standardize the nomenclature of lateral-line canals. Consequently, one may find many epithets for the same canal in the literature. However, in general the primary-canal names correspond to the names given to the primitive neuromast lines discussed above. Excepting these lines, which are always present in one form or another, authors often have to develop special nomenclature for specialized groups of fishes (Illick, 1956; Hubbs and Cannon, 1935; and many others). In North America perciform fishes the terminology of Hubbs and Cannon, with some reservations, is generally satisfactory. The names for the skull bones of teleostomian fishes have been standardized by Harrington (1955).

Innervation of the acoustico-lateralis system is accomplished by the Acoustic (VIII), branches of the Facial (VII) and Glossopharyngeal (IX), and a large branch of the Vagus (X) (Hyman, 1956). All of these nerves enter the anterior part of the medullary sensory-column known as the "acoustico-lateral area" (Hyman, loc. cit.). The eighth nerve, of course, as the prefix "acoustico-" implies, serves the ear and is not a part of the lateralis system per se.

In animals with a well-developed, movable tail and/or a lateral-line system some large nerve cell bodies are found in the medulla at the level of the roots of cranial nerve VII. The axons of these cells, which are called Mauthner's cells, extend the length of the spinal cord to reach the tail (Healey, 1957). The lateral-line branches appear to end on these cell bodies in the form of "end feet," "boutons termineux" or "Endfusschen" (Barbey-Gampert, 1943), but there is some disagreement as to whether each nerve has a separate medullary center (Kingsley, 1926) or one medullary center receiving many nerves (Herrick, 1899) on Mauthner's cells.

Many morphological studies have revealed that innervation of the neuromast lines and of canal organs is always by the same nerves for given lines in any group of fishes. It has been argued that in very primitive fishes the lateral-line system was restricted to the head region as it is now in some clupeids (Tretyakov, 1938) and that during phylogeny, as it extended farther and farther caudad into the trunk, it carried its innervation with it (Garman, 1888), which accounts for the extensive length of the lateralis branch of the Vagus. This branch always occupies a fixed position in the septum (horizontal skeletogenous septum) between the epaxial and hypaxial musculature (Rode and Rabaus, 1926). At each neuromast in the lateralis a small, heavily myelinated nerve twig is given off (Kingsley, 1926). Since the lateral line does not exactly follow the septum in deep-bodied fishes, the twigs are of lengths varying according to the distance from the main nerve to the neuromasts (Branson, in press). In addition to innervating the organs of the lateralis, the Vagus also sends branches to the canal organs of the supratemporal canal and external neuromasts just in front of it (Lekander, 1949; Bonin, 1940). The remaining organs of the lateral line are innervated by branches of cranial nerves VII and IX.

The supraorbital line receives branches from the superficial Opthalmic ramus of nerve VII, which also innervates the organs of the supraorbital commissure. The infraorbital line is ramified by fibers of the Buccal branch of VII whereas the Otic ramus of VII sends fibers to the retro-orbital line of Bonin (op. cit.) or postorbital sinus of Branson (in press). The operculomandibular canal organs are innervated by the relatively large hyomandibular ramus of the Facial. The few organs associated with the part of the supratemporal canal contained in the posttemporal bone receive fibers from the supratemporal branch of the Glossopharyngeal (Bonin, 1940).

The acoustico-lateralis system, omitting the function of hearing, has been defined in several ways, many of the definitions being purely semantic in nature. The system has often been credited with a "sixth sense" function (Parker, 1905; Ewart, 1895; Knox, 1925) but more often it is referred to as an accessory auditory organ (Pumphrey, 1950) or "Akzessorisches Gehororgan" by several German workers (Dijkgraaf, 1952); a true external labyrinth (un véritable labyrinthe externe) (Piveteau, 1935), and a "poor relation to the auditory organ" (Hillier, 1931). Other workers, notably DeSéde (1884), have implicated the series of organs as being very sensitive touch receptors. In general, the idea that the lateral-line system is auditory in function has not met very wide acceptance by physiologists and behaviorists. The research of Dijkgraaf, who conducted physiological and behavioral studies, has been widely cited. Dr. Dijkgraaf's (1934) term for this system is long-distance touch receptor (Ferntastsinnes) which has often been used without proper credit

(Tretyakov, 1950).

Before going into the literature concerning the various functions which have been assigned to the lateral line, a few words should be said concerning the terminology that has been developed for the sense organs of this system. These organs, as seen above, are often termed neuromasts but have been given several other names. Dercum (1879), because of their resemblance to the maculae of the ear, suggested the name "maculae laterales"; Garman (1888), thinking they were functional in detecting vibrations in the water, called them "tremognosters" and Bonnier (1896), reasoning along the same lines as Garman, termed them "seisesthesic organs." Some of the lateral-line organs in specialized fishes have become modified so much as to deserve special names. Specific instances of the latter are the so-called "Mormyromastes" and "organs of Fahrenholz" (Cordier, 1938) and the "Ampullae of Lorenzini (Druckrezeptoren)" (Daget, 1949). Leydig (1850), discoverer of the neuromast (auct.), called the normal neuromasts "nervenhugeln," or nerve hillocks.

If the list of synonymy for the lateral-line organs is long, the list of functions ascribed to it is even longer. Many of these so-called functions have been assigned strictly from a morphological view; others have resulted from brief behavior experiments in which the morphology of the system was unknown. Some of these functions are listed below without comment: perception of wave motion (Beard, 1884); communication with other members of the same species (Bonnier, 1896); static function (Carpenter, 1928); relative pressure perception (Freeman, 1928); sex recognition (Noble, 1934); orientation of the animal in space and in currents (Piveteau, 1935); detection of electrical currents (Regnart, 1931); perception of minute temperature differences (Ryder, 1890; Rubin, 1935);

obtaining food (Scharrer, 1932); testing the physical and chemical changes occurring in an aquatic habitat (Smith, 1930; 1933); and perception of light (Andrews, 1952; Young, 1935). Recent experimental evidence by several workers has shown that many, if not all, of the above may actually be functions of the lateral-line system. There are a few specialized groups of fishes in which generalizations concerning these functions will not apply.

In one of these taxa, Mormyridae, Cordier (1938) discovered some very interesting peculiarities concerning the lateral-line system. The sensory cells of some of the neuromasts (Mormyromasts) pass through very definite cycles which terminate when the sense cells become degenerate and are passed to the exterior as some sort of a secretion. The sense cells are later regenerated, presumedly by the supporting cells below. Such holocrine functions have also been described for the organs of Fahrenholz (Cordier, op. cit.) in the Dipneusti and in <u>Polypterus</u>. Sand, according to Daget (1949) has shown that the chondrichthine ampullae of Lorenzini are specialized organs of the lateral line which are responsive to temperature changes at magnitudes of 0.1 degree Centigrade.

The general function of the lateral-line system has been worked upon by scores of investigators all of whose works are not pertinent in this connection; a few of the more important contributions are considered here. The reader is directed to Daget's (1949) excellent review of the subject for more comprehensive coverage.

Parker (1905) early realized that it was essential for anyone interested in studying animal behavior to first familiarize himself with the animal's sense organs. Dijkgraaf (1952) suggested the same sequence for physiologists, i. e., study of sense organs before attempting research.

This last author has also suggested that there are two main methods for studying the function of the lateral-line system: (1) the behavior method and (2) the electro-physiological method. He further concluded that these two techniques are complementary. In surveying the literature one is struck by the many negative and conflicting results obtained by the very early investigators. This is not surprising since the treatment of test animals was often very harsh and they more often died than not. These experiments were also quite inconsistent with what modern scientists call the "scientific method" since often control animals were not used (Bonnier, 1896).

Parker (1905), an early American behaviorist, subjected some cyprinodonts, flatfishes and sharks to an array of stimuli and concluded that light, temperature, varying concentrations of salt, foods, oxygen and carbon dioxide tensions, pollution, pressure changes, water currents and high frequency vibrations did not stimulate the neuromasts. Furthermore, he did not find the system to be any more functional than the general skin in equilibration. His single positive stimulating device was low frequency vibrations.

Hoagland (1933a) is the first to receive credit for discovering that the neuromasts send repetitive discharges (spontaneous activity) to the medulla when not under any particular stimulation. This spontaneous activity has been confirmed by other workers, among them Dijkgraaf (1952) who considers this "resting" discharge to be an "intracentral tonus." This same sort of activity has been described in the ampullae of Lorenzini and in the organs of the semi-circular canals (Daget, 1949). Furthermore, in this and subsequent experiments Hoagland (1933b, 1933c, 1934 and 1936) found that if the spontaneous activity was absent no response could be elicited from the lateral-line organs. He discovered that low velocity vibrations, light stroking of the side, streams of water directed against the canals and bending of the body increased the impulses transmitted by the lateral line and concluded that these organs may offer kinesthetic cues in swimming, acting to regulate speed of swimming and direction of turning. He also found that constant stimulation of the sense organs causes very rapid adaption (sensory inhibition) which may be a corollary of the spontaneous activity. The rate of spontaneous activity of the neuromasts appears to be a function of temperature (Hoagland, 1933c).

Sand (1937), in a series of experiments designed to confirm Hoagland's results, made some rather startling physiological findings. There were two different kinds of sense cells in the neuromasts which acted antagonistically. When the organ was stimulated from one direction a certain electrical response was obtained, but when stimulated from the opposite side a different response was noted. Further experiments by Sand resulted in the discovery that still another type of cell was indicated with a third level of excitability (threshold). These results have been duplicated by Monnier (Daget, 1949) in Mustelus canis. Different kinds of cells in lateral-line organs have never been described histologically and Daget (1949) does not believe that they are equally distributed in all of the neuromasts.

In addition to the above findings, physiologically, the existence of more than one kind of cell in the neuromasts, has been indicated by Dijkgraaf (1952), who made some definite statements concerning the function of the lateral-line system. If the lateral-line sense hairs or cupulae are deformed anteriad an increased response results. If on the other hand, these structures are deformed in the other direction a decrease in response obtains. It is clear to Dijkgraaf that the lateral-line system is responsible for extending touch, viz., it operates under low-frequency vibrations, whereas the semi-circular canals register angular acceleration; the utricular organs serve in spatial orientation; and the pars inferior responds to sound. He also stated that in an intact fish it may be impossible to separate the function of the ear and the lateral line.

The lateralis components of the acoustico-lateralis system, then, are organs intermediate between that of hearing and that of touch; a member of the somatic-sensory division of the nervous system; and whose sensory cells are the seat of certain physico-chemical reactions resulting in the perception of low frequency waves.

One aspect of lateral-line studies which has received only cursory notation is that of correlating observed morphology with the habits and/or ecology of the species involved. Garman (1888) noted in selachians and ratfishes that animals which were lethargic of habit possessed a much more abbreviated lateral-line system than those which were active swimmers. Disler (1941), in the Plagistomidae, and Tretyakov (1938), in flying fishes, also concluded that the habits of these species were related to the development of the lateral-line system in some way. Dijkgraaf (1952), after having observed many species, has shown that fast-swimming species generally have a more extensive canal system than sluggishly-swimming fishes which have correspondingly more external neuromasts and fewer canals. Hoagland (1933a), contrasting a trout and a catfish, found that, in the sluggish catfish, the greater number of neuromasts were located anteriorly and in the active trout were concentrated more caudad.

According to Lowenstein (1957) the free-swimming fishes have, along with other modifications, their sensitive cupulae and neuromasts protected by canal systems whereas sluggish bottom-dwelling types (also Dijkgraaf, 1952; Hoagland, 1933a), and fishes which are intermittent swimmers (Dijkgraaf, 1952), such as Esox, more often than not have primarily or secondarily reduced lateral lines. However, this system may remain highly developed even in slow-swimming species or bottom dwellers if they inhabit fast-moving bodies of water such as the surf or mountain streams (Dijkgraaf, 1952; Lowenstein, 1957). Lepomis humilis has much inflated lateral-line canals and some other peculiarities which Moore (1956) considered as adaptations for living in the turbid streams of the American Great Plains; he also reached similar conclusions while studying other sensory systems in some barbeled minnows (Moore, 1950). Tsukazu and Yoshiro (1957) have recently published a paper (not available for reference) which apparently deals with this subject.

The centrarchid lateral-line system has been utilized on several occasions for the purpose of constructing diagnostic keys (Hubbs, 1926; Moore, 1957), and in one instance, as a generic character (Allotis) (Ortenburger and Hubbs, 1927). There have also been one or two passing remarks on the function of the system in Centrarchidae (Noble, 1934). Otherwise, the knowledge concerning the system in sunfishes is slight. Allis (1904) presented a diagrammatic representation of the osseous elements in Micropterus dolomieui and stated elsewhere (1889) that the lateral-line canal did not pass through the angular of this fish but through the articular. Likewise, the work of Schufeldt (1884, 1901), which has apparently been completely overlooked by many recent workers, and Gregory (1933) are of such a general nature as to be of little use in the study of lateral-line bones. Dineen and Stokley's (1956) description of the osteology in Archoplites interruptus, with the exception of one minor error, is useful because osseous affinities of the lateral line are clearly delineated. The only published papers definitely concerned with histological and external morphology in the Centrarchidae is that of Moore (1956), who compared the systems of Lepomis humilis, L. cyanellus and L. microlophus, and that of Curd (1959), who made some observations concerning certain abnormalities in L. humilis. The author (Branson, unpublished) considered the system in Elassoma zonatum. As far as can be determined this is all of the work completed to date with direct bearing on the lateral-line system in members of the sunfish family.

CHAPTER II

MATERIALS AND METHODS

With two exceptions the names used for the species considered in this discourse agree with Moore (1957). Bailey (1956) uses *Chaenobryttus gulosus* instead of *C. coronarius* for nomenclatural reasons and the name *Elassoma okefenokee* was not available when Moore's manuscript went to press.

Methods of Collecting and Species List

Obtaining specimens for study proved to be one of the more difficult aspects of this project. At present there are 30 valid species of centrarchid fishes. However, since one species, *Ambloplites cavifrons* Cope appears to be extinct or so rare as to be seldom collected (E. C. Raney, personal communication, 4:IV:1958), only 29 of the 30 are discussed herein. In obtaining specimens several techniques were used. Some were caught by hook and line, some were seined or trapped, and some were collected with the aid of rotenone. Many specimens were donated by interested fellow workers who employed one or more of the above methods in collecting them. Since the list is rather lengthy, these data are presented below without comment. The number of specimens taken from each site is given in parentheses.

Micropterus dolomieui Lacépède: (1), 27:VIII:1953, Chenowettis Fork, Sunfish Creek, Scioto River System, Pike County, Ohio (formalin), S. L.

203.2 mm.; (5), 10:V:1957, Spring Creek, Adair County, Oklahoma (P. F. A.), S. L. 63.5 to 71.8 mm.

Micropterus punctulatus (Rafinesque): (1), 28:VIII:1947, James Fork Creek, LeFlore County, Oklahoma (formalin), S. L. 152.4 mm.; (1), 29:VII: 1956, Luksukelo Creek, 1 ½ miles north of Eagletown, McCurtain County, Oklahoma (P. F. A.), S. L. 61.8 mm.

Micropterus treculi (Vaillant and Bocourt): (3), 8:II:1950, San Marcos River, 20 miles south-east of San Marcos, Caldwell County, Texas (formalin), S. L. 75.9 to 231.4 mm.; (1), VII:1958, two miles north of New Braunfels, Comal County, Texas (P. F. A.), S. L. 72.1 mm.

Micropterus coosae Hubbs and Bailey: (12), 15:III:1950, University of Alabama (formalin), S. L. 218 mm.

Micropterus salmoides (Lacépède): (1), 1:VI:1955, Yost Lake, near Stillwater, Payne County, Oklahoma (formalin), S. L. 218 mm.; (8), VIII: 1957, Snedden Pond, 3 ½ miles west, ¼ mile north of Centralia, Craig County, Oklahoma (P. F. A.), S. L. 78.6 to 330.2 mm.

Micropterus notius Bailey and Hubbs: (6), 3:IV:1957, University of Florida, (formalin), S. L. 102.0 to 277.0 mm.; (15), 28:I:1956, Santa Fe River, Ft. White, Florida (formalin), S. L. 200.0 mm.

Chaenobryttus gulosus (Cuvier): (8), 8:V:1948, Lake Murray, Murray County, Oklahoma (formalin), S. L. 58.7 to 111.3 mm.; (1), 27:V:1957, Mudline Creek, three miles south of Eagletown, McCurtain County, Oklahoma (P. F. A.), S. L. 118.6 mm; (12), VIII:1957, Snedden Pond, Craig County, Oklahoma (P. F. A.), S. L. 76.2 to 118.5 mm.

Lepomis cyanellus Rafinesque: (1), 29:V:1948, Gates Creek, Ft. Towson, Choctaw County, Oklahoma (formalin), S. L. 11.0 mm.; (112), 27:VIII: 1957, Snedden Pond, Craig County, Oklahoma (P. F. A.), S. L. 10.0 to

228.6 mm.

<u>Lepomis</u> <u>symmetricus</u> Forbes: (3), 27:VII:1948, swamp three miles north-east of Eagletown, McCurtain County, Oklahoma (formalin), S. L. 31.6 to 47.2mm.; (2), 27:VII:1957, creek at Tom, McCurtain County, Oklahoma (Helly's fluid), S. L. 41.0 mm.

<u>Lepomis</u> <u>punctatus</u> (Valenciennes): (121), VI:1958, San Marcos Spring, San Marcos, Hayes County, Texas (formalin), S. L. 16.1 to 72.0 mm.; (1), IV:1957, a small tributary to the Neches River, highway 21, Texas (P. F. A.), S. L. 68.2 mm.

<u>Lepomis</u> <u>gibbosus</u> Linnaeus: (11), 29:VIII:1958, Dixon Lake, Otsego County, Michigan (formalin, P. F. A. and Helly's), S. L. 101.6 to 113.4 mm.; (11), 29:VIII:1958, Loon Lake, Ogemaw, Michigan (formalin, P. F. A. and Helly's), S. L. 78.3 to 92.4 mm.; (1), 20:XII:1937, Washtenaw County, Michigan (formalin), S. L. 118.2 mm.

<u>Lepomis</u> <u>microlophus</u> (Gunther): (16), 2:VII:1947, Lake Okmulgee, Okmulgee County, Oklahoma (formalin), S. L. 61.6 to 152.4 mm.; (3), VIII:1957, Snedden Pond, Craig County, Oklahoma (P. F. A.), S. L. 138.2 mm.

<u>Lepomis</u> <u>auritus</u> (Linnaeus): (2), San Saba River, Menard County, Texas (formalin); (22), VII:1958, below Lake Austin, Austin, Texas (formalin, P. F. A.), S. L. 38.6 to 142.8 mm.

<u>Lepomis</u> <u>marginatus</u> (Holbrook): (143), 4:VI:1958, Massey Lake, Hardin County, Texas; S. L. 42.1 to 66.8 mm.; (3), 27:VII:1957, creek five miles south of Tom, McCurtain County, Oklahoma (P. F. A.), S. L. 51.2.

<u>Lepomis</u> <u>macrochirus</u> Rafinesque: (18), 20:VII:1948, Pennington Creek, U. S. Fish Hatchery, Tishomingo, Johnston County, Oklahoma (formalin), S. L. 14.0 to 176.8 mm.; (6), 27:VII:1957, Waterfall Creek, south of Idabel. McCurtain County, Oklahoma (Helly's).

Lepomis megalotis Rafinesque: (12), 14:IV:1947, tributary to Little River, four miles north of Broken Bow, McCurtain County, Oklahoma (formalin), S. L. 20.3 to 88.3 mm.; (1), 27:VII:1957, creek at Tom, McCurtain County, Oklahoma (Helly's).

Lepomis humilis (Girard): (23), 25:IV:1955, Horse Creek, three miles east of Afton, Ottawa County, Oklahoma (formalin), S. L. 20.6 to 75.6 mm.; (1), 25:VII:1959, mouth of Blue River, Red River, Bryan County, Oklahoma (P. F. A.), S. L. 63.5; (3), 27:VII:1957, creek near Harris, McCurtain County, Oklahoma (P. F. A.), S. L. 46.2 to 76.2 mm.

Enneacanthus obesus (Girard): (12), University of Florida, 4.4 miles south of Baxter, Baker County, Florida (formalin), (3), 8:XI:1952, one mile north of Trenton, Highway 47, Florida (formalin), S. L. 51.2 mm.

Enneacanthus gloriosus (Holbrook): (7), 19:I:1947, ditch 1.1 miles north of Alachua, Alachua County, Florida (formalin), S. L. 29.8 to 43.3 mm. ; (4), Brasenia Pond, 3.5 miles north of Sneads, Butler Road, Florida (formalin).

Mesogonistius chaetodon (Baird): (4), University of Florida, Florida Lake, 1.5 miles north of Altoona, State Highway 42, Florida (formalin), S. L. 31.6 to 42.0 mm.

Ambloplites rupestris (Rafinesque): (4), V:1957, Spring Creek, Mayes County, Oklahoma (P. F. A.), S. L. 35.4 to 52.4 mm.; (4), VII:1958, San Marcos River, San Marcos, Hayes County, Texas (P. F. A.), S. L. 184.6 to 256.3 mm.

Pomoxis nigromaculatus LeSeuer: (7), 18:VII:1950, Poteau River, near Shady Point, LeFlore County, Oklahoma (formalin), S. L. 196.3 to 228.6 mm.; (3), 27:VII:1957, slough near Harris, McCurtain County, Oklahoma (P. F. A.), S. L. 76.2 to 84.3 mm.

Pomoxis annularis Rafinesque: (100), VIII:1957, Snedden Pond, Craig County, Oklahoma (formalin and P. F. A.), S. L. 50.8 to 206.8 mm.; (12), 24:VIII:1946, small stream, Sequoyah County, Oklahoma (formalin), S. L. 77.2 to 192.6 mm.

Acantharchus pomotis (Baird): (1), University of Florida, Dismal Swamp, north of Jerico Ditch, Norfolk County, Virginia (formalin), S. L. 42.1 mm.; (2), V:1914, Pocataligo River, Manning, South Carolina (formalin), S. L. 38.1 and 41.0 mm.

Centrarchus macropterus (Lacépède): (1), ditch one mile north of Wamba, Bowie County, Texas (formalin), S. L. 76.2 mm.; (3), 27:VII:1957, creek five miles south of Tom, McCurtain County, Oklahoma (formalin and P. F. A.), S. L. 48.1 to 88.7 mm.

Archoplites interruptus (Girard): (15), 3 and 6:VII:1957, Carson River, three miles north-north-east of Fallon, Churchill County, Nevada (formalin), S. L. 84.2 to 330.2 mm.

Elassoma zonatum Jordan: (7), Magnolia Springs, near Millan, Jenkins County, Georgia (formalin), S. L. 23.2 to 24.5 mm.; (50), 24:VIII: 1956, Forked Lake, three miles south-east of Eagletown, McCurtain County, Oklahoma (formalin, P. F. A. and Helly's), S. L. 17.2 to 31.6 mm.

Elassoma evergladei Jordan: (3), Alachua County, Florida (formalin), S. L. 20.8 to 27.1 mm; (6), creek two miles northwest of Mullis, on Gunn Highway, Hillsborough, Florida (formalin).

Elassoma okefenokee Böhlke: (13), Lewis Pond, Seminole County, Georgia (formalin), S. L. 22.4 to 26.8 mm.

Fixatives, Fixation and Preservation

A fixative is any substance used to preserve as faithfully as possible the cytological, histological or gross morphological anatomy of a part of or a whole animal. In selecting fixatives for the material to be used some other considerations had to be met, namely the solution also had to function as a killing agent and certain biological stains had to follow these fixatives well. As indicated above, three main fixatives were utilized in preparing specimens for study. Ten per cent formalin is a standard fixing solution long used by ichthyologists (Hubbs and Lagler, 1958). Helly's fluid was used because it fixes very rapidly (Dawson, 1934; Denny, 1937). The third fixative indicated, P. F. A.$_3$, a modified Bouin's solution, was originally designed as a cytological agent for insect material but has been found to fix neuromasts with very little shrinkage (Branson, in press). The formulae for all of these agents may be found in several handbooks of microtechnique (Jones, et al., 1950).

After fixation the specimens were washed in running tap water if they had been treated with formalin, in 50 per cent ethanol if killed in P. F. A. and in several changes of 50 per cent ethanol containing a trace of iodine if fixed with Helly's fluid. All specimens were stored in 70 per cent ethanol until needed. An additional solution was used to kill and fix 11 specimens of <u>Elassoma</u> <u>zonatum</u>. These small fish were placed alive in a ten per cent formalin solution containing small amounts of the blue stain thionine. These specimens were stored in the fixing solution.

In addition to the specimens listed above, each of the following species were preserved in a saturated solution of table salt for use in skeletal work: <u>Micropterus</u> <u>dolomieui</u>, <u>M</u>. <u>punctulatus</u> and <u>M</u>. <u>salmoides</u>, all from the mouth of Little River, McCurtain County, Oklahoma; <u>Chaenobryttus</u> <u>gulosus</u>, <u>Lepomis</u> <u>cyanellus</u>, <u>L</u>. <u>megalotis</u>, <u>L</u>. <u>macrochirus</u> and <u>Pomoxis</u> <u>annularis</u>, all from Lake Texoma, Marshall County, Oklahoma;

Lepomis microlophus and *L. humilis* from Boomer Creek, Stillwater, Payne County, Oklahoma; *Centrarchus macropterus*, three specimens from Waterfall Creek south of Idabel, McCurtain County, and three from a small creek five miles south of Tom, McCurtain County, Oklahoma; *Pomoxis nigromaculatus* from Horse Creek, Afton, Ottawa County, Oklahoma; *Ambloplites rupestris* from the Illinois River east of Tahlequah, Cherokee County, Oklahoma; and *Lepomis auritus* from the Austin City Lake, Austin, Texas.

Sectioning, Staining and Mounting

The lachrymal component of the infraorbital canal was chosen for the purpose of studying the histological nature of the lateral-line system. This choice had its basis in a cursory observation of the external morphology of various members of the family in which it was noted that the lachrymal bone was present in all species concerned (many components of the lateral line are absent in one species or another) and that the bone was easily removed. After removing these bones from both sides of the heads of fixed and preserved specimens and immersing them for 48 hours in two per cent hydrochloric acid for decalcification, they were dehydrated and embedded in celloidin according to Walls (1932). This technique was modified slightly in the three species of *Elassoma* in which the entire head was removed and bilaterally split and processed. The specimens thus embedded were sectioned with a rotary microtome at five and ten microns thickness, the sections being stored in 90 per cent isopropanol. From these sections certain ones were visually selected by using a dissecting microscope and stained with Mallory's triple connective tissue stain and a modified Heidenhain's iron hematoxylin method (Moore, 1933). The sections were cleared in beechwood creosote and mounted in piccolyte, a synthetic resin.

Preparations for Studying External Morphology

Three of the thionine-treated specimens of E. zonatum and one skin from each of the following species, stained with borax carmine, erythrosine or phloxine, were mounted in piccolyte for survey of external neuromasts and location of canal organs; Elassoma okefenokee, E. evergladei, Lepomis cyanellus, L. gibbosus, Centrarchus macropterus, Micropterus dolomieui, Enneacanthus obesus, Mesogonistius chaetodon and Acantharchus pomotis. Observation of these specimens was augmented by inspection of formalin-fixed specimens.

With the exception of Acantharchus, of which only three specimens were available, the canal systems of three specimens of each species were dried by jets of air and injected with black India ink. This procedure greatly facilitates the study of canal courses and has been used to advantage in previous studies (Moore, 1956; Branson, in press; Illick, 1956). These observations were also augmented by inspecting non-injected, formalinized fishes.

The scales of the lateralis were studied by various means. In some instances they were observed in situ after injection of the canals with India ink. In other specimens, strips of skin, bearing the scales, were stained and mounted as in the skins discussed above, the latter also being used for this purpose. Further observations were made upon intact, formalinized specimens.

Skeletal Preparations

The specimens preserved in concentrated NaCl solution were gently boiled until the flesh fell away from the bones upon the touch of a dissecting needle or of the fingers. The lateral-line bones were removed one at a time, thoroughly dried, and marked for identification. Additional specimens were treated in the same manner, whether fresh or salt-preserved, whenever available. Dr. Kirk Strawn's large collection of centrarchid bones was used to augment our own collections for purposes of illustration.

To aid in proper orientation and identification, especially of the smaller osseous elements, one specimen of each of the more common species, and three to five specimens of those which were not available for dissection, were stained in toto by the alizarin method of Hollister (1934) as modified by Evans (1948). Some of the larger, more opaque species, such as *Archoplites interruptus*, *Micropterus notius* and *M. coosae*, had to be dissected before the deeply-placed elements could be discerned even after staining and clearing.

Concomitant with the osteological aspects of the project an attempt was made to borrow fossil centrarchids for study. However, as much of the material is in a very poor state of preservation this venture produced little results. Sixteen specimens of *Chaenobryttus kansasensis* Hibbard were made available by the Museum of Comparative Zoology, Harvard University, and two specimens of the same species plus two of *Pomoxis lanei* Hibbard by the University of Kansas. All of the above mentioned material, mostly crushed and otherwise deformed, was in slabs of the diatomaceous marl characteristic of the middle Pliocene rocks of Logan County, Kansas. These specimens are virtual topotypes, most of them being less than 100 mm. in standard length.

Counts, Measurements and Terminology

All measurements of histological preparations were made with a filar micrometer mounted on a compound microscope. Measurements of fishes and/or their parts were made with a pair of needle-nosed calipers and a steel scale calibrated to 0.1 mm.

Lateral-line scale counts always started with the first scale in the lateral series and continued caudad. The lateralis is termed complete if every scale in the series bears a tube; incomplete when the series ends anywhere short of the end of the hypural plate; and interrupted if there are intervals of scales in the series which do not bear lateral-line tubes, even if only single scales are involved.

The nomenclature herein utilized, in contrast to that of several other investigators, is not that of a single fellow worker. The names of the several neuromast lines are those of Sâto (1955a) and Stensiö (1947). The canal names are modified from Hubbs and Cannon (1935), Robins and Miller (1957), Illick (1957) and Branson (in press).

In deciding upon a method of notation for pore counts there are several factors to be considered. One of these, which prevents us from using the method of Hubbs and Cannon (op. cit.) is that the sunfish supratemporal canal is unlike that in Etheostominae. Another aspect that should enter into any method of notation is that of embryology. As has been seen, the lateral-line canals begin to form near the eye and spread both caudad and cephalad from this position. It would seem, then, that the most logical place to start counts would be somewhere in that region. Modifying this concept, however, is knowledge within any group under consideration. That is, pre-existing knowledge concerning the extent of development of canals and their pores will dictate where counts should start and end. Nonetheless, it should be possible for one to subjectively delimit the canals so that a method would be utilizable in any group of fishes within a certain order. This is attempted here for the order Perciformes. Since the lateralis system completes its development rather early in life, this notation should be as valid for small specimens (11.0 mm. or so) as for large adults.

The *cephalic lateralis* begins with the opening in the posterior edge of the upper end of the supracleithrum and extends to the point where the supratemporal canal exits. Its pores are numbered from the one in the posterior edge of the supracleithrum forward. When a pore is lacking in the canal system it is indicated thus by the interpolation of a "0" into the formula. The *supratemporal canal* extends dorsad from its junction with the cephalic lateralis. In sunfishes this canal is never complete, so the pore count starts with the dorsal-most pore and is continued to its ventral junction. The *postocular commissure* extends anteriad from the junction of the supratemporal to the *postocular sinus*; the latter term is discussed more fully in the text. The pore count begins at the posterior junction and ends with the sinus. If a pore arises directly from the sinus it is included in the count. The *infraorbital canal* extends from the postocular sinus to the anterior end of the lachrymal bone and its pore count starts with the first pore below the sinus and continues to the dorsal pore of the lachrymal. The *preoperculomandibular canal* begins in a junction with the postocular commissure and the cephalic lateralis and extends the length of the preopercle and, except in *Elassoma*, the articular and dentary bones. If this canal is not connected at the junction mentioned above the formula begins with (IN) 1. If it is joined, but a pore occurs at the junction, then the junction pore is indicated by (JP). The supraorbital commissure is always complete, except in *Elassoma*, and begins in a coronal pore (CP) on the midline and extends to a junction with the supraorbital canal, its pore count starting with the coronal and continuing to the supraorbital junction. The supraorbital canal proper extends anteriad from the postocular sinus onto the snout where it ends. The pore count for this last canal begins with the first pore anterior to the postocular sinus and continues to the last one on the snout. Ectopic pores occasionally appear and some specimens abnormally lack certain pores. These will be noted in the text. Most of these terms are illustrated in Text Figure 1.

Methods of Illustration

Several kinds of illustrative materials have been prepared: some are simple, unscaled, line drawings; others are stippled line drawings made by freehand methods, using a pair of calipers to obtain proper proportions. All of the bone drawings were made to scale by the last method and shaded with hard charcoal. All drawings of histological preparations were made with a camera lucida mounted on a compound microscope.

CHAPTER III

OBSERVATIONS

During the investigations requisite to a clear understanding of the lateral-line system in the 29 species of sunfishes herein considered, a large amount of information has been gleaned. This mass of details, for the sake of logical order, is presented under three captions: external morphology, osseous components and histological morphology. Under each caption one species is described in detail and followed by a comparison with other members in the family and with members of other taxa.

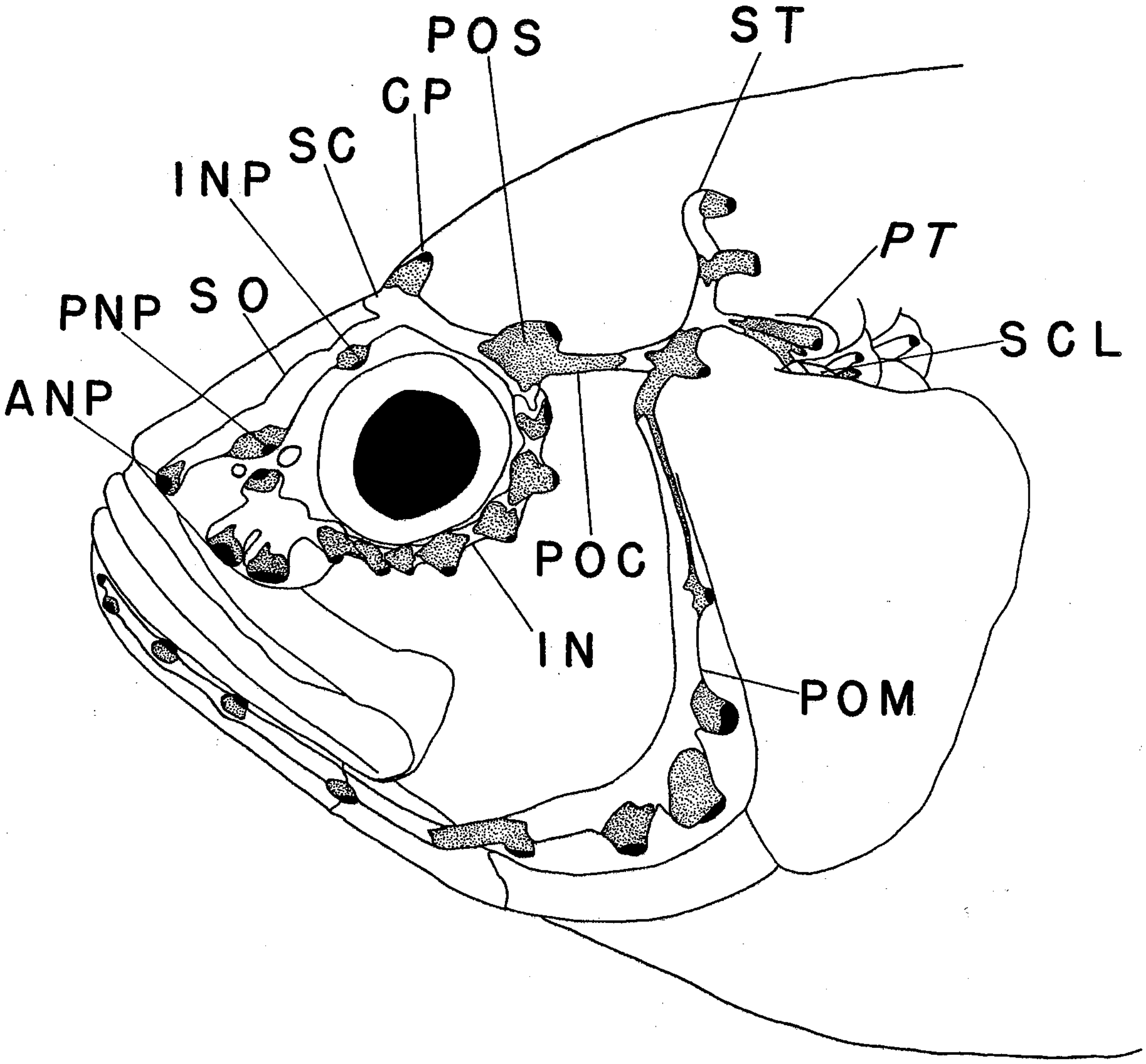
External Morphology: Canal Systems

Chaenobryttus gulosus. Text Figure 1. This species was chosen as a prototype for description for several reasons. Its morphology is probably near that of the ancestral lepomine stock (Bailey, unpublished), but *Archoplites* or *Ambloplites* would have been equally logical, or, in some respects, a more logical choice.

As pointed out in the section concerning terminology, the cephalic lateralis is a relatively short canal which extends from the posterior edge of the upper end of the supracleithrum to a point where the supratemporal canal is given off dorsally. This canal is the connecting piece between the lateralis proper and the cephalic canals, the point of union being made between the surpacleithral opening and the first scale of the lateralis. From this point the canal is directed diagonally upward and forward to the junction with the supratemporal. The connection with the lateralis will be described in detail below, but an open pore is usually lacking at this point. The only two pores occurring in this canal are at the ends of two rather short, posteriorly-directed tubes of connective tissue (Text Fig. 1). These connective tissue tubes are termed "external canaliculi" (Tretyakov, 1938) because they are not enclosed in bone or scales. The pore formula for this canal is 2 (0 + 2 + 0). The "2" in front of the parenthesis refers to the bilateral nature of the system.

The supratemporal is a relatively abbreviated canal, which is slightly sigmoid in shape, bearing two round pores at the tips of caudally-directed canaliculi. The canal proper, in this species, is covered by scales, between which the external canaliculi exit onto the skin. The pore formula is 2 (1 + 1). Connection is made with the postocular commissure and the preoperculomandibular canal at a junction in connective tissue, actually a sinus, where another posteriorly-directed canaliculus is formed (Text Fig. 1). As already stated, when such a pore occurs it is by definition a part of the preoperculomandibular system.

The preoperculomandibular canal, as it leaves the above-mentioned sinus, becomes narrow but progressively increases in diameter until a point near the middle of the preopercle is reached. Anteriad from this area the canal very slowly decreases in diameter, becoming constricted at the anterior end of the preopercle where it is suddenly deflected downward for a short distance (when the mouth is closed), then diagonally extends the length of the mandible. The angularly-deflected portion of the canal is not enclosed in bone but in connective tissue which forms a flexible connecting piece, allowing the canal to straighten when the mouth is opened. The formula for this canal is 2 (JP1 + 10). All



Text Figure 1. External Morphology of the Lateral-line System in <u>Chaenobryttus</u> <u>gulosus</u>. Standard length 118.5 mm. ANP, anterior nasal pore; CP coronal pore; IN, infraorbital canal; INP, interorbital pore; PNP, posterior nasal pore; POC, postocular commissure; POM, preoperculomandibular canal; POS, postocular sinus; PT, posttemporal; SC, supraorbital commissure; SCL, supracleithrum; SO, supraorbital canal; ST, supratemporal canal. India-ink injection.

of the pores are at the ends of short canaliculi, except the anterior-most one, which opens directly forward near the symphysis of the dentaries. Canaliculi seven and eight are positively deflected (toward the head); all of the others are negative.

The postocular commissure, with pore formula 2 (0 + 1), becomes increasingly narrowed from its origin at the supratemporal-preoperculomandibular junction. In India ink-injected specimens it appears as a very narrow black line. This is a very short tube which enters the enlarged postocular sinus just behind the eye. This sinus is externally covered only by skin and connective tissue. An inflated, caudally-directed canaliculus arises from it and bears a smallish, round pore at its tip.

Two other canals, the supraorbital and the infraorbital, find origin in the postocular sinus. From the junction with the postocular sinus the supraorbital canal, 2 (0 + 3) follows the curvature of the head downward until it ends on the snout just behind the lip sulcus. The canal maintains a relatively constant diameter until the middle of the eye is reached where it is suddenly constricted. Just in front of this constriction a laterally-directed canaliculus is given off, the interorbital canaliculus, which bears a very small round pore near the orbit. Distal to the interorbital pore the canal assumes a diameter very nearly that of its portion near the origin and curves downward and slightly laterad. Near the posterior nostril the canal opens into a vacuity covered by connective tissue. A very short canaliculus (posterior nasal canaliculus) arises from this sinus which opens in a small pore near the posterior nostril. In front of this canaliculus the canal decreases in diameter and bends gently laterad to end in a pore opening directly from the end of the canal. Near the posterior border of the eye the supraorbital gives off a mesially-directed branch which nearly meets a similar branch from the opposite side of the head. On the midline these two branches open into a sinus which gives rise to an unpaired, caudally-directed canaliculus ending in the small, circular, coronal pore. This is the only canalular connection between the right and left sides of the body. The supraorbital commissural arms never bear additional pores so there is no need for a formula.

The infraorbital canal, formula 2 (10), is also complete, with lateral walls composed mostly of connective tissue and presenting an aspect similar to a pea pod in which there are strong constrictions between each pea. Here the constrictions lie between each external canaliculus, canaliculi eight and nine being the longest in the series. All of the canaliculi are directed away from the eye. The infraorbital ends in front of the eye in a small pore directed toward an area between the nostrils. All of the pores in the infraorbital series are small and nearly round except the slit-like ones of canaliculi eight and nine.

In general, the external canaliculi are triangular in shape, the pores occupying the apex of the triangle. The exact positions of the canaliculi are best understood when the osteological components, discussed below, are known.

The lateralis, communicating with the cephalic canals via an opening in the supracleithrum, begins in a lateral-line scale located about two-thirds the width of a single scale below the posterior end of the posttemporal, about seven or eight scale rows below the middorsum. It usually is not completely covered by the "ear flap" and is obviously modified in relation to the other scales near it. It is smaller than other scales of the lateral-line series and those of the general body. The course of the lateralis is delineated as follows: from the connection with the supracleithrum it curves dorsad, for five or six scales, to a point seven scale rows below the origin of the dorsal fin then gently curves caudoventrad to a point three or four scales behind the posterior margin of the dorsal fin. Three or four scale rows below the middorsum of the caudal peduncle the line is directed in very nearly a straight line, ending on the penultimate or ultimate large scale in the lateral series. This point lies over the end of the hypural plate. Normally every scale in this series is pored, completing the lateralis. Occasional specimens may lack one or two pores on one side or the other.

The lateral-line tubes borne by the scales are straight-sided or very slightly lagenated distally. The external canaliculi are very short and normally directed along the axis of the mother tube. In very few instances were any of these found to be deflected from the major axis.

Comparison of C. gulosus with Other Centrarchids

Cephalic Canals. The general course of the lateral-line canals is identical to that described for Chaenobryttus in all of the centrarids except Elassoma, which will be discussed presently. There are, however, many variations to be seen from genus to genus and within genera. It seems best to discuss these differences in related groups rather than cover the family as a whole.

Centrarchinae--Amblopiitini. This taxon includes three genera and four species, Ambloplites rupestris, A. cavifrons, Archoplites interruptus and Acantharchus pomotis (Pl. I, Figs. 4, 5 and 6). The lateral-line canals are about as capacious as those in the warmouth. In Chaenobryttus the posterior edge of the supracleithrum is not notched at the junction with the lateralis. In *Ambloplites* and *Archoplites* there is a slight notch at this point; in *Acantharchus* the supracleithral junction is like that of the warmouth. There are, however, marked differences in the cephalic lateralis. The pore formulae for the latter three genera are as follows: *Ambloplites*, 2 (0 + 2 + 1); *Acantharchus*, 2 (0 + 1 + 0 + 1); and *Archoplites*, 2 (1 + 2 + 1). In *Ambloplites* and *Acantharchus* there is no opening at the posterior edge of the supracleithrum. In *Archoplites* and *Ambloplites*, as in the warmouth, there are two posteriorly-directed canaliculi. In *Acantharchus* there is a single canaliculus which is comparable to the ventral-most component of the two in other species. As noted above in the formulae and in Figures 4, 5, and 6 (Pl. I), there is an element present in these three species which was not seen in *Chaenobryttus*. This is a ventrally-directed canaliculus near the anterior end of the cephalic lateralis. In 18 examined specimens of the rockbass, one specimen, 117 mm. in standard length, lacked the fourth canaliculus on the right side. The cephalic lateralis is slightly longer in these three species as compared with that of the warmouth and nearly lacks lateral hard walls in *Ambloplites* and *Acantharchus*. In *Archoplites*, only the canaliculi are composed of connective tissue and in *Acantharchus* the cephalic lateralis is covered by large scales.

The supratemporal canal and external canaliculi are essentially like those in *Chaenobryttus*. In *Ambloplites* the canal is composed mostly of connective tissue laterally, whereas in the other two genera it contains considerable bone. In *Acantharchus* the supratemporal canal, except the external canaliculi, is covered by scales.

Observation of the preopercular elements disclosed some further differences. The canal begins at the same junction as that of the warmouth.

It will be noted in the figures that where two or more canals meet, or where external canaliculi are given off, an enlarged area covered by connective tissue is formed. This is true in all of the centrarchids and of fishes in general (Allis, 1904). Comparing the preoperculomandibular canal formulae for these three species we find the following: Ambloplites, 2 (JPl + 12); Acantharchus, 2 (JPl + 12); and Archoplites, 2 (IN 1 + 1 + 11). In Chaenobryttus, which has a complete preoperculomandibular and junction pore, as in Ambloplites and Acantharchus, the first canaliculus, below the junction, is formed about one-third the length of the ascending arm of the preopercle below the upper end of that bone. In Acantharchus and Ambloplites a short canaliculus is directed backward immediately below the junction canaliculus and a second one very near the upper end of the preopercle. In Archoplites the canal is not joined at the junction, therefore it is termed incomplete. Near the position where the first canaliculus is formed in Acantharchus and Ambloplites a small canaliculus extends dorsally for a short distance then turns caudad and ends in a tiny round pore. A second canaliculus, immediately above this, opens directly downward at a point where the preopercular canal would attach if complete. The junction pore and tube are about in their normal position, and the remaining tubes and pores are homologous to those found in Acantharchus and Ambloplites.

The postocular commissure is a term recently introduced (Branson, in press) as a name for the connecting canal between the junction of the preopercular, supratemporal and cephalic lateralis canals and the postocular sinus. The reason for this introduction was simply to avoid use of the confusing terms "lateral canal," "posterior end of the infraorbital canal," and other such terms. The term "postocular sinus" was introduced in the same work for the enlarged vacuity contained in connective tissue where the infraorbital, postocular commissure and supraorbital canals meet. This term refers to the same structure called the "tympanic receptacle" by Tretyakov (1950), which may lead to some confusion because of the word tympanic.

In general, the configuration of the postocular sinus in these three genera agrees with *Chaenobryttus*. However, in *Archoplites* the canaliculus of the postocular sinus opens on the ventral side of the commissure rather than dorsal to it and, in the three specimens available of *Acantharchus*, there was a minute canaliculus, possibly ectopic, opening anteriorly from the postocular sinus and deflected toward the eye (Pl. I, Fig. 5). The postocular canal of *Acantharchus* and *Ambloplites* contains very little bone in its lateral walls, but in *Archoplites* the central part of the canal is composed of osseous material.

The infraorbital canalicular formulae for members of this tribe are: *Ambloplites*, 2 (6 + 1 + 0 + 1 + 3) (occasionally complete with ten pores); *Acantharchus*, 2 (9); and *Archoplites*, 2 (5 + 1 + 0 + 0 + 1 + 3). In *Ambloplites* and *Archoplites*, as shown in the formulae, the infraorbital canal is incomplete, the break occurring between pores 7 and 8. In *Ambloplites* canaliculus 7 has been lost and in *Archoplites* both 6 and 7 have disappeared. There are terminal pores on both sides of the interruption. Although the infraorbital has remained complete in *Acantharchus*, there seems to have been a loss of canaliculus 6.

The supraorbital and supraorbital commissure are essentially as in *Chaenobryttus*. In one of 18 specimens of *Ambloplites* a minute ectopic canaliculus occurred at the point where the supraorbital begins to curve around the orbit. In one of three specimens of *Acantharchus* there was a very short canaliculus, probably ectopic, directed anteriorly from the junction of the two supraorbital commissural canals.

Centrarchinae--*Centrarchini*. The tribe Centrarchini contains *Centrarchus macropterus* and the two species of *Pomoxis* (Pl. I, Figs. 1, 2, and 3). The external morphology of the canal systems are, again, similar to that of *Chaenobryttus* and to the members of the Amblopltini. The supracleithrum is deeply notched posteriorly and opens in a pore in *Pomoxis*, but is smooth and poreless in *Centrarchus*. The pore formulae for the cephalic lateralis in *Centrarchus* is like that of *Ambloplites* and is the same as *Archoplites* in *Pomoxis*. All of these formulae differ from that of *Chaenobryttus*. The external canaliculi, in addition to being arranged differently, are also slightly larger. Furthermore, pore 4 opens directly from a connective tissue sinus in the flyer and the black crappie rather than being at the ends of canaliculi. However, this is rather variable and short tubules do appear frequently in both species at this point (28 of 100 *P. nigromaculatus* and 6 of 31 *Centrarchus*).

The supratemporal is like that of the previously discussed species. The dorsal-most canaliculus is occasionally strongly deflected ventrally in *Centrarchus* (Pl. I, Fig. 2). In the last-named species the supratemporal excluding the external canaliculi is always covered by scales.

The preoperculomandibular canal in this group is characterized by the following pore formulae: *Centrarchus*, 2 (JP1 + 10); *Pomoxis nigromaculatus*, 2(JP1 + 10); and *P. annularis*, 2 (IN 1 + 1 + 10), which, excluding *P. annularis*, is identical to that of *Chaenobryttus*. At the upper end of the canal, near the point of union with the junction, a pinhole-like pore, which is inconstant in position, often occurs in all three species, but may be absent on one side while appearing on the other. In P. annularis, where the canal is incomplete (one of 25 specimens had the canal complete on the left side), the junction canaliculus and pore are normal in position and a slight canaliculus and pore occur at the upper end of the incomplete part of the canal. Pore 6 is directed dorsally rather than ventrally as in the warmouth and in all Centrarchini.

The postocular commissure is like that of Chaenobryttus except that the anterior canaliculus is lacking in most specimens of P. nigromaculatus, the pore thus opening directly from the postocular sinus. In 3 of 25 P. annularis a tiny pore opened from the lateral wall of the commissure (Pl. I, Fig. 1).

The infraorbital canal is interrupted in all three species, differing from the complete condition in the warmouth. The formulae are: Centrarchus, 2 (4 + 1 + 0 + 0 + 0 + 1 + 3); P. nigromaculatus, 2 (4 + 1 + 0 + 0 + 0 + 1 + 3); and in P. annularis, 2 (3 + 1 + 0 + 0 + 0 + 0 + 1 + 3). Centrarchus and P. nigromaculatus have lost three canaliculi whereas the white crappie has lost four during the process of reduction. The external canaliculi of Pomoxis are very short and the pores often open directly into the canal walls. In one specimen of P. nigromaculatus pore 10 was double.

The supraorbital canal and its commissural branches are like those discussed above except that the posterior end of the main canal and the commissures are much more deeply covered by muscle. This, of course, is in consequence of the gibbous body. The coronal canaliculi are also lengthened as a result of the deeping of this part of the body, a general feature of gibbous centrarchids.

Lepominae--Lepomini. (Pls. 1 and 2; Figs. 7, 8, 9, 10, 11, 12, 13, 14, 15 and 16; Text Fig. 1). There are two genera, Chaenobryttus (already described) and Lepomis, and eleven species included in this tribe.

The cephalic lateralis pore formula given for the warmouth is the same for only Lepomis punctatus and L. megalotis. In L. punctatus the entire supracleithrum and the ventral half of the posttemporal are covered by the opercular flap. Neither a notch nor a pore is found at the posterior edge of the supracleithrum in any member of the tribe. In the rest of the tribe there are two cephalic lateralis formulae: 2 (0 + 0 + 1 + 0) and 2 (0 + 2 + 1). The first of these is found only in L. symmetricus, which possesses only the dorsal component of the two posteriorly-directed canaliculi seen in Chaenobryttus (Pl. I, Fig. 8). The remaining seven species possess a cephalic lateralis corresponding to the second formula, although Moore (1956) indicated only a single posterior pore in L. humilis, L. cyanellus and L. macrochirus and a tube through the supracleithrum was not seen. The last-named formula, it will be noted, is identical to that of Ambloplites. In L. marginatus, L. cyanellus and L. gibbosus pore 4 is normally very tiny and occasionally may be lacking on one or both sides of the head; it opens directly into the canal wall. In L. microlophus, L. humilis, L. auritus and L. macrochirus the pores are at the ends of ventrally-directed, short, canaliculi, but are sometimes directed upward on one or both sides of the fish. The supratemporal canal is like that of Chaenobryttus except that it is strongly tilted forward in the deep-bodied species. In one of 100 L. macrochirus a third, ectopic canaliculus was observed (Pl. II, Fig. 14) and in one specimen of L. megalotis breviceps (one of 27) two short, anterodorsally-directed ectopic canaliculi were observed (Pl. II, Fig. 9). The canal is covered by scales only in L. punctatus and Chaenobryttus.

The interrupted nature of the preoperculomandibular canal noted by Moore (1956) in L. humilis occurs normally only in that species. In all other *Lepomis* the canal is complete. The pore formula given for the warmouth also applies for *L. macrochirus*, *L. punctatus* and *L. marginatus*. A very tiny, anteriorly-directed tube was noted in one bluegill (Pl. II, Fig. 14). There are three other formulae normally found in this tribe: 2 (IN 1 + 1 + 10); 2 (JPl + 11); and 2 (JPl + 12). From what has been said the first of these obviously belongs to *L. humilis*; the second formula illustrating the condition in *L. megalotis*, *L. auritus*, *L. microlophus* and *L. cyanellus*. The extra canaliculus has arisen at a point just below the origin of the junction canaliculus. In addition to the normally-occurring tubes and pores an anteriorly-directed ectopic tube lying near the preoperculomandibular-postocular commissure junction is seen in about one of each 50 specimens of *L. microlophus*. In specimens of *Lepomis cyanellus* which are 11.0 to 25.0 mm. in standard length a posteriorly-directed canaliculus is intercalated between the junction pore and the first preoperculomandibular pore (Pl. I, Fig. 7). By the time a fish attains a size of 75.0 to 100.0 mm. in length the tube and pore have both disappeared. *Lepomis gibbosus* and *L. symmetricus* both possess preoperculomandibular pores which are represented by the third formula above. Two extra canaliculi, then, have been added over the same system in *Chaenobryttus*. One of these is located near the junction pore and the other is found near the upper end of the preopercle.

In all of the species of *Lepomis*, except *L. humilis*, the next to the last and third from the last pores (numbers 7 and 8 of *Chaenobryttus*) are directed toward the lip. In *L. humilis* the next to the last two (number 8 and 9 of the warmouth) are so directed. Moore (1956) indicated that all of the preoperculomandibular tubes and pores were directed away from the lip in all three of the species mentioned above.

There are only two postocular commissural formulae in this tribe: 2 (0 + 1) in Chaenobryttus, L. symmetricus, L. gibbosus, L. marginatus, L. humilis and L. cyanellus; and 2 (1 + 1) in L. punctatus, L. megalotis, L. auritus, L. microlophus and L. macrochirus. In one specimen of L. microlophus, a blindly-ending tube was formed near the junction of the commissure with the supratemporal and in L. punctatus a third ectopic canal is often (12 of 100) seen near the postocular sinus. Moore's (1956) observations are in accord with those described above.

As in the last-described portion of the canal system there are two formula types found in the supraorbital canal. The one exhibited by L. symmetricus, L. macrochirus, L. cyanellus and L. humilis is 2 (0 + 3), as in Chaenobryttus. In L. gibbosus, L. marginatus, L. microlophus, L auritus, L. punctatus and L. megalotis the pore formula for this canal is 2 (1 + 3), which is different than any species thus far discussed. The placement of the posterior canaliculi varies slightly from one species to the next. In 100 specimens observed from Horse Creek, near Afton, Ottawa County, Oklahoma, 33 L. humilis possessed a slender canaliculus (not observed by Moore, 1956) directed rostrally from the anterior edge of the sinus connecting the two supraorbital commissural canals (Pl. II, Fig. 16). The coronal pore and commissural canals are otherwise as in the warmouth.

It is possible to write five different formulae for the infraorbital canal in the Lepomini. Five species, L. cyanellus, L. gibbosus, L. marginatus, L. auritus and L. punctatus possess the same formula as Chaenobryttus, 2 (10). In L. auritus, one specimen of 37 observed had a small ectopic, dorsally-directed canaliculus (Pl. II, Fig. 11) located between canaliculus five and six. One other species, L. megalotis, has a complete infraorbital canal, but a different pore number than those discussed above. The pore formula for this species, 2 (13), obviously represents specialization since, if one counts only the normal-sized tubules the pore count would be the same as the other six members with a complete infraorbital canal. Three, very small canaliculi have been added, one between pore 1 and 2, one between 2 and 3 and one between 6 and 7. It is not known how constant this condition is from one population to another. Our specimens were mostly all L. m. breviceps and an unnamed subspecies from northeastern Oklahoma. There are three possible, usual formulae in species which possess an interrupted suborbital series. In L. symmetricus and L. macrochirus the formula is 2 (5 + 1 + 0 + 0 + 1 + 3), indicating the loss of canaliculi 6 and 7. The bluegill, in about 25 per cent of the specimens, sometimes has a second interruption occurring between tubules 4 and 5 so that the infraorbital has three segments instead of two. Moore (1956) illustrated the bluegill as having a complete infraorbital, but the canal was definitely interrupted in over 100 specimens observed in this study. Lepomis microlophus has apparently lost only canaliculus 7 as its pore formula is 2 (6 + 1 + 0 + 1 + 3). In one instance the terminal end of the proximal segment had a second small pore (Pl. II, Fig. 13). Lepomis humilis has lost three external canaliculi, 5, 6 and 7, but this is not so apparent at first glance because of the inflated nature of the canal system in this species. The terminal pore of the proximal segment is often doubled (Pl. II, Fig. 16), but the formula 2 (4 + 1 + 0 + 0 + 0 + 1 + 3) does not take this into consideration because the double condition is actually only a subdivision of a single opening and is not constant.

Lepomis humilis is an abberant member of this series in that most of the lateral-line pores, with the exception of the lachrymal component, are very large and slit-like, whereas other Lopominae have rounded pores. Bailey (unpublished) has also noted this condition. In fact, all of the canals are so enormously inflated that Hubbs (Ortenburger and Hubbs, 1927) erected a new genus (Allotis) for this species on the basis of the large head canals. The width of one of the supraorbital canals is greater than the distance between the two canals. Moore (1956) has also commented upon these large canals, inferring that they were an adaptation for living in the muddy waters of the Great Plains. The last author's pore counts for the infraorbital are in agreement with those made herein. The entire cephalic canal system of L. humilis possesses very little bone in the lateral walls, being covered instead with connective tissue. In certain populations (Curd, 1959) the lateral-line canals lose even the connective tissue covering and appear as open grooves.

Lepominae--Micropterini. (Pl. III, Figs. 17, 18, 19, 20, 21 and 22). This tribe includes the six species of Micropterus, the blackbasses. The most obvious characteristic of the canal system in an adult Micropterus, when compared with the other members of the family, is the small diameter of the canals. Furthermore, the external canaliculi are very long and slender (much longer than the width of the canals which emit them), and the pores are comparatively minute.

The cephalic lateralis and supratemporal canals bear the same number of pores as in Chaenobryttus, with some individual variation. One specimen of M. notius possessed a small opening into the canal at about the position of pore 4. One of the few available specimens of M. coosae, in addition to possessing this ectopic pore, had only a single posterior canaliculus in the cephalic lateralis. This last-named canaliculus corresponds to the dorsal component.

As far as the preoperculomandibular system is concerned there are two groups found in *Micropterus*, those corresponding to *Chaenobryttus* and those which have the formula 2(JPl + 11). Only two forms, *M. dolomieui dolomieui* and *M. punctulatus*, fall into the first group. The second formula characterizes *M. dolomieui velox*, *M. coosae*, *M. notius*, *M. treculi* and *M. salmoides*. The extra canaliculus, as seen above for *Lepomis megalotis*, is formed just below the junction pore. This pore is usually not borne at the end of a canaliculus in *M. notius* but opens instead directly into the connective tissue connecting piece between the preopercle and the postocular commissure. In one specimen each of *M. salmoides* and *M. dolomieui* (Pl. III, Figs. 17 and 22) the third from the last pore was directed away from the lip instead of toward it.

In the specimens observed during this study it was again possible to divide the Micropterini into two groups based, this time, on postocular commissure morphology. Three species are similar to *Chaenobryttus* (*M. dolomieui dolomieui*, *M. salmoides* and *M. notius*) and four species, *M. dolomieui velox*, *M. punctulatus*, *M. coosae* and *M. treculi*, have the same formula as *Lepomis auritus*. *Micropterus coosae* and *M. dolomieui* are extremely variable in this respect, about 50 per cent of the specimens falling into the first category.

The general plan for the supraorbital and its commissural branch described for the warmouth is found in the basses. The interorbital pore, however, is located at the end of a relatively long, slender, external canaliculus which is strongly deflected caudad. In all species a small directly-entering pore is occasionally seen near the junction of the commissural arm. An ectopic, anteriorly-directed tube, similar to the one described in *Lepomis humilis*, arises from the coronal sinus in one largemouth bass.

The infraorbital canal is complete in all six species and the basic plan of Chaenobryttus is found in M. treculi, M. punctulatus, M. salmoides and M. coosae. One specimen of M. coosae was found to possess an abnormal lachrymal opening (Pl. III, Fig. 21) which caused an additional canaliculus to appear. Micropterus dolomieui and M. notius were again found to be extremely variable. These two species ranged from nine to 11 canaliculi and pores per side. This condition also varied from side to side in a single specimen, one side having 11, the other nine, ten or 11. The single formula which seems to be the most prevalent is 2 (9), or one tube less than Chaenobryttus and two less than the other members of the bass tribe.

Lepominae--Enneacanthini. (Pl. III and IV, Figs. 23, 24 and 25). This tribe, comprised of Enneacanthus gloriosus, E. obesus and Mesogonistius chaetodon, possess several specializations not seen elsewhere in the family. The cephalic lateralis is like that of Acantharchus in having only the single posterior canaliculus. This element, instead of being a straight tubular structure, is bulbously inflated and occupies nearly the whole width of the posttemporal. In Mesogonistius (Pl. IV, Fig. 25) a pore often occurs at the posterior edge of the supracleithrum. One specimen of E. obesus lacked any sign of a posterior opening in the cephalic lateralis. The supratemporal canal exhibits the same pore condition as other centrarchids, but it is a relatively larger canal than seen in the others, with the possible exception of L. humilis. The supratemporal and cephalic lateralis, except the external canaliculi, are completely covered by scales in all three species.

The preoperculomandibular canal, 2 (JP1 + 8), is likewise different than that of any of the other centrarchids. The loss of the canaliculus corresponding to number 8 in Chaenobryttus seems to have occurred so that there is only a single canaliculus directed toward the lip on the mandibular arm. The other loss was probably the tube corresponding to number 1 of Chaenobryttus. The preopercular portion of the canal is covered by scales between the external canaliculi in all three species.

The postocular commissure is characterized by the same formula as that of the warmouth. It is extremely short in Mesogonistius, nearly completely enclosed in bone in all three members of the tribe, and is covered by scales in the two species of Enneacanthus.

The supraorbital canal is difficult to characterize in this tribe because of extreme variation. It is interrupted in all three species, but the amount of interruption is seldom the same from specimen to specimen or from side to side. The anterior segment of the canal is, however, morphologically constant and differs drastically from all other centrarchids. In other sunfishes, except Elassoma, there are two anteriorly-directed pores in the lachrymal segment but in the Enneacanthini there is only one. This will be better understood when the osteology is compared. In all specimens observed the proximal portion of the canal extends downward past the middle of the eye in M. chaetodon and E. obesus, both having at least three pores, two canaliculi directed away from the eye and an anterior terminal pore. About 50 per cent or more of the Florida specimens of M. chaetodon had five tubes (Pl. IV, Fig. 25), four laterals and the terminal one. Bailey (1941), in his discussion of the geographic variation of M. chaetodon, did not consider the lateral-line system beyond stating that the head canals were "fairly well-developed." Over half of the specimens of E. gloriosus had only a single pore at the posterior margin of the eye. Some specimens (Pl. IV, Fig. 24) have a brief tube a short distance below the one mentioned above, and in a few individuals the canal is continuous to just below and behind the middle of the eye.

Elassominae. (Text Figs. 2, 3 and 4). This is a peculiar group of fishes which has unfortunately been retained as a member of the Centrarchidae. Three species are presently recognized and a fourth is in the offing (personal communication, Böhlke). All of the species examined, Elassoma zonatum, E. evergladei and E. okefenokee, are nearly identical in their lateral-line morphology, the resemblence to that of the true sunfishes being very slight. The process of reduction has been extreme and the canals which are left are relatively large, being composed mostly of connective tissue.

The cephalic lateralis and supratemporal canals are represented by straight tubes which bear terminal pores. There are no external canaliculi, unless one wishes to term the canals such. The preoperculomandibular canal, a misnomer in this instance, could be represented by the following formula: 2 (IN 1 + 1 + 0 + 0 + 3 + 0 + 0 + 0 + 0 + 0). This, compared with Chaenobryttus, would mean that the first two and the last five pores of the canal have disappeared. There is, then, no mandibular component in Elassoma.

The postocular commissure is a straight tube which does not bear external pores or canaliculi, nor do such arise from the postocular sinus.

The infraorbital is greatly interrupted, consisting only of a short tube behind the eye and the lachrymal component in front of the eye (Text. Fig. 2). As will be noted in the figures, the lachrymal differs from that of all other species in the Centrarchidae in lacking anterior canaliculi.

The supraorbital canal is also strikingly different although it roughly follows the same course as in the other species. There is no interorbital canaliculus and the commissure is never complete. There are two rather large terminal pores, one from either commissural branch, directed toward the midline of the fish (Text Fig. 4). The two nasal pores are rather normal in position except that the posterior nasal pore is in the posterior nostril. This has not been observed, at least not recorded in the literature, in any other fish. The supraorbital canals, actually the whole dorsal part of the head (Böhlke, 1956), is covered by scales in *E. evergladei*.

Lateralis

The lateralis is the conspicuous line that usually extends along the sides of the body in most fishes. As has been intimated above, it communicates with the cephalic system through the upper end of the supracleithrum, a fact that has very often been overlooked in perciform fishes by recent investigators. Most authors illustrate the lateralis as being a posterior continuation from the dorsal or ventral canaliculus of the cephalic lateralis. It is also common practice to speak of the scales in the lateralis as the "lateral series," which may lead to some erroneous conclusions.

The scales of the lateralis bear small tubes of varying shapes and lengths according to the group observed. These canals are not isolated entities but are connected to one another by certain linking mechanisms and by connective tissue similar to that which imparts continuity to the cephalic canals. As in the cephalic system there may be varying degrees of interruption or incompleteness. There may be, as shown below, some lateral-line scales which are isolated from the others.

In a typical centrarchid lateralis scale, such as the one seen in Fig. 27 (Pl. IV), it is seen that the neuromast (here represented by a stippled area) occupies approximately the center of the tube, implanted on the proximal wall. The tube is rather lagenate, or ampulla-like in shape, being smaller posteriorly than anteriorly. There are usually three openings per scale: an anterior and a posterior, terminal one opening on the outer surface and a subterminal one opening through the scale to the inner surface. Ectopic openings may occur anywhere on the scale and there may also be abnormal scales which have only two, one or no pores in the canals. There is usually a slight depression close to and paralleling the lateral-line tube for its entire length. The apical or anterior end of each lateral-line tube is peculiarly modified (Pl. IV, Figs. 26 and 28) to form a firmly united socket with the scale immediately anterior to it. The flat plate slips under the anterior scale and the elevated spinous processes fit into a pair of socket-like structures located near the pore which opens on the inner side of the scale. Thus, the scales are rather rigidly held to each other. Furthermore, the connective tissue lateral-line canal, which passes into the scale tube through its lateral surface and out through the proximal surface, insures continuity from scale to scale. The connection is achieved by the anterior pore being placed nearly directly under the inner opening of the subterminal pore of a preceding scale (Pl. IV, Fig. 28).

Apparently external canaliculi of the lateralis in North American fishes have never been discussed. These tiny tubules are of the same nature as those of cephalic canals, i. e., contained in the skin alone.

These usually originate from each scale canal at the posterior end, where two scales overlap and may be directed along the major axis of the lateral series as in *Chaenobryttus* (Pl. IV. Fig. 27) or be deflected from the axis as in *L. Gibbosus* (Pl. IV. Fig. 28). The canaliculi open to the exterior by a small round pore. The length, diameter and general configuration of the external canaliculi are variable, but the picture for a given species is fairly constant. The external canaliculi of the Centrarchini, Micropterini and *Enneacanthus obesus*, *Lepomis symmetricus*, *L. macrochirus*, *L. humilis* and *L. marginatus* are similar to those of *Chaenobryttus*, whereas the other centrarchids, except *Elassoma*, which lacks lateralis tubes completely, bear canaliculi that exhibit some variation of the condition found in *L. gibbosus*. In *L. microlophus* the canaliculi range from very short to longer than the main tube and are nearly always deflected upward. Some of the tubes may be bent back so as to be directed toward the head. Most of those in *L. cyanellus* are quite short and usually deflected ventrally, but occasional tubes appear which are dorsally-directed. There does not seem to be any particular pattern of arrangement in *L. megalotis*, *L. auritus*, *L. punctatus*, *Enneacanthus gloriosus* and *Mesogonistius*, the tubes following a course in either direction from one scale to the next. The canaliculi are usually very short in the first three of the last-named species and about one-half the length of the main tube. They are deflected at about a 90° angle from the main canal in the last two.

Course of the Lateralis Proper. It is possible to divide the Centrarchidae, if the Elassominae are included, into four groups based upon the gross morphology of the lateralis, as seen in Table 1. There is no need for discussion of the Elassominae as the lateralis is lacking. The tabular rubrics shown below, are relative.

TABLE I

COMPARISON OF THE RELATIVE MORPHOLOGY OF THE LATERALIS IN THE CENTRARCHIDAE

Complete	Interrupted	Incomplete
A. rupestris	L. symmetricus	E. obesus
A. interruptus	L. megalotis (in part)	E. gloriosus
P. nigromaculatus	L. cyanellus (in part	A. pomotis
P. annularis (in part)	P. annularis (in part)	L. megalotis (in part)
C. macropterus		
L. punctatus		
L. macrochirus		
L. humilis		
L. marginatus		
L. auritus		
L. microlophus		
L. gibbosus		
L. cyanellus		
L. megalotis (in part)		
Micropterus		
M. chaetodon		

As is true in all of the species with a lateralis, the first scale is a modified one. Its position is always the same, i. e., just below the posterior end of the posttemporal abutting the supracleithrum. In Chaenobryttus this point lies seven or eight scale rows below the middorsum, but this varies with the scale size in individual species. In Ambloplites rupestris it is 13 to 14 rows; Archoplites, 11 or 12; in P. nigromaculatus, Lepomis punctatus, L. gibbosus, L. symmetricus, M. salmoides and Enneacanthus, six or seven; in Centrarchus, L. microlophus and P. annularis five or six; in L. macrochirus and M. notius, eight or nine; in *L. humilis*, *L. marginatus*, *M. treculi*, *M. punctulatus* and *L. megalotis*, seven or eight; in *L. auritus*, seven to nine; in *L. cyanellus*, nine or ten; ten to 12 in *M. coosae*; 12 or 13 in *M. dolomieui*; and four or five in *Acantharchus*. This first scale is partially or wholly covered by the opercular flap in *L. cyanellus*, *L. punctatus*, *M. chaetodon*, *A. pomotis*, *P. annularis* and *Enneacanthus*. However, this condition is quite variable in *M. chaetodon* and some specimens are to be found in which the scale is completely visible.

The size of the lateralis scales, in relation to other body scales, also varies from species to species. They may be equal in size to the epaxial and smaller than the hypaxial scales, as in *Ambloplites*, equal to the rest of the body scales in size, as in most of the Lepomini, or smaller than those above or below them, as in the Micropterini and Enneacanthini.

The general course of the lateralis, like other aspects of the system, varies from species to species. In all species, except the basses, the lateralis curves upward for sevaral scales from its point of origin, gently in the more parallel-sided forms, and declivitously in the deep-bodied species. In *Micropterus* the lateralis first loops downward for two or three scales, then gently slopes upward for three to eight scale rows from which point it extends in a nearly straight, diagonal line to its termination on one of the last four normal-sized scales in the lateral series. Every scale in the lateralis is usually tubed, but there may be short stretches of incompleteness amounting to one or two scales in length. For all practical purposes the genus *Micropterus* is considered to possess a complete lateralis.

In other sunfishes, except *Pomoxis* and *Ambloplites*, the canal line immediately begins curving upward and continues to do so for four to nine scales. In Ambloplites the length of the descent is from ten to 11 scales and in Pomoxis, which is variable for this character, the number of scales involved is from five to 11. The point where the curvature becomes negative lies at varying distances below the dorsum. In all species, except Archoplites, this point lies nearly directly below the origin of the spinous dorsal fin. In the 15 specimens of Archoplites, the lateralis began to curve downward seven or eight scale rows below the fourth spine of the dorsal fin. In the greater number of the remaining species the negative curvature begins at a point five to seven scale rows below the dorsal origin. In Mesogonistius and E. Gloriosus it starts at four or five rows and in Ambloplites eight or nine rows below the origin. Most of the centrarchids, excluding the basses, then, resemble Chaenobryttus in this respect.

The negative curvature in the species with a complete lateralis, again excluding the basses, since they have already been discussed, ends either at the posterior end of the dorsal fin, one or two scales below the dorsum and proceeds directly caudad from that point, or the line curves to the posterior end of the dorsal base, three to five scale rows below the dorsum, and then abruptly drops down from one to six scale rows and extends straight back as in L. humilis, L. microlophus or L. gibbosus. In other species with a complete lateralis the series declines to a point from two to six scales behind the posterior end of the dorsal base, two to five scale rows below the caudal peduncle dorsum, from which point the line straightens and extends, as in the other species, to one of the last three normal-sized scales. In some specimens of L. macrochirus, L. cyanellus, L. auritus and L. microlophus there was a very small lateral-line tube on the first small scale behind the last normal lateral-line scale. It will be noticed in Table I that L. cyanellus, L. megalotis and P. annularis have been included in more than one column. The reason for this is that the species are variable and exhibit more than one lateralis phenotype. The variation observed in the other species possessing a complete lateralis was not great. Short interruptions of one to three blank scales were noted in most of the species and in certain regions of the lateralis where blank scales occurred there was a tube observed on a scale above or below the main course of the normal series.

Those species which possess a markedly interrupted lateralis are few: Lepomis symmetricus, L. megalotis (in part), L. cyanellus (in part) and Pomoxis annularis (in part). The point of interruption and of recovery is variable. In L. symmetricus the break usually occurs nine to 15 scales posterior to its beginning. Following the interruption there is a stretch of scales, averaging 20 to 21 in number, which may completely lack lateral-line tubes or possess a few anomalous tubes scattered through the 20-odd scales. The series then recommences four or five scale rows behind the posterior end of the dorsal base and extends to the last large scale of the series. In specimens of L. cyanellus the interruption may occur almost anywhere in the lateralis and varies from two to eight or nine scales in length. Another condition seen in this species is that of many of the tubes in the series are staggered above and below the main course of the lateralis, giving it a sinuous appearance. Lepomis megalotis, as noted in Table I, is an extremely variable species. The interrupted area, in specimens with such a condition, may be only two or three scales in extent, or may be 12 or more scales in length. The series may end near the posterior extremity of the dorsal base and the last three normal scales of the lateral series bear tubes, or there may be several gaps of two or three scale lengths along the canal system. In some specimens of *P. annularis* the interruption occurred any place from five to eleven scales from its commencement followed by a gap of 18 to 25 tubeless scales (an occasional tube or two occurs within the blank area in some individuals) then takes up again, ending on the penultimate large scale in the lateral series. In other specimens the interruption amounts to one to four or more short blank areas of two to four scales in length. This was not observed in *P. nigromaculatus*.

There are likewise four species which have or sometimes exhibit, as in *L. megalotis*, an incomplete lateralis. In addition to the above species, the two species of *Enneacanthus* and *Acantharchus pomotis* also have an incomplete lateralis. In the variable *L. megalotis* the degree of incompleteness ranged from only one scale short of the end of the hypural plate to the series ending near the middle of the dorsal base. In *Acantharchus* the end of the lateralis may be found from two to six scales behind the posterior end of the dorsal base, three to four scales below the dorsum of the caudal peduncle. There are usually only six or seven tubed scales behind this point. The degree of incompletness is likewise variable in *Enneacanthus*. The series may end seven scales before the end of, just below the end of or two to four scales behind the posterior end of the dorsal fin or may be within two or three scales of being complete. In our specimens, it most usually ended near the posterior end of the dorsal base.

The lateralis tubes are rather variable in all of the species and may be straight-sided or slightly lagenate. In *L. punctatus* they are attenuate-lagenate. Some of the abnormalities which were observed are as follows: several tubes in *L. cyanellus* were found which occupied parts of two different scales; in *L. humilis* a few of the canals were bifurcate posteriorly and in a few instances there were two canals on single scales; in *L. auritus* some small abnormal scales were formed over the lateral-line canals in some areas of the lateralis; and in *Mesogonistius* several canals on the caudal peduncle did not have lateral walls, but appeared as open grooves. In *Archoplites* and *Acantharchus* the anterior lateral-line scales are so strongly imbricated by the body scales above and below them that only the lateral-line canals are free.

CHAPTER IV

DISTRIBUTION OF EXTERNAL NEUROMASTS

With the exception of the genus Elassoma no adult centrarchids have extensively-developed neuromast lines. Consequently, the distribution of these external lateral-line organs will be described in E. zonatum and comparison made with the other members of the family.

Elassoma zonatum. (Text Figures 2, 3 and 4). The neuromast lines of E. Zonatum, with a few minor variations, are quite like those in the other two species of the genus. Of Stensiö's (1947) six cheek lines only four are represented in the adult of this species: the infraorbital line, the oral line, the mandibular line and the postmaxillary line (Text Fig. 2). The other lines have either been included in canals or they never develop.

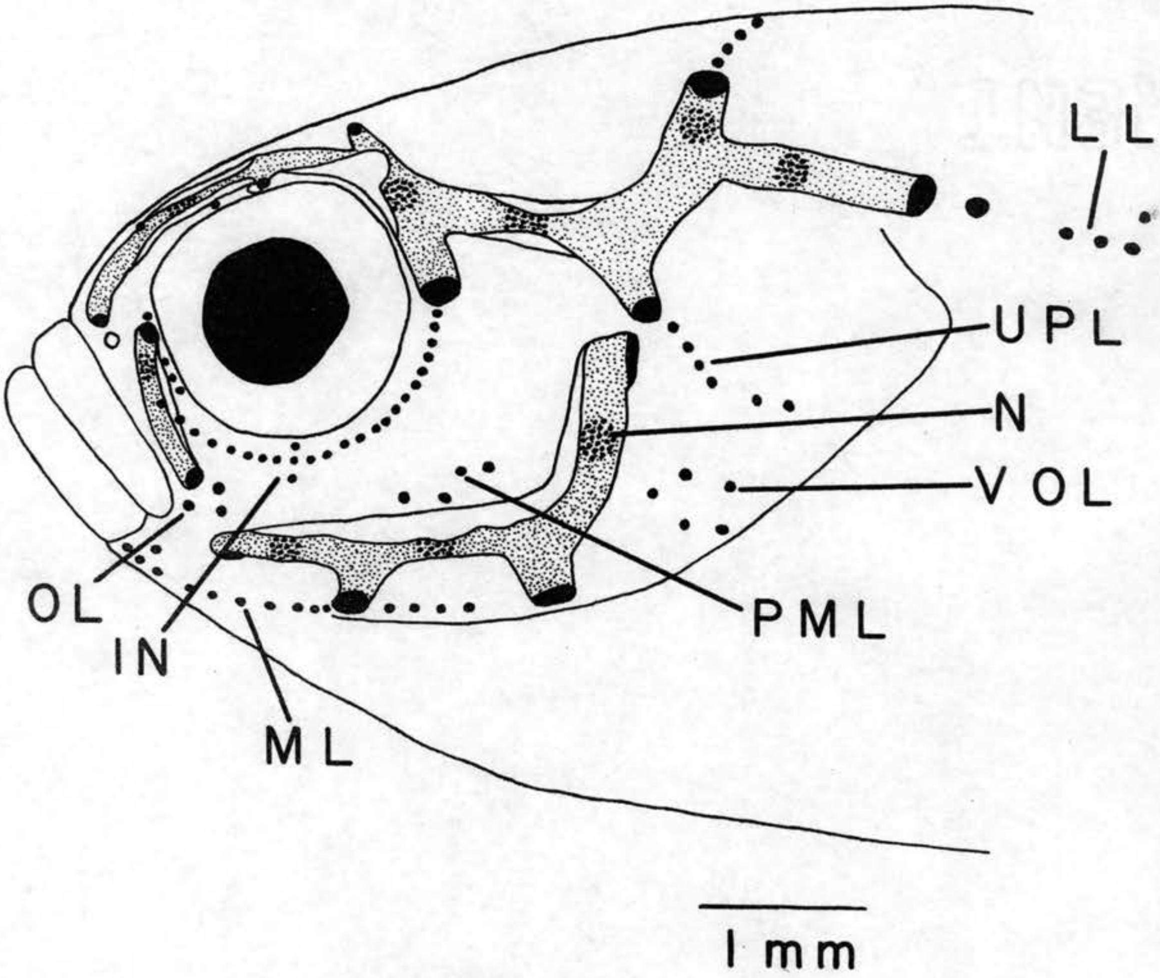
The infraorbital line is represented by a continuous row of neuromasts from a point just behind and above the middle of the eye to an anterior terminus just in front of and above the middle of the eye. The number of organs in the series averages 27 but in some specimens it seems that one or more of the primary neuromasts occasionally undergoes division to form secondary organs above and/or below the main line. This line usually possesses, at its anterior end, two or three neuromasts which are located in the skin covering the much reduced lachrymal bone, and about four of these organs between the eye and the lachrymal. Only the infraorbital proper is developed, the postorbital segment is included in the short canal behind the eye.

The mandibular line is a ventral continuation of the preopercular line. The preopercular line has been included in the preopercular canal, but its mandibular extension is very well-developed, replacing the canal of this segment (Text Figs. 2 and 3). This line, unlike the infraorbital series discussed above, does not take up at the point where the canal ends, but starts somewhat below this junction and extends both anteriorly and posteriorly. The posterior continuation is doubtless the result of division and migration of the primary organs. The anterior part of the line extends onto the lower jaw and is continuous with the line from the other side of the head (Text Fig. 3). The caudally-directed portion extends backward to a position below the middle of the ventral arm of the preopercular canal. There are usually 54 organs in the line, 27 on each side of the head.

There are usually four or five neuromasts located just above the ventral arm of the preopercular canal. Their position indicates that they are rudiments of the postmaxillary, a connecting line between the anterior and posterior supramaxillary lines, when these are present. Actually the supramaxillary and postmaxillary lines are only different reduced parts of the same morphological line in different fishes. In Elassoma the only part of this complex line remaining is the postmaxillary portion and perhaps a small segment on the opercle (Text Fig. 2).

The ventral opercular line, represented in Text Figure 2 by five black dots (neuromasts), is possibly the remains of the supramaxillary line of Stensiö.

Three or four small neuromasts were observed posterodorsal to the ventral angle of the mouth. It is thought that these organs, which are of very common occurrence in teleost fishes (Stensiö, 1947), represent an oral line, actually only another segment of the postmaxillary line. This is especially probable since the mandibular canal is lacking.

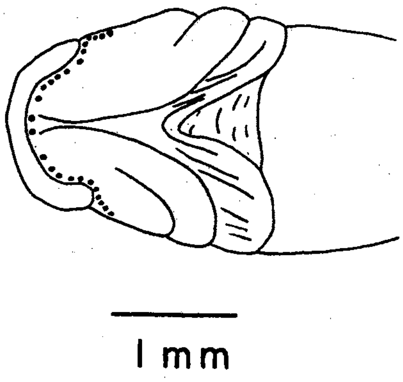


Text Figure 2, Lateral View of Cephalic Canals and Neuromast Lines in Elassoma zonatum. IN, infraorbital line; LL, lateralis; ML, mandibular line; N, canal neuromast; OL, oral line: PML, postmaxillary line; UPL, upper opercular line; VOL, ventral opercular line.

The upper opercular line varies from three to six neuromasts in length and is directed posteroventrally on the upper part of the opercle. This line is obviously only a ventral continuation of the supratemporal neuromast line.

The neuromast lines on top of the head are considerably less well developed than those on the cheeks (Text Fig. 4). Sâto's (1955a) nasal line is a very short one, two neuromasts occupying the area between the nostrils.

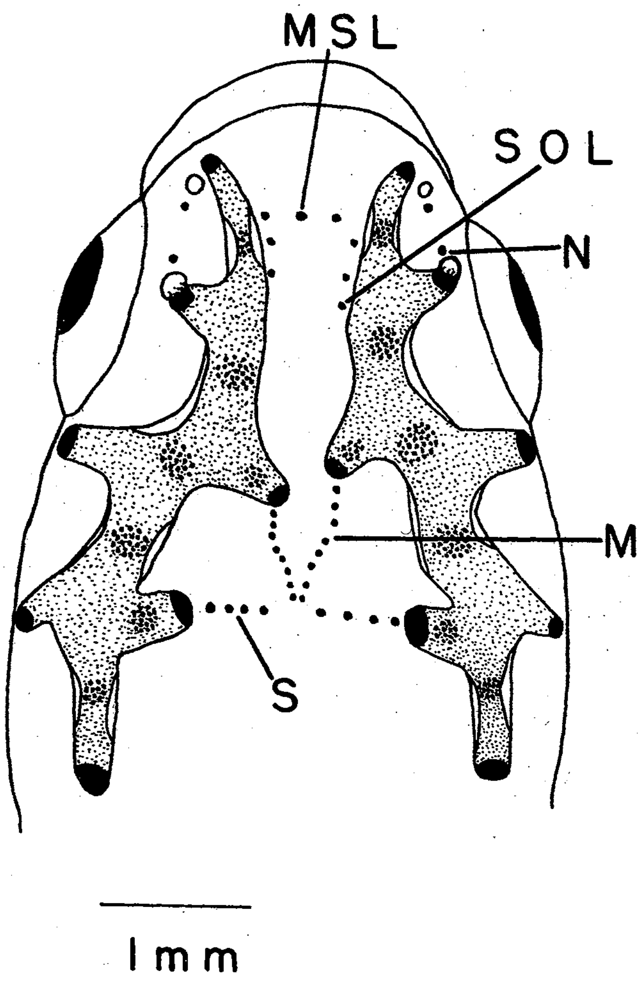
The supraorbital line, although most of it has been included in the supraorbital canal, consists of three neuromasts on the anteromesial margin of the supraorbital canal. Sâto's medial supraorbital line is nothing more than a subdivision of the supraorbital line and is here represented by two neuromasts situated on each side of the median line, between the two supraorbital lines. There is no rostral commissural line.



Text Figure 3. Ventral View of Head in E. zonatum showing Mandibular line.

As previously indicated, the supraorbital commissural canal is incomplete. However, a row of neuromasts, on each side of the head from the posteriorly directed pores, are in a position comparable to Sâto's (1955a) extrascapular line and are obviously a continuation of the supraorbital-commissural canals. The former row, usually comprised of eight organs per line, is directed caudad to a point near the medial ends of the supratemporal, discussed below.

The supratemporal canal is also much reduced but is continued dorsally by four or five neuromasts on each side of the head.



Text Figure 4. Dorsal View of Cephalic Canals and Neuromast Lines in *E. zonatum*. M, medial extrascapular line; MSL, median supraorbital line; N, nasal line; S, supratemporal line; SOL, supraorbital line.

There are no pitfields and only occasional compounding in the cephalic neuromast lines of E. zonatum. As shown below, there has been some subdivision of primary neuromast lines and the formation of some small pitfields in the caudal parts of the lateralis.

The lateralis is the most extensively developed of the neuromast lines, both in length and in number of individual organs. The line commences in a neuromast, which is approximately twice the size of any other external lateral-line organ on the body, at the posterior end of the cephalic lateralis and extends to the morphological base of the caudal fin. These neuromasts, averaging 44 in number, are not arranged in a single straight line, but occupy a band about two organs deep along the sides of the fish back to about the end of the soft dorsal. From this position caudad the neuromasts are arranged in a small pit field consisting of 18 to 20 organs.

Comparison with Other Centrarchids

The external neuromast lines of E. zonatum, and the other members of the family, with few exceptions, represent regions where the lateral-line canals have been reduced during phylogeny, or, in the instances of the supraorbital, median supraorbital, nasal, postmaxillary, oral and the two opercular neuromast lines, represent vestigial lines which never were included in a canal. As indicated, neuromast lines are rare in the centrarchids with well-developed canal systems.

Elassominae. The infraorbital line in E. evergladei and E. okefenokee varied slightly from that of E. zonatum. In the former two species the neuromasts are formed in a continuous series from the posterior origin to the anterior terminus, with none of the organs out of line. The maximum number of organs observed was 23 per side in E. evergladei and the minimum

21 in E. okefenokee.

Only in the anterior portion of the mandibular line was seen in the other two Elassoma and the organ series started not below the canal as in E. zonatum, but at the anteriorly-directed terminal pore of the preopercular canal. The series was again found to be continuous from one side of the head to the other. A total of 18 organs, or nine per side, was found in E. evergladei and E. okefenokee, or less than half the number found in E. zonatum.

The oral line is essentially the same in all three species of Elassoma, consisting of three organs.

The postmaxillary is apparently a variable line, but was consistently composed of at least five neuromasts in all three forms. The ventral opercular line is often represented by only a single organ and is sometimes altogether absent.

The supratemporal line was not observed in E. evergladei and E. okefenokee, but, because of the inadequate sample of these two species, may be found when a longer series is examined. The ventral continuation of this line, or the upper opercular line, was invariably found to be present but was never composed of more than three neuromasts.

Considerable differences between the neuromast lines on the head dorsums of E. zonatum and E. evergladei, but similarity between the former and E. okefenokee were observed. The nasal line of E. evergladei contained five or six organs per side (only two in E. zonatum) and the supraorbital and median supraorbital lines were completely lacking. The reason for the absence of these two lines may be linked to the fact that the head is fully scaled in E. evergladei and naked in the other two species.

With the exception that only five or six organs per line were observed, in the two species compared with E. zonatum, the medial extrascapular line is like that of the latter.

In three examples of Elassoma evergladei, an additional line of four neuromasts was observed in a position above the postocular commissural canal. This line is interrupted as a modified portion of the supratemporal line and is probably quite variable in nature.

The lateralis line is alike in all three forms but varies from 31 to 59 in the number of organs contained.

Centrarchinae--Centrarchini. The only external neuromasts observed in this tribe were in the two species of Pomoxis (Pl. I, Figs. 1 and 3). These neuromasts occur in the gap between the two ends of the interrupted infraorbital canal. In P. annularis there was usually one neuromast, occasionally two, in this position. This number varied from one to three in specimens of P. nigromaculatus.

Centrarchinae--Ambloplitini. External neuromasts were not observed.

Lepominae--Enneacanthini. Mesogonistius chaetodon (Pl. IV, Fig. 25) possesses several remnants of neuromast lines not seen in Enneacanthus. In the interrupted infraorbital canal, between the lachrymal and the anterior terminus of the proximal part, two neuromasts are usually found. Both of the opercular lines are represented, the upper one possessing two or three organs and the lower one, one or two. Three neuromasts were observed in the same position as the postmaxillary line in Elassoma, one in the position of the oral line and one near the leading border of the supratemporal canal.

Since the specimens of Enneacanthus were not optimally fixed for observation of the external organs it is possible that these same lines are present but in such a state as to escape observation.

Lepominae--*Micropterini*. In the Micropterini external neuromasts were observed only in *Micropterus punctulatus* (Pl. III, Fig. 18). A line of six organs was seen in the position of the ventral opercular line.

Lepominae--*Lepomini*. Scattered or symmetrically-distributed neuromasts were observed in eight species of *Lepomis*. In most specimens of *L. macrochirus* from one to five small organs were counted just behind the eye, between the infraorbital and preoperculomandibular canals. These may be secondary neuromasts budded off from the postocular series. Two neuromasts, in very close approximation to each other, bridge the interruption of the infraorbital canal in *L. symmetricus*, *L. microlophus* and possibly in other species.

Lines or groups of neuromasts, one or three in *L. cyanellus* (Pl. I, Fig. 7) and nine or ten in *L. gibbosus* (Pl. II, Fig. 15) represent the supratemporal line. In *Lepomis gibbosus* an additional line of four organs, which may represent a posterior continuation of the supratemporal, was observed in a few specimens. The ventral continuation of this primitive line, the upper opercular line, was found to be well formed in the pumpkinseed and the green sunfish. In *L. gibbosus*, the line is continuous with neuromasts which are in the position of the ventral opercular line. The entire line is comprised of eight organs, whereas that same line possesses five organs in *L. cyanellus*. A group of four or five organs, located on the opercle near the posteroventral edge of the preopercle, are probably the vestiges of a ventral opercular line in *L. cyanellus*, and a straight, dorsoventrally dispersed row of neuromasts, six in *L. punctatus* and seven in *L. megalotis breviceps*, situated just behind the ventral arm of the preopercle, are probably members of the same element.

The tubes of the scales in the lateral series are usually accompanied by accessory neuromasts (pit organs) in four lepomine species. In L. auritus only a few of these appear on each side, but in the other species involved there are usually 40 to 50 of them and sometimes more.

Some observations made upon a five-specimen series of Lepomis cyanellus, 10.5 to 76.0 mm. in standard length, may be instructive as to the origin of these "extra" neuromasts. In the 10.5 mm. specimen, the anterior lateralis tubes had not become completely covered laterally and appeared as shallow, open grooves. The canal organ was clearly visible, implanted on the proximal wall at about the center of the scale. A secondary neuromast appeared above and/or below the presumptive canal. Near the posterior end of the lateralis no tubes were formed and the neuromasts were arranged one above the other in a vertical line. In specimens above 15.0 mm. in length the canals are completely roofed, leaving the one or two external neuromasts free on the skin covering the scales. In adult specimens, with few exceptions, there was at least one of these secondary organs on each scale in the lateralis. From the foregoing it seems clear that these secondary neuromasts are the product of subdivision of the primary organs before the canals start to form. The accessory neuromasts of the lateralis in L. gibbosus are variable in number from scale to scale and in position on the scales. There may be single neuromasts above and/or below the tube, one above and two below, or vice versa. Sometimes the scales are barren of external neuromasts. The distributional pattern of these free organs in L. punctatus is similar to that of L. gibbosus

CHAPTER V

COMPARISON WITH OTHER TAXA

Cephalic Canals

Although various orders of fishes have innovated their own peculiarities as regards the cephalic lateral-line system, the course of the canals, as seen externally, is very similar in all Teleostomi. This basic pattern has been retained by the Centrarchidae.

Very early fishes, such as the Coelacanthiformes (Stensiö, 1922; Moy-Thomas, 1937), apparently possessed the same canal lines as more recent forms, but were characterized by very complex systems of external canaliculi and tremendous numbers of pores. The preoperculomandibular canal may have anastomosed with the infraorbital canal rather than with the postocular canal as in the centrarchids. The supratemporal canal was nearly always complete across the back of the head, as it is in several groups of recent forms. It is difficult to say whether or not the supraorbital commissural canal was always complete, but there was a complete rostral commissure in many forms. The last-named canal has been obliterated in most of the recent species of teleosts, but is represented in a few as a rostral neuromast line. The major difficulty in dealing with the coelacanths is that the lateral-line canals most often did not penetrate deeply into the bones but were probably connective tissue in nature, the course of the canals being indicated by slight to deep grooves in the bones over which the canals traversed. This last condition is considered to be a holocephalan character, but it is also found in such fishes as suckers and some catfishes (personal observation).

Canal organization in the acipenseriform fishes, although remaining quite complex in the large number of external canaliculi (many of which have become terminally bifurcated), is considered to be an advancement over the condition observed in the coelacanths. The preopercular canal, as in most of the higher groups, no longer effects a communication with the infraorbital, but is directed upward toward the cephalic canals, as in Acipenser (Allis, 1904; Norris, 1924) and connected to the cephalic lateralis in Polyodon (Nachtrieb, 1912). This condition persists, except where secondarily reduced, in the sunfishes and other percomorphs.

The course of the cephalic canals delimited in Amia calva by Allis (1889) and in Sinamia zdanskyi by Stensiö (1936) is the basic blueprint followed in the Centrarchidae and other more highly evolved groups. Consequently, the centrarchid system will be compared, canal by canal, with those of several of these taxa.

Cephalic Lateralis

The sunfish lateralis canal series communicates with the cephalic lateralis through the supracleithrum as it does in Amia, salmonidae (Berg, 1940), Aphredoderus and Serranidae (personal observation), Percidae (Allis, 1904) and Cichlidae (Branson, in press). However, in many fishes, such as the ganoids (Allis, 1904), Clupeiformes (Tretyakov, 1950), Ostariophysi (Lekander, 1949) and Cyprinodontidae (Denny, 1937; Techernavin, 1946), the connection is made directly with the posterior end of the posttemporal opening which ends in one or two pores in the centrarchids. In many of the fishes mentioned above, especially in Lepisosteus (Collinge,

1893) and clueids (Bramford, 1941), there are extensively-developed external canaliculi and pores in this region. It will be recalled that the centrarchids never possess more than five external pores in this canal line, which is essentially as found in the Cichlidae (Branson, op. cit.).

Supratemporal Canal

The supratemporal canal is another of the more or less constantly persistent canals in fishes (Stensiö, 1947; Allis, 1904). However, its relative length varies from group to group. It is always complete in Amia (Allis, 1889), Lepisosteus (Collinge, 1896) and in several siluroids (Pollard, 1892). In other taxa this canal may be complete in some species and incomplete in others, as in the Percidae (Hubbs and Cannon, 1935) and Cyprinidae, (Illick, 1956). The canal has completely given way to a line of neuromasts in such fishes as the Cyprinodontidae (Gosline, 1949; Denny, 1937). The canal is never complete in the Centrarchidae and there are usually only two pores in its walls. Suckers, clupeids, Amia and Lepisosteus possess numerous pores in this canal.

Postocular Commissure

This connecting piece is of rather simple design in most teleost fishes. The two-or three-pored tubes seen in sunfishes are similar to those in Aphredoderus (Moore and Burris, 1956), Chichlasoma (Branson, op. cit.), Hololepis and Villora (Hubbs and Cannon, 1935), Cobitis taenia (Lekander, 1949) and some catfishes (Pollard, 1892). In many, supposedly less advanced groups, the canal is even simpler than in the above species. Menidia notata and M. gracilis, for example, have no pores in the canal and in many cyprinodonts (Gosline, 1949; Denny, 1937; and

Tchernavin, 1946) the canal does not exist, having been replaced by external neuromasts. In the Cyprinidae (Illick, 1956) there seems to be considerable variation in this character from group to group. Some species, such as Orthodon microlepidotus (Ayres), have as many as ten pores, opening directly into the canal walls, whereas others have fewer, five in Pogonichthys macrolepidota (Ayres) and three in Agosia chrysogaster Girard. In Iotichthys phlegethontis (Cope) there are three pores but the canal is interrupted and very incomplete, which, of course, is to be considered a result of specialization. In still lower-grade fishes, i. e., Lepisosteus and Clupeidae, the postocular commissure is not simple, in fact the degree of complexity in all of the canals of these fishes is amazing. The external canaliculi in the gar are very numerous but can be traced (Collinge, 1893). In the clupeids, if the representations of Bamford (1941) and Tretyakov (1938, 1950) are exact, this canal is so complex that the task of tracing the ramifications, which actually extend downward and backward over the branches of some other canals, would seem a most difficult task.

Postocular Sinus

In all fishes in which the postocular commissure, supraorbital and infraorbital canals coalesce just behind the eye there is found a cavity of variable size in connective tissue. As pointed out above, this is termed the postocular sinus (tympanic receptaculum of Tretyakov, 1950; posterior dilation of Bamford, 1941). In all of the perciforms, Amia, siluroids (Pollard, 1892), Lepisosteus (Collinge, 1893) and many others this is a generality. The structure has become tremendously inflated and complicated in the herring-like fishes, giving rise to some highly dendritic branches

(Bamford, 1941; Tretyakov, 1950). Bamford (op. cit.) found in Clupea that the sinus opened into the cranial cavity near the optic lobes, the only separation of the lateral line from the brain being effected by the dura mater and the basement membranes of the lateral-line canal.

In Cyprinodontidae (Denny, 1937; Gosline, 1949), and Cyprinidae (Illick, 1956), except the carp and goldfish, Catostomidae and a few others (Allis, 1904), there is no postocular sinus because the supraorbital does not communicate with the postocular commissure.

Supraorbital Canal and Commissure

There are many differences between fish taxa with regard to the supraorbital complex. The supraorbital canal communicates with a well-formed postocular sinus in the cichlids, very much the same as in centrarchids, Aphredoderus (Moore and Burris, 1956), Amia (Allis, 1889), Medidia (Herrick, 1899) and darters of the subgenera Hololepis and Villora (Hubbs and Cannon, 1935). The canal usually ends in front of and lateral to (in a few, mesial to) the anterior nostril. The supraorbital commissure, which Allis (1904) does not consider to be a true commissure because of its bilateral origin, may be incomplete, as in Elassoma, or complete as in all of the other sunfishes, many percids, Amia and others. One major difference between the higher percids and lower fishes is that external canaliculi are very few or absent in the former. In the ganoids (Allis, 1904; Collinge, 1893) and Amia (Allis, 1889) the supraorbital is unique in passing between the nostrils and joining the infraorbital either by the terminal pore or by a side branch. This does not occur in any other known group of fishes. The most striking dissimilarity between the Centrarchidae and other taxa is found in the Ostariophysi and cyprinodonts. In these taxa (excluding the exceptions mentioned above) the supraorbital does not communicate with the postocular canal at all. In Fundulus (Gosline, 1949) the canal may loop downward behind the eye, occupying a region similar to that of the upper infraorbital and postocular canals, but in the Cyprinidae (Illick, 1956) the supraorbital extends nearly straight back, paralleling the postocular commissure to its posterior terminus. In some species of Fundulus (Gosline, op. cit.) and Hybopsis (Illick, 1956) the canal is interrupted in several places, and in Iotichthys the structure is nearly lacking. Furthermore, these fishes do not possess the slightest indication of a supraorbital commissure.

Infraorbital Canal

Although the pore counts and degree of interruption vary, and in some groups secondary complete reduction occurs, the general infraorbital morphology of the sunfishes is very similar to that of most percomorphs, siluroids (Pollard, 1892), clupeids (Bamford, 1941; Tretyakov, 1938, 1950), Amia (Allis, 1889), Polypterus and other ganoids (Collinge, 1893), except for the anteorbital connection with the supraorbital in the last three taxa. In Clupeidae (Tretyakov, 1938, 1950) this canal, as well as all of the others in these fishes, is very complex and often sends dendritic branches downward and caudad, which may overlap other canals as in Alestes (Allis, 1904). In Fundulus (Denny, 1937; Gosline, 1949) and several cobitids (Miyadi, 1929) the infraorbital is quite lacking, being similar in this respect to Elassoma. In minnows and suckers the canal curves upward and backward to fuse with the postocular commissural line.

Preoperculomandibular Canal

In one form or another this canal, or parts of it, is present in all fishes. However, the simplicity found in cichlids, centrarchids, catfishes, Amia and percids in general, is vastly different from the complex organization of the system in some ganoids (Collinge, 1893), clupeids (Tretyakov, 1938, 1950) scombricids (Tretyakov, 1941b) and flying fishes (Tretyakov, 1938b). In Polypterus the canal is relatively simple but in the gar (Collinge, 1893) there are many small anastomosing tubules. The external canaliculi of the preopercular canal of the flying fish, Exocetes, have become much enlarged, elongated and branched at the angle of the preopercle, as in Scomber. The mandibular component is rather unmodified in appearance and does not bear the aberrant bi- or trifid canaliculi seen at the position mentioned above. The greatest complexity in this canal occurs in the Clupeidae, in which the external canaliculi may become so highly anastomosed and branched as to cover the entire side of the head. In a species of anchovy there is a massive connection with the infraorbital canal and such connections also occur in some herrings. As far as can be told from Tretyakov's drawings, the mandibular component is not involved in this extensive development.

In all of the sunfishes, except Elassoma, the preoperculomandibular canal extends the length of the preopercle and mandible, though, as in most groups of fishes, there may be a break at its upper end. Elassoma, in lacking a mandibular canal resembles some species of Fundulus (Gosline, op. cit.) and members of the Clupeidae (Tretyakov, 1938b, 1950). Cyprinids, which usually have the canal free at its upper end, always have at least a part of the mandibular canal, but the preopercular portion may be very short, as in Phoxinus (Lekander, 1949), or absent, as in some specimens of Tiaroga (Illick, 1956).

Some fishes, i. e., Lefua echigonia and L. nikkonia (Miyadi, 1929) completely lack canal systems, others may have the canals reduced to open grooves (some cyprinodonts, Gosline, 1949) and a few peculiar muraenids, (Allis, 1904) possess well-developed canal systems but lack external canaliculi and pores. In other groups, such as suckers (Moxostoma, Allis, 1904) and catfishes (Pollard, 1892) the lateral-line canals are mostly not enclosed in bone, but are attached to the osseous components by connective tissue.

When compared with the lower percoid fishes (Tretyakov, 1944) the centrarchids are seen to be much modified in the external anatomy of the lateral-line system. The lower forms possess much longer and more numerous external canaliculi.

Lateralis

In many teleostomian fishes the course of the canal series of the lateralis is very similar to that of the Centrarchidae and Amiidae. However, there are several examples in which this is not true. The peculiar situation of the lateralis in cichlids has been noted elsewhere by this author (Branson, in press) and others. In this group of fishes the lateralis is anteroposteriorly continuous to a point near the middle of the soft dorsal where it ends. Two or three scale rows below and in front of the upper terminus, the series is resumed to continue to the end of the hypural. Many flatfishes, probably as the result of embryological transfiguration, possess two lateral canal series. The lateralis may also vary, within any group, from entirely lacking to complete, a condition reminiscent of sunfishes. As in Elassoma, several fishes, including Fundulus

(Denny, 1937), several cobitids (Miyadi, 1929) and some species of Menidia (Herrick, 1899), completely lack tubiferous scales in the lateral series. In a few aberrant species, such as Trachurus (Tretyakov, 1938), the lateralis series is complete, but is not connected with the cephalic canals at all. This seems to be an exception to Miyadi's law, which states that ". . . when the degeneration of the canal system takes place, it is in the anterior portion of the trunk that this process occurs last of all." In general the mode of progressing from one scale to the next in most fishes is similar to that described above for the Centrarchidae, in Amia (Allis, 1889) and Lepisosteus (Collinge, 1893). However, there are other fishes in which differences have been observed. In Cichlasoma cyanoguttatum (Branson, in press) it appears that each scale canal is a separate entity, and in some Etheostoma the connective-tissue tube passes directly from one canal to the next (Vaillant, 1874).

The connection of the lateralis with the cephalic canals is made in two main ways, directly with the end of the posttemporal part of the cephalic lateralis, as in suckers and minnows, or indirectly through the supracleithrum, as in the centrarchids and Amia. In Amia (Allis, 1889) this union is marked by the largest pore in the canal system, as it is in Pomoxis and Cichlasoma and some other sunfishes, though the pore is usually somewhat smaller in the latter fishes. In the last-named fishes the pore is usually at the end of a small external canaliculus.

The tubes borne by the scales of the lateralis are not, as suggested by Rode and Rabaud (1926), simply raised folds on a longitudinal series of scales. As a matter of fact, these tubes appear, and often ossify when the scales are absent, as in some catfishes. Usually the lateral-line tube is fused immovably to the flat plate of the scale, but in some fishes, Grammistes and Ryptieus (Vaillant, 1874), the tubes lie free in the skin covering the scale. In percids, however, the arrangement is as shown above.

The external canaliculi described for centrarchids are quite simple when compared with those in certain other species. There are apparently two kinds of branches formed from lateralis tubes, those enclosed in the same substance as the mother canal and those which are composed only of connective tissue. The first type is found in some species of Lutjanus and Serranus (Vaillant, 1874). These bony branches probably come about by subdivision of the connective-tissue procanal before ossification has occurred, as do some of the external canaliculi in Clupea (Bamford, 1941). Some abnormal bony branches from the main canal are often seen in regenerated lateral-line scales (Takebe, 1934). The second type of external canaliculi are widespread in most groups of higher fishes but seldom have been the object of investigation. Nachtrieb (1912), who called these secondary canals "branchlets" or "pore tubes," observed as many as eight canaliculi per single mother canal in Polyodon, and Allis (1889) noted that the main canals on the scales break up into a fan of smaller tubules on the posterior margin of a scale in Amia. A single paper (Tretyakov, 1938) presumedly is the only work dealing specifically with this facet of lateral-line study. Although he made a few observations concerning these structures in other fishes, this work is mainly concerned with the morphology of the canaliculi in Clupeidae. In the species studied the tubules varied from three or four simple tubes to many dendritically-branched ones.

The interruptions and incompleteness noted above in several sunfishes occurs in almost every taxon of fishes which has been studied in detail. The variability within a species, in which short gaps occur where one or two scales lack lateral-line canals, may be explained in one of two ways, both being correlated with the absence of branches from the vagus nerve. If a branch from the vagus lateralis fails to develop embryologically then a neuromast and consequently the tube, will fail to develop. On the other hand, if one or more scales are lost accidentally (Mori, 1931) regeneration of the scale may or may not involve replacement of the canal, according to whether the nerve was destroyed or left intact by the injury.

External Neuromasts

Although Cole, according to Herrick (1899), considered naked neuromast lines to be an indication of primitiveness, there is general agreement among modern workers that this condition represents specialization (Stensiö, 1947; Herrick, 1899; Sâto, 1955a). As seen in the above discussion, one or more of the cephalic canals may become degenerate in phylogeny and disappear. The ancient course of the canals, when critically observed, is usually replaced by external neuromast lines. We have made the generalization that fishes with well-developed canal lines usually do not have equally well-developed neuromast lines, but there are exceptions to this statement. Sâto (1955c) and Moore and Burris (1956) have observed both well-developed neuromast lines and canals in the carp and pirate perch respectively. The opercular lines, which, according to Pehrson (1945), have escaped notice, except in Menidia (Herrick, 1899), Esox and Gymnarchus niloticus (Pehrson, op. cit.), are actually much more widespread than the above records indicate. Pehrson overlooked Bamford's (1941) work on the herring (Clupea harengus), in which ten neuromasts were clearly illustrated on the opercles and subopercles of that species, and Denny's (1937) discourse on Fundulus heteroclitus, in which she showed four or five surface organs on the opercles. Moore and Burris (1956) demonstrated 73 neuromasts on the opercles (and hundreds elsewhere on the head) of *Aphredoderus*, and they are recorded herein for *Elassoma* and several of the true sunfishes.

Reports upon the neuromast lines of the body in fishes are only occasionally published. The condition observed in *Elassoma*, in which the series of naked neuromasts start out as a thin line, then extend caudad to end in a pit field is apparently not the usual condition. In *Fundulus*, Denny (1937) showed the line commencing in a field of scattered pits and ending as a single-file series. The initial large neuromast of the series, mentioned in the pygmy sunfish, is not of uncommon occurrence. Herrick (1899) observed the same phenomenon in *Menidia*. The accessory organs accompanying the lateralis canals are of very common occurrence in fishes (Allis, 1899; Herrick, 1899).

CHAPTER VI

OSTEOLOGICAL COMPONENTS OF THE LATERAL-LINE SYSTEM

In recent years there has been a tendency to overlook the osseous affinities of the cephalic canals in lateral-line studies. This is a definite shortcoming because the true nature of the canals and of their external canaliculi is known only when the internal bones associated with them are understood. The rockbass, *Ambloplites rupestris*, has been chosen as a subject species for the same reason that the warmouth was used in describing the external morphology.

Ambloplites rupestris

The cephalic lateralis canal (Text Fig. 5) is associated with two bones, the supracleithrum and the posttemporal. The supracleithrum, a compound bone having anasmestic and lateral-line elements, is the second from the last dorsal element in the pectoral girdle and is articulated dorsally and mesially with the posttemporal by ligaments. The lateral-line canal passes diagonally downward in an anteroposterior direction through the bone, to end in a small foramen at the posterior edge where connection is made with the lateralis. The point of departure is marked by a slight notch. The anterior entrance into the supracleithrum, indicated by a dotted line in the figure, opens on the lateral aspect and lies in direct contact with the ventral opening of the posttemporal. The passageway through the supracleithrum, not markedly raised above the surface of the bone, apparently bears no nerve foramina.

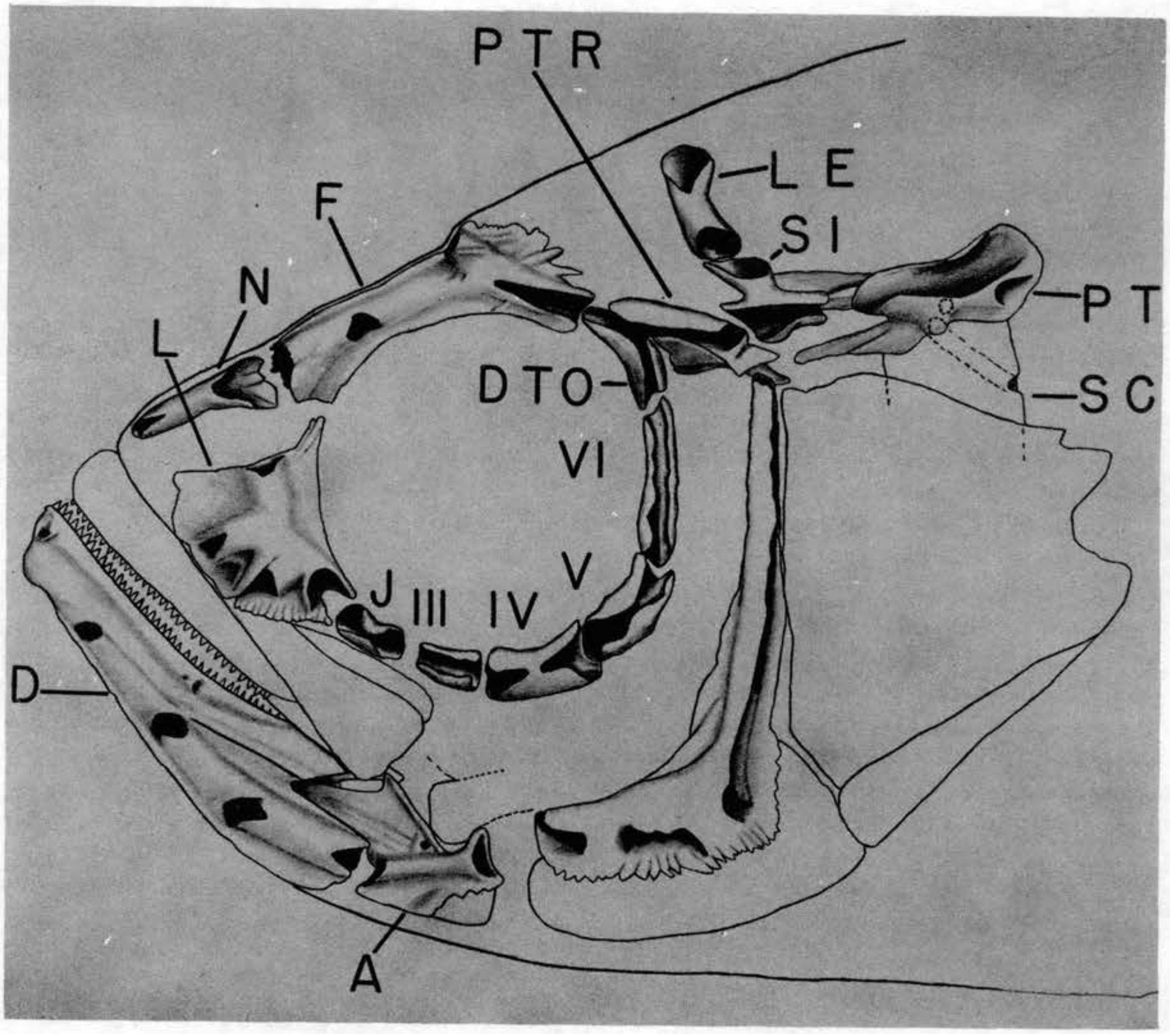
As shown below, the posttemporal is also a compound bone. The primitive function of this element is to hang the pectoral girdle to the skull by two prongs (Text Fig. 5), a dorsal one articulating with the dorsal surface of the epiotic and the ventral one with the opisthotic by a strong ligament. The lateral-line element has become welded to the posttemporal, which, in the rockbass, appears boat-shaped in lateral view. The large groove thus formed is depressed anteriorly, elevated caudally and is covered laterally by connective tissue. From the posterior end of this groove the more dorsal of two caudally-directed external canaliculi opens. The ventral external canaliculus finds origin at the end of a very short canal, completely enclosed by bone, on the ventroposterior margin of the posttemporal. At about the middle of the ventral edge of the large groove a small opening marks the beginning of the commissural canal to the supracleithrum. This small branch is also completely enclosed by bone. The edges of the posttemporal lateral-line complex are strongly raised above the body of the bone and a small nerve foramen pierces the anteroventral portion.

In life the cephalic lateralis canal progresses anteriorly from the posttemporal, enclosed only by connective tissue, from which the last canaliculus of the cephalic lateralis emerges to enter a small, inverted, T-shaped bone embedded in tissues over the lateral aspects of the parietal, between the posttemporal and pterotic bones. This small ossicle is the supratemporal-intertemporal and is the first member of the supratemporal canal. As seen in Text Fig. 5, the dorsally-directed leg of the "T" is tubular in nature and is slightly asymmetrically flared at the dorsal opening. The arms are incompletely tubular, the lateral wall being absent.

The posterior arm, which receives the canal from the posttemporal, is of uniform diameter, but the anterior arm is slightly inflated above, and strongly below, so that the canal may exit to make connection with the sinus that occurs at this junction. The dorsal portion is tilted forward, allowing the canal to pass into the small bone (lateral extrascapular) above it. The mesial and anterior walls of the dorsal part of the supratemporal-intertemporal are ligamentously attached to and nearly touch the lateral extrascapular, but the lateroposterior wall is much reduced. A small nerve foramen penetrates the mesial wall near the point of bifurcation of the ventral arms.

The lateral extrascapular is the second of the two osseous elements of the supratemporal canal. This is a very small tubular bone which is bent in the middle so that its two openings, dorsal and ventral, are directed slightly caudad. Portions of the lateral and posterior walls, adjacent to the apertures, are absent, causing the ends to be notched. The nerve foramen opens through the mesial wall near the center of the bone's length. The dorsal external canaliculus of this canal arises directly from the end of the lateral extrascapular then bends sharply backward; the ventral canaliculus arises from the connective tissue which covers the open area between the supratemporal-intertemporal and the lateral extrascapular. Both of these are pure lateral-line bones.

Immediately in front of and slightly below the supratemporal-intertemporal is the pterotic, the only osseous element containing the postocular commissural lateral-line canal. This is a compound bone consisting of a lateral-line element, the dermopterotic and a cranial bone, the autopterotic. The autopterotic articulates with the sphenotic anteriorly, prootic anteromesially, the opisthotic posteromesially and the exoccipital post-



Text Figure 5. Osteological Components of the Lateral-Line System in Ambloplites rupestris. A, articular; D, dentary; DTO, dermosphenotic (suborbital 7); F, frontal; J, jugal; L, lachrymal; LE, lateral extrascapular; N, nasal; PT, posttemporal; PTR, pterotic; SC, supracleithrum; SI, supratemporal-intertemporal; III--VI, suborbitals 3 through 6.

eroventrally. The dermopterotic, which is immovably fused to the cranial element, forms the lateral aspect of the pterotic complex. It is open laterally for its entire length and the posterior end is moderately depressed below the level of the anterior. The posterior opening is slightly turned upward toward the anterior end of the supratemporal, but the two bones are not in physical contact. In life, the lateral-line tube opens into a connective tissue sinus, formed at this point, which also connects with the preoperculomandibular canal. The anterior end of the groove is slightly flared and is almost in direct contact with the dermosphenotic. A foramen of moderate size penetrates into the lateral-line canal near the posterior end of the bone on the ventromesial border.

There are three bones associated with the preoperculomandibular canal; the preopercle, articular and dentary. As pointed out above, the upper end of the preopercle opens into the connective tissue sinus in common with the supratemporal-intertemporal and dermopterotic. It is rather L-shaped, the lower arm forming an angle of 100 to 105^{0} with the upper. The upper two-thirds of the ascending arm is tubular except for its posterior margin (Text Fig. 5). The bony canal of the inferior one-third of the upper and the entire lower arm is fused to a somewhat flattened mesial plate which bears 25 to 30 relatively strong spine-like serrae, with some striae above them on the plate of the preopercle. These serrae are distributed along the entire ventral edge of the bone. Six to ten similar, but weaker, striate serrae are found along the posteroventral one-fourth of the ascending part of the plate. The incomplete, slit-like posterior edge of the tubular portion of the preopercle is extended downward for approximately two-thirds of the total length of the ascending arm, from whence a thin lamella of bone is inserted between the lateral wall and the flat plate that is continuous to the angle of the preopercle. A slight carina on the lateral wall marks the length of this lamella. The canaliculus, which we have termed the junction pore, arises directly from the sinus at the upper end of the preopercle and the next three external canaliculi (Pl. I, Fig. 6) arise from the unossified part of the ascending arm. At the preopercular angle, a U-shaped opening into the wall of the completely tubular, bony passageway of the lateral line, is found a short distance in front of the posterior edge of the flat plate. Canaliculus 5 emerges here and extends nearly to the margin of the bone. Its course, as well as the one just anterior to it, is marked by a shallow depression in the preopercular plate. The next opening is W-shaped (Text Fig. 5) and gives rise to canaliculus 6, located midway between the two extremities of the horizontal arm. The anterior aperture of the preopercle opens directly forward into a connective tissue sinus. In this region the wall of the preopercular canal is free on three sides, appearing as a shelf which extends anteriad over the mesial plate. The sixth canaliculus leaves the sinus between the preopercle and the articular, extending directly ventrad. There are six nerve and/or blood vessel foramina into the preopercular canal, all of them being located on or near the leading edge of the bone. The first of these is located just below the upper end, the second is found about one-third the length of the ascending arm below the upper end, the third near the middle of the ascending arm, the fourth on the anterior edge in front of the preopercular angle, the fifth a short distance anterior to the fourth and the sixth near the middle of the horizontal arm. The preopercle is a compound bone, the anasmestic element being represented by the mesial plate.

The articular represents a bone composed of a lateral-line segment fused to the suspensory element of the lower jaw. A dorsal, laterally-compressed prong fits into Meckel's canal effecting articulation between the dentary and quadrate. The small, triangular angular is firmly attached to the posteroventral margin of the articular. The lateral-line canal passes diagonally downward through the middle of the articular and its anterior opening, slanted backward, lies below the posterior end of the maxilla. The posterior opening is shaped somewhat like an eye cup and is of considerably greater diameter than the anterior one. The nerve entrance lies near the middle of the bone through its mesial wall.

Canaliculus 8 opens to the exterior from another connective tissue sinus found between the anterior end of the articular and the caudal end of the dentary. The dentary is a triradiate bone with a long, tooth-bearing anterior ramus and a caudal bifurcation, the dorsal and ventral rami. The lateral-line canal passes through the middle of the ventral part of the bone, the caudal entrance being deeply notched laterally with the apex of the notch directed anteriad. Below the anterior edge of the mecklian opening, near the ventral edge of the lateral-line canular bulge, lies the next opening. This aperture is peculiarly formed, appearing as two inverted V-shaped structures, their apices directed away from each other, the dorsal arms of the posterior "V" being partially covered by the caudally-directed dorsal arm of the anterior one (Text Fig. 5). The two ventral arms fall short of each other so that a short diastema is formed on the dentary plate between them. This is the point of exit for canaliculus 9 which is directed toward the lip, as is the one just anterior to it. The opening underlying external canaliculus 10 is located nearly in the center of the canal and is suboval or round in shape. The exit for canaliculus 11 is likewise round and lies very near the ventral margin of the jaw. Anterior to this point the canal becomes very constricted, being of much lessened diameter than the part behind it. The anterior portion of the canal is not elevated above the general contour of the dentary, and is rather steeply bent upward, ending in a tiny pore situated near the mandibular symphysis. The dentary, then, is another bone composed of fused elements. Four foramina, approximately one-fifth the diameter of the lateral-line openings, penetrate the canal through the inner wall. The smallest of the four enters the canal near the dentary symphysis. The next three foramina enter the canal opposite the next three lateral-line openings respectively.

Whether the canal is complete or interrupted the infraorbital series consists of seven individual ossicles in this species. The peltate, anterior element is the lachrymal, which possesses four openings, two terminal ones (dorsal and ventral) and two anterior ones. The posterior margin of the lachrymal fits the curvature of the eye, forming the anterior rim of the orbit. The main course of the lateral line through this bone lies approximately over the center of the flattened lachrymal plate. The bone is about as wide as high with a raised tube passing through it. The tube is bent in the middle so that the dorsal and ventral ends seem to be pulled back. The posteroventral margin of the plate bears 12 to 15 short, blunt serrae with striae above them. Canaliculus 10 or 11, according to whether the canal is complete or incomplete, arises directly from the end of the dorsal extremity of the lachrymal and 9 (10) and 8 (9) from the two anterior openings respectively. As shown in Text Fig. 5, these two openings, borne at the ends of two side branches entirely surrounded by bone, are deeply notched, the apex of the notch being directed toward the orbit. The ventral aperture, which receives the lateral-line tube from the ossicles behind it, is broadly U-shaped and deeply cleft laterally and mesially (Text Fig. 5). Five blood-vessel and nerve foramina enter the posterior edge of the lachrymal, one near the posterodorsal tip, one just in front of it, and three evenly-spaced ones in a dorsoventrally-dispersed line. Then the canal is interrupted, a short, caudally-directed canaliculus appears from the ventral opening; but when complete, this aperature opens into a sinus between suborbital 2 (jugal) and the lachrymal, from which the canaliculus shown in the drawing arises. Actually this can be stated as a generality for all of the external canaliculi in the infraorbital canal; they all arise between the ends of two suborbital bones, except those of the lachrymal, and open ventrally or caudally, according to their position in the series. The jugal is a tiny bone which is usually attached to the hyomandibula by a ligament. The shape of this element is best described as a flat sheet which has the edges rolled upward but not meeting over the center of the groove thus formed. Suborbitals 3 through 6 present varying degrees of completeness on the lateral margin, element 4 very often possessing a thin strap of bone transversely across its center (Text Fig. 5). The posterior end of 4 and the anterior end of 5 are usually in contact, which is probably the reason that these two bones are fused in many teleost fishes. The last suborbital (7), or the dermosphenotic, is funnel-shaped and lies in a receptacular groove in the autosphenotic at the posterodorsal margin of the eye. It is flared out dorsally and bent around the orbit, making it possible for the infraorbital canal to open into the postocular sinus.

The infraorbital ossicles are purely lateral line bones, although in a few cases they may have some extraneous secondary limy deposits on them, such as a flat mesial plate, which develops in older individuals. A tiny nerve foramen usually penetrates each ossicle, including the dermosphenotic, through the center of the mesial wall.

The frontal, obviously a compound structure, covers a large percentage of the skull dorsum and is the largest lateral-line bone in the skeleton. This is the only osseous member of the supraorbital canal and commissural branch, except the nasal. The frontals are strongly articulated posteriorly with the parietals and supraoccipital, posterolaterally with the sphenotics and anteroventrally with the mesethmoid. There are some strong cartilages below the frontals. These bones are slightly curved in all directions and the lateral margin forms the dorsal part of the orbit.

The frontal lateral-line segment is raised above the general surface and opens posterolaterally into the postocular sinus (Text Fig. 5). The opening in this position is usually very deeply cleft dorsally and ectopic canaliculi occasionally arise at this point. From this beginning the canal curves around the orbit, gives off the very short commissural branch toward the midline and extends the length of the frontal, gradually increasing in diameter. About one-fourth of the width of the orbit from that structure's posterior margin, an opening is found in the lateral wall of the canal which in life opens into the interorbital canaliculus. The frontal canal becomes mesolaterally and dorsoventrally flared just in front of the orbit, where it ends. The lateral-line canal here connects with a sinus, between the frontal and nasal bones, which emits the posterior nasal canaliculus, then enters the last ossicle of the supraorbital canal, the nasal.

The commissural canals meet near the midline at the posterior margin of the frontals. Their anterior and dorsal edges form an elongate, U-shaped sinus but are not articulated. The coronal canaliculus originates from this sinus.

There are usually four obvious foraminal penetrations into the frontal lateral-line canal, three ventral and one dorsal. The very tiny dorsal foramen is located on the mesial side of the canal, a short distance in front of the commissural branch. A relatively large one enters the canal floor almost directly under the posterior nasal opening; a second, but smaller one enters the floor near the point where the commissural canal is given off and the last one penetrates the commissural canal slightly behind the last-mentioned foramen.

The nasal bone lies free in the tissues of the dorsal rostrum. It is moderately flexed near the middle so that the anterior end is deflected laterad. The bone is widely flared posteriorly, in which region the dorsal wall is marked by a small notch. The anterior diameter is less than the posterior and the dorsoanterior wall is usually narrowly but deeply cleft. The two nerve foramina penetrate the floor of the bone a short distance anteriad to the posterior lateral-line opening.

CHAPTER VII

COMPARISON OF AMBLOPLITES WITH OTHER CENTRARCHIDAE

Although many differences exist between the various groups of centrarchids, in regard to lateral-line bones, no extensive deviations from the rockbass pattern were noted except in the aberrant species of *Elassoma*.

Centrarchinae--Ambloplitini

Dineen and Stokely (1956) have described the osteology of the Sacramento perch, *Archoplites*, in considerable detail and in a general way delimited the course of the lateral-line through the bones. However, these bones were not considered in detail and cannot be used for comparative purposes. In addition, there are several points, mostly of a minor nature, in which this author differs with Dineen and Stokely. Therefore, before comparing *Archoplites* and *Acantharchus* with *Ambloplites*, some points will be discussed briefly.

Dineen and Stokely, following a rather common practice, described the canal system as "extending over the dorsal and lateral surfaces of the head," but these canals actually penetrated and progress through the bones with which they are associated. The nasal bones are not continuations of the frontal canals, although a continuance of the lateral-line canal passes through them, but are separate, well-defined lateral-line bones. The lateral-line canal does not extend from the sphenotic to the pterotic, since the former bone does not bear a lateral-line tube. The connection is made as described in *Ambloplites*. The "Y"-shaped bone mentioned by Dineen and Stokely, but left unnamed, between the epiotic and pterotic is the supratemporal-intertemporal. The bone above this one, likewise unnamed, is the lateral extrascapular.

Supracleithrum

The upper end of the supracleithrum in *Archoplites* and *Acantharchus* is similar to that of *Ambloplites*. However, some differences were observed. In *Archoplites* the posterior edge of the upper one-fourth of this bone bears some rather heavy serra (Pl. V, Fig. 29) which are not found elsewhere in the family, and the anterior opening is not completely covered by the posttemporal in either of the compared species. In this they differ from the rockbass. In the mud sunfish the canal is nearly straight, very short and bulbously inflated. The posterior opening is notched in *Archoplites*.

Posttemporal

There is considerable difference between the other two members of this tribe and *Ambloplites* as concerns the posttemporal bone. Some very strong, spine-like serra (11 to 14) ornament the posterior and posterodorsal one-fifth of the bone in the Sacramento perch. With the exception of the three species of the tribe Centrarchini, the posttemporal is aspinose in all centrarchid fishes. The anterior and posterior end of the posttemporal is tubular in both species compared with *Ambloplites*, but a relatively large, unevenly-walled vacuity occurs in the middorsal section of the canal in *Archoplites*. The dorsal, posteriorly-directed canaliculus springs from this region in the Sacramento perch, immediately behind which, and a short distance below, a third aperture occurs. This is the opening for the exit of the ventral canaliculus. The middle opening is lacking in Acantharchus, and the only canaliculus present in that species arises from the single posterior breach. This is supporting evidence for the statement (see discussion of external morphology) that this canaliculus is the ventral homologue rather than the dorsal. The conspicuous commissural canal seen in Ambloplites is lacking in Archoplites and is much reduced in Acantharchus. In the Sacramento perch the opening for the passage of the lateral-line canal into the supracleithrum is a simple hole in the ventral floor near the posterior end of the bone (Pl. V, Fig. 29) and in two specimens (2 of 15) an ectopic opening occurred in the lateral wall of the canal. The proximal opening of the commissural canal of Acantharchus is very large and opens through the floor of the bone, midway between the anterior and posterior openings, into the short canal which quickly funnels posteriad to a relatively small ventral aperture that communicates with the supracleithrum.

Supratemporal-intertemporal

Unlike the ossicle of Ambloplites the supratemporal-intertemporal (including the ventral arms) of the mud sunfish and Archoplites is almost completely tubular. However, like Ambloplites, the anterior, ventral arm is of greater diameter than the posterior. In Acantharchus both of the ventral arms are deeply notched at their extremities and the dorsal arm possesses a low, lateral keel, directed diagonally downward toward the leading arm. In both of the species now being compared with Ambloplites, the posterior arm is dovetailed into the anterior opening of the posttemporal.

Lateral Extrascapular

This small bone is about like that of the rockbass, but it is completely tubular and unnotched.

Dermopterotic

This element differs markedly from the observed morphology of *Ambloplites*. In *Archoplites* the bone takes the form of a half-tube, being completely uncovered, except by connective tissue, dorsally (Pl. V, Fig. 40). Near the posterior one-third of the bone a gap is seen in the lateral wall which allows the junction canaliculus (JPl) to leave the canal. In *Acantharchus* the form is even more divergent. Instead of being an open sulcus the bone is tubular, but very thinly so, which, in an India-ink injected specimen, causes the canal to appear to be open laterally, except at the posterior end, where a deep dorsal and ventral notch occurs. These notches allow connection between the supratemporal-intertemporal and preopercular junction respectively. The bone is very strongly declined posteriad.

Preopercle

Instead of possessing the very long upper slit seen in the ascending arm of *Ambloplites*, there is a short open space at the upper end of the preopercle in *Archoplites* (Pl. VII, Fig. 49), from which the first two canaliculi arise, whereas the ones below them have individual apertures. The leading edge of the bone is slightly wrinkled in front of this dorsal slit. The anterior breach of the horizontal arm is subdivided by a thin lamina of bone, making a total of six lateral-line apertures in the preopercle of Archoplites as contrasted with the four of Amblopiites and seven of Acantharchus. The posterior edge of the lower three-fourths of the ascending arm is moderately spinose and the horizontal arm, from just above the angle forward, is very heavily serrate in the Sacramento perch (Pl. VII, Fig. 49). The lower arm forms an angle of almost 90° with the upper, being less depressed than that of the rock bass. The preopercular openings in the last-named species are less capacious than in the other two. Dineen and Stokely (1956) did not illustrate this bone.

The preopercle of Acantharchus, when compared with that of Ambloplites or Archoplites, is an aberrant-looking structure. It is boomerang-like in general appearance, the lower arm being nearly equal to the upper in length and forming an angle with it of 110° or more. The whole bone is considerably more compact than either of the others and the lateral-line canal, except for the seven openings for canalicular exit, is entirely tubular. There is no open slit on the posterodorsal margin of the ascending arm. Instead, there is a slightly notched dorsal pore and a smaller one immediately below it (Pl. VII, Fig. 50). The hinder edge is entirely aspinose and the upper end is very strongly bent toward the eye in life.

Articular

The articular lateral-line canal is very similar to that of Ambloplites in both of the compared species, but in Acantharchus it is not so strongly cupped posteriorly.

Dentary

The dentary of Archoplites is like that of Amboplites in shape and number of openings. Dineen and Stokely (op. cit.) erroneously illustrated the dentary of the Sacramento perch as possessing four lateral-line openings. Acantharchus and, except Elassoma and the Enneacanthini, most centrarchids have five openings. In Acantharchus the bone is more like that of a short-jawed Lepomis in shape than the rockbass or Archoplites.

Suborbital Series

The number of suborbital ossicles in Acantharchus is five and six in Archoplites, Acantharchus thus differing from Ambloplites. The dermosphenotic of both compared species is unlike that of the rockbass. In the mud sunfish the bone is not curved around the orbit, but is very short, straight, funnel-shaped and does not have open areas in its walls. In Archoplites, the bone is curved around the orbit and dorsally flared as in the rockbass, but is is also flared at the ventral end and constricted in the middle. Near the constriction a small strap of bone extends transversely across the middle of the groove, or the entire anterior half of the bone becomes tubular. The five ossicles anterior to the dermosphenotic are usually of equal length and diameter and are either simple groovular bones or have a thin strap of osseous material across the lateral aspect of the open area. All, or any one of the small bones may, and usually do bear ventrolateral spines (Pl. VIII, Fig. 80). In very large individuals some of these ossicles may become tubular in their central parts. The jugal is about like that of Ambloplites.

The reduced number of suborbitals in Acantharchus is probably the result of the extensive shortening of the rostrum, for, although there are only five ossicles in the suborbital series, the infraorbital canal is complete. The suborbitals of this species are the heaviest in the family, often bear denticulations similar to those described in Archoplites, and are all usually groovular, or are only tubular near their center. All of the bones appear to have been physically shoved one into the other at their anterior and posterior ends, accounting for some of the shortening of the line. There is no true jugal, since a ligamentous attachment of the first ossicle behind the lachrymal with the hyomandibula is lacking. Ossicles 3 and 4 have become ankylosed and a short grooviform, ventrally-directed, bony branch occurs where external canaliculus 5 arises. These last facts account for the additional shortening derived from the pushing upward of the mouth, which is nearly terminal.

Lachrymal

The lachrymal of Archoplites is essentially the same as that of Ambloplites, but the spination, which is localized in the same region, is intensely heavy. The first suborbital of Acantharchus, however, differs greatly from that of the other two members of this tribe. It is aspinose, and about twice as long as wide (Pl. VIII, Fig. 77). The bone lies in a nearly vertical position before the orbit, being only slightly curved behind. Its canals are inflated, roundly tubular, and the two anterior branches are quite short. These changes are likewise apparently a modification for the abbreviated rostrum and terminal mouth.

Frontal

In Archoplites the frontal canal is T-shaped but otherwise very similar to Ambloplites, whereas in the mud sunfish the same bone is more like that of a Lepomis. In Acantharchus the commissural arm is very short, bulbously inflated and of a much greater diameter than any of the other frontal canals. The anterior opening is slightly deflected laterad.

Nasal

All members of the tribe Amblоplitini are alike in this respect.

Centrarchinae--Centrarchini

Most of the lateral-line bones in members of this tribe are more flattened than in the preceding tribe.

Supracleithrum

The supracleithrum (Pl. V, Fig. 32) is identical in the two species of Pomoxis, agreeing with the findings of Hofstetter, Dineen and Stokely (1958), which showed very few consistent skeletal differences between the two crappies. Centrarchus is like Pomoxis and all three are very similar to Ambloplites, but the anterior pore is not covered by the posttemporal and the posterior edge of the bone is notched. The canal, instead of passing diagonally downward in the supracleithrum, passes almost directly backward.

Posttemporal

In the species of Centrarchini the posterior end of the posttemporal is serrate as in Archoplites. These serrae are quite strong in Centrarchus (Pl. V, Fig. 30), especially in young fishes, but rather weak or obsolete in Pomoxis (Pl. V, Fig. 32). The bone is nearly always widely open dorsally in the flyer, with the exception of narrow straps of bone anteriorly, from which groove the two external canaliculi open. The commissural canal is represented by a simple hole in the floor of the groovular portion near the middle of the bone.

The posttemporal of Pomoxis is more like that of Archoplites than of Ambloplites, but a short commissural canal is found near the posterior one-third of the bone. The degree of dorsal covering is variable, but the posterior end is nearly always covered by bone in the white crappie, the condition being reversed in the black. In 38 of 100 specimens of P. annularis the anterior one-sixth of the dorsal canal was open; the remaining 62 specimens exhibited a completely covered canal as seen in Fig. 1 (Pl. I). In both species, when the entire canal is covered by bone, the origin of the two external canaliculi is indicated posteriorly by short raised areas in the bony covering. Ectopic openings are of common occurrence in both crappies.

Supratemporal-intertemporal

This small bone is of the usual shape but is entirely tubular, except for the deep notches in the lateral walls of the three open ends, rather than being an open gutter as in Ambloplites. The posterior arm is closely applied to the anterior opening of the posttemporal in Centrarchus, which simulates the condition seen in Enneacanthus. In Pomoxis the morphology of the supratemporal-intertemporal is variable. Ectopic openings into its walls are common and in one specimen of P. annularis the posterior arm was entirely free from the rest of the unit so that the bone was composed of a J-shaped part and a short straight segment behind. In another specimen of the same species the posterior opening was subdivided by a thin bony lamina.

Lateral Extrascapular

With the exception of flattening of this element in Pomoxis, it is similar to the one in Amblopitini.

Dermopterotic

Morphologically, this bone is like that in Ambloplites in being open laterally (in a few specimens it becomes tubular at the extreme anterior end) but differs from that species in being T-shaped at the posterior end. The dorsal arm of this "T" is twisted toward the anterior opening of the supratemporal-intertemporal and the ventral segment is skewed anteriad so that delivery of the lateral-line to the upper end of the preopercle can be effected. The preoperculomandibular canal of P. annularis is interrupted dorsally (Pl. I, Fig. 1). The osteological basis for this interruption is seen in the dermopterotic, in which the ventral arm of the "T" is lacking, the sides of the canal in this region being completely filled in with bone.

Preopercle

The upper one-third of the preopercle is open on the posterior edge and an additional five openings occur ventrally (Pl. VII, Fig. 57). The lower one-third of the ascending and nearly the entire length of the horizontal arm are deeply serrate, the individual denticulations being striate above. The horizontal arm describes an angle of about 90° with the ascending one. In 108 specimens each of both species of Pomoxis the upper half of the preopercle was narrowly open posteriorly. In 12 specimens of P. nigromaculatus and 14 of P. annularis the vertical wall separating the next to the last and third from the last openings of the horizontal arm were incompletely formed. In these specimens the preopercle possessed a long open dorsal slit, a raised tube at the angle and a slit-like aperture anterior to the angle, the latter being separated from the anterior terminus by a raised keel from the floor of the bone.

Articular

The articular canal in the crappies is slightly longer than that of Ambloplites, otherwise in this tribe it closely approximates that of the Ambloplitini in shape.

Dentary

The dentary of Pomoxis approaches that of the rockbass in shape, but the flyer possesses a shortened bone in this position which is more like one of a short-jawed Lepomis. In addition, the symphyseal opening in Centrarchus is the largest observed in the family.

Suborbital Series

The suborbitals are similar to those of Ambloplites in shape, varying from open grooves, or narrowly-covered grooves, to tubular structures, which are flared at each end. Including the dermosphenotic, which is like that of Archoplites, there are six in Centrarchus, usually five in P. nigromaculatus (rarely four and occasionally six) and usually four in P. annularis (occasionally 5). The jugal, correlated with the interrupted infraorbital canal, is lacking in all three species.

Lachrymal

In shape, suborbital one is similar to the same bone in Ambloplites, but the openings are relatively much longer and the spines much more numerous and longer. In Centrarchus these serrae are mostly restricted to the area between the ventral-most opening and the one just above it. In Pomoxis the spines extend along the lower one-half of the leading edge and ectopic openings are very common in the lateral walls of the canal (Pl. VII, Fig. 62).

Frontal

In general, the frontal elements are of a smoother texture and the lateral-line openings into them of considerably larger diameter than in the Amblopitini. The posteroventral opening is usually not cleft as in the rockbass, and the very large posterior nasal opening (Pl. VI, Fig. 41), instead of opening into the lateral wall of the canal, opens directly through the dorsal wall.

Nasal

These bones are generally more dorsoventrally flattened and flared than in the Amblopitini.

Lepominae--Enneacanthini

There are several lateral-line peculiarities which distinguish the Enneacanthini from all other sunfishes. There is very close rapport between Enneacanthus gloriosus and E. obesus in regard to morphology of the lateral-line bones and, in general, great similarity between these two and Mesogonistius. Although the same elements are involved, there is considerable divergence expressed in these elements when compared with the Centrarchinae. All lateral-line bones are inflated in this tribe.

Supracleithrum

Unlike Ambloplites, the supracleithral canal in this tribe is bulbously expanded anteriorly and reduced posteriorly (Pl. V, Fig. 33 and 35). In Enneacanthus the anterior opening is in contact with the posttemporal aperture but separated from it by a short diastema. In Mesogonistius the posttemporal covers the opening.

Posttemporal

As can be seen in Figs. 33 and 35 (Pl. V), there is considerable dissimilarity between the posttemporals of the Enneacanthini and any of the species thus far discussed. In Enneacanthus the posterior openings cover about two-thirds of the bone's width and the canal narrows only slightly anteriorly. The anterior opening is tubular except at the ventrolateral margin, where a prong of bone (Pl. V, Fig. 35) extends cephalad. About one-third of the total length of the bone, from the posterior end, a relatively large, but short, commissural canal is given off. In Mesogonistius the posttemporal is entirely different (Pl. V, Fig. 33). The lateral-line component is not unlike one of the valves of the great clam, Tridactna, the whole complex being widely open. There is a V-shaped depression near the middle of the mesial wall and the anterior end is ventrally constricted and gently depressed. A commissural canal is lacking, connection being made with the supracleithrum by a simple hole in the posterior floor of the groove.

Supratemporal-intertemporal

Compared with other centrarchids this bone is huge, being as large or larger than the posttemporal. In Mesogonistius the posterior arm is not in direct contact with the anterior end of the posttemporal but is otherwise like that of *E. gloriosus*. In the last-named species the bone has the shape of an asymmetrical "Y" (Pl. V, Fig. 35), the posterior arm being as long as the dorsal one and nearly twice as long as the anterior, ventral arm. The greatest diameter of the upper arm is found at the dorsal extremity, from whence it funnels downward to the point where the lower branches join it. The long posterior arm is in direct, very intimate tandem with the anterior end of the posttemporal. The ventral projection, mentioned above, from the last-named bone fits neatly into a depression on the ventral side of the supratemporal-intertemporal and a V-shaped prong from the last bone enters the posttemporal. This is the only centrarchid genus in which such a connection was observed. The anterior arm is largest anteriorly and is definitely deflected downward toward the dermopterotic.

Lateral Extrascapular

Like the others, this lateral-line bone is inflated. It is pipe-like and closely abuts the upper end of the supratemporal-intertemporal in Enneacanthus, but is slightly removed from that junction in Mesogonistius. It is completely tubular in all three species.

Dermopterotic

This bone is morphologically similar in the three enneacanthine species but differs from that of Ambloplites. The ossicle is a closed, tubular structure, except for its lateral-line openings, and is Y-shaped posteriorly. There is no osseous connection with other lateral-line elements posteriorly, but the anterior opening lies in direct contact with two bones. The dermopterotic is notched ventrolaterally, the dorsoposterior edge of the dermosphenotic fitting into the notch. Anteromesially the bone touches the ventromesial tip of the frontal, forming a postocular sinus closed on three sides.

Preopercle

As in the other elements discussed above, the preopercle is very similar in these three species and differs from Ambloplites and its allies. The lateral-line diameter is relatively larger than in the rockbass and the upper end is equal to the lower in this respect. The angle between the two arms is about 90°. Except for the five lateral-line apertures the entire bone is tubular and aspinose on the posterior margin (Pl. VIII, Fig. 57). The mesial, flat plate nearly extends the entire length of the canalular portion.

Articular

The lateral-line segment of this bone is about like that of any other centrarchid, but runs directly through the bone rather than diagonally downward as in Ambloplites.

Dentary

The lower tooth-bearing jaw bone in this tribe is very different from those of other centrarchids, shaped as in a short-jawed Lepomis, but with only four lateral-line apertures including the terminal pores.

Suborbital Series

In contrast with the sunfishes thus-far discussed, there are never more than three suborbitals present per side in the tribe Enneacanthini. The dermosphenotic is usually present (sometimes lacking in E. gloriosus) and is a short funnel-like bone. In Mesogonistius the two suborbitals anterior to the dermosphenotic are most often pipe-like bones notched at either end. These two elements are rather long and slender in E. obesus, extending slightly beyond the middle of the eye. The most variability, with respect to this series, was observed in E. gloriosus. The suborbital immediately below the dermosphenotic is usually a tiny, flattened, scale-like particle and the ossicle anterior to this, probably number 4, varies from a well-formed tube to a U- or V-shaped open gutter. In about 50 per cent of the specimens observed all of the suborbitals, except the dermosphenotic were lacking on both sides of the head in E. gloriosus.

Jugal

This bone is always lacking in the tribe Enneacanthini.

Lachrymal

This peltate bone diverges sharply from the morphology of all other sunfishes and observations of it, as with other elements of a gross morphological nature, give some insight into the reason for the peculiarities of the external anatomy mentioned earlier. The bone, in all three species of the tribe, is smooth, its upper end being broadly V-shaped. The lateral-line tube possesses only three openings (Pl. VII, Fig. 71), dorsal, ventral and anterior. One specimen of E. obesus from Gilcrest, Florida lacked the anterior branch of the right lachrymal.

Frontal and Nasal

The general configuration of these bones is similar to those in the rockbass.

Lepominae--Micropterini

Although Allis (1904) illustrated the lateral-line bones in Micropterus dolomieui, his figure does not portray the anatomy of these bones in such a way as to be usable for comparative purposes. The same is true of Gregory's (1933) figures. The most outstanding feature of the lateral-line habitus in the Micropterini is the relative smallness of the canals when compared with those in the Ambloplitini and Enneacanthini.

Supracleithrum

The supracleithrum of the black bass is not markedly different from that of Ambloplites. The canal is of greater diameter posteriorly than at the anterior opening, which is covered by the posttemporal. In Micropterus salmoides and M. punctulatus the canal does not attain the trailing edge of the bone, but opens on the mesial side a short distance anteriad to it. From this point the canal continues caudad as a connective tissue tube where connection is made with the lateralis. This course is indicated on the bone by a shallow groove.

Posttemporal

There is some variation from the condition seen in Ambloplites in that this bone is always at least partially tubular in nature. The anterior portion is generally tubular, whereas the remaining part is often a short open groove. At the posterior end of the groove a dorsal element, which in life gives rise to the dorsal external canaliculus, originates and continues as a rather deep, open furrow to within a short distance of the posterior edge of the bone, or as a furrow proximal to its origin. In some specimens the entire branch is tubular throughout its length. The ventral canalicular branch is subject to the same kind of variation as the dorsal one and is about one-third shorter than the branch above, except in M. punctulatus, in which the ventral branch is usually slightly longer than the dorsal one. This tube is unlike any in the other centrarchids in that it does not originate from the main canal but as a ventral diverticulum from the dorsal branch, the point of origin varying from near the origin of the dorsal one to a point close to the middle of that branch. The commissural canal is similar to that in other sunfishes, always tubular and short, but differs from other members of the family, except Lepomis, in arising as a diverticulum from the ventral canalicular branch rather than from the main canal, as in Ambloplites and Enneacanthini.

Supratemporal-intertemporal

This small bone has the usual Y-shape and is entirely tubular except for the lateral notches at the openings. As shown by Allis (1904) the posterior end of the arms of the "Y" is in direct contact mesially with the posttemporal and is longer than the anterior one. The anterior end is separated from the dermopterotic by a short gap.

Lateral Extrascapular

Contrary to Allis' (1904) figure, the lateral extrascapular is not a straight bone but is slightly sigmoid. When the bone is entirely tubular both of the openings are flared and notched laterally but it varies from an open gutter to a pipe-like structure.

Dermopterotic

In most respects this bone is very similar to that of Ambloplites, but it is Y-shaped where communication with the supratemporal-intertemporal and the preopercle occurs. The "Y" is always open and cup-shaped, but the rest of the canal varies from a narrowly-open, V-shaped slit to a bone with a tubular anterior portion and an open posterior part (or vice versa). Thin straps of bone may occlude lateral areas anywhere along the bone's length. The anterior opening, as in the tribe immediately above, touches the frontals and dermosphenotic to form a postocular sinus completely closed by bone on three sides (Allis, 1904).

Preopercle

The shape of the micropterine preopercle is strongly suggestive of Acantharchus, e. g., boomerang-shaped, and the posterior edge is always smooth. An angle of 100^{0} to 105^{0} is formed by the horizontal with the vertical arm, the leading edge of the mesial plate nearly always being wrinkled opposite the angle of the bone. Triangular depressions opposite the three middle apertures of the lateral line mark the exit of external canaliculi)(Pl. VII, Fig. 52). Normally there are two terminal and three middle openings, one each above and below the angle, and one at the angle of preopercle. However, the anterior terminal pore may become subdivided by an additional bony strut, in which case six exits are formed. These observations are in agreement with Allis (1904).

Articular

The articular canal is generally like that of the other species, except that the entire posterior part of the canal is sharply deflected upward to receive the lateral-line canal from the preopercle.

Dentary

The dentary canal, as in all centrarchids except the Enneacanthini and *Elassoma*, possesses the typical five lateral-line openings. Although the bone is greatly prolonged, these exits retain the same relative position, but are considerably smaller than in other species. Most of the elongation of the jaw seems to have occurred between the posterior end of the bone and the third opening of the dentary canal. This observation also applies, as seen in Table 3, to the long-jawed species in the tribe Lepomini, such as *L. cyanellus* (Pl. VI, Fig. 44).

Suborbital Series

In adult *Micropterus* there are almost invariably seven suborbitals, if the dermosphenotic and jugal are counted, but there is some evidence that ossification is not complete in the series before a size of 100 to 150 mm. in standard length is attained. This matches the largest number of ossicles found in the Centrarchidae and is the same as found by Allis (1904) in *M. dolomieui*. The dermosphenotic is usually funnel-shaped and is either an open gutter or a tubular pipe. All of the suborbitals are variable, but large adults tend to have tubular bones, deeply notched at each end and resting on a flattened plate. This latter condition is illustrated by the jugal of *M. salmoides* (Pl. VII, Fig. 65). The bones fit together end to end like a series of tile pipes, the V-shaped notches, their apices directed away from each other, leaving a spindle-shaped opening through which the narrow external canaliculi communicate with the exterior.

Jugal

In all of the basses the jugal is present and similar to that drawn for M. salmoides. However, in M. coosae, the jugal sometimes fuses with the suborbital behind it to form a compound bone like the one in Fig. 79 (Pl. VIII). Since only a few specimens of this species were observed, no data as to the frequency of this fusion are available. An ectopic aperture is also shown in the figure.

Lachrymal

The shape of the bass lachrymal is different from that of Ambloplites, being narrower at the ventral end than dorsally as in that species. In the other species-groups thus far discussed almost the entire posterior margin of the lachrymal has been involved in forming the anterior orbital rim, but, as seen in Fig. 78 (Pl. VIII), only about the upper one-half of the bone is thus involved in Micropterus. Contrasted with the Ambloplitini (except Acantharchus) and Centrarchini, the bass lachrymal lacks serrae completely. From a lateral view the highest part of this bone is the anterodorsal corner, i. e., the bone is prolonged. As is usual, the ventral aperture is the largest and opens near the margin of the bone. The other openings, at the ends of fairly long, slender branches fall quite short of the margin (Pl. VIII, Fig. 78). Their lateral walls are very deeply cleft and the flat plate before them bears shallow grooves. The shape of these grooves corresponds to that of the external canaliculi which occupied them during life.

Frontal

The frontals of Micropterus are much flatter dorsoventrally than in most of the other centrarchids, especially at the posterior end. In other species the posterolateral portion of the canal is curved around the orbit, but in basses the canal is nearly straight in this region and suddenly inflated where it contacts the postocular sinus. The entire frontal complex is strongly Y-shaped posteriorly, the arm discussed above extending nearly straight backward and downward. The commissural canal, except in M. treculi, with arms of approximately of equal length, is about one-half the length of the other, and bends forward to end in an opening near the midline. The coronal opening is protected by a slightly raised, thin bony lamina. The interorbital opening opens into the dorsal wall of the canal, but is peculiar in that it is covered dorsally by a rampart (Pl. VI, Fig. 46). The anterior portion of the canal continues forward and widens to empty into the sinus between the frontal and the nasal.

Nasal

Although the nasal canal is relatively small, the bone itself is fairly large (Pl. VI, Fig. 48). Unlike most other centrarchid nasals, which are circular or subcircular in section, the bass counterpart is flattened, very widely flared posteriorly, and is nearly straight rather than being curved outward.

Lepominae--Lepomini

There are some distinctive characteristics of the lateral-line elements in the tribe Lepomini which are pointed out below.

Supracleithrum

There are two morphological groups in the Lepomini as regards this bone, those with a short, broad supracleithrum and those with a long slender one. These relationships are shown in Table 2. The anterior supracleithral opening is covered by the posttemporal in L. auritus, L. megalotis, L. microlophus, L. cyanellus and L. gibbosus; in the remaining species it is partially free from the posttemporal. The canal, as is usual, passes through the supracleithrum to open on the mesial side of the bone a short distance in front of the posterior edge. In most of the species the canal is only slightly inflated, but in L. humilis, in which the canal extends nearly straight back instead of declining, it is two or more times greater than in any other centrarchid and bears a notch near its origin. The supracleithrum of L. cyanellus possesses the most acutely depressed lateral-line canal in any of the Lepomis (Pl. V, Fig. 31). In this species the supracleithrum is many times higher than wide, having a height-width index of 4.00 (Table II). Other peculiarities observed in this tribe concerning this bone are: low keel marks the course of the lateral-line canal in L. symmetricus; in L. microlophus, a second short branch opening freely on the skin, is occasionally found; few spines (2 or 3), located posteroventral to the posterior lateral-line aperture, are often seen in specimens of L. megalotis breviceps.

Posttemporal

The posttemporal is similar to that of Micropterus in general character, but there are some specific differences. The bone is seldom boat-shaped, as in Ambloplites, except in immature forms and exceptional specimens of L. humilis (Curd, 1959). The canal is usually proximally tubular (Pl. V, Figs. 34 and 37), the tubular part being followed by an open area. It is from this central open region that the dorsal canaliculus originates, differing in this regard from the basses. Another point of divergence from *Micropterus* and other centrarchids is the mechanism giving rise to the ventral canalicular branch. In the Centrarchinae the branch originates as a continuation from the main canal; in *Micropterus* a branch from this canal forms the commissural canal; and in the Lepomini, this last condition is reversed, i. e., the ventral branch is a diverticulum from the commissural canal. The ventral canalicular branch is of variable length, being long and slender in *L. auritus* (Pl. V, Fig. 37) and short in *L. microlophus* (Pl. V, Fig. 34) and *Chaenobryttus*. In the last-named form and *L. macrochirus* the ventral canal is very often subobsolete and in one specimen of the bluegill (one of 18) was completely lacking.

TABLE II

LENGTH/WIDTH RELATIONSHIP OF THE SUPRACLEITHRUM IN THE LEPOMINI. WIDTH AT WIDEST POINT. N = 50

Species	Length/Width
Chaenobryttus	3.50
L. macrochirus	2.25
L. auritus	2.50
L. punctatus	2.67
L. marginatus	2.25
L. megalotis	2.33
L. microlophus	2.90
L. humilis	3.00
L. symmetricus	3.67
L. cyanellus	4.00

Usually, the commissural branch originates as a simple hole in the ventral wall of the posttemporal canal at about the middle of the bone and continues diagonally downward to meet with the supracleithrum. The ventral canalicular branch originates from about the middle of the posterior edge of the commissural branch, except in L. microlophus (Pl. V, Fig. 34), in which the very short canal arises at the extreme posteroventral edge of the tube, and L. auritus, in which the long slender branch originates near the point of divergence from the main canal of the commissural branch. A second, ectopic commissural branch, of much smaller size than the normal one, is sometimes seen in the orangespotted sunfish, where the canals are enormously inflated (Pl. VI, Fig. 42).

Supratemporal-intertemporal

This bone, as in the other sunfishes, is Y-shaped. In L. microlophus the lower arm is longer than the dorsal one. The anterior branch is about two-thirds longer than the posterior one and is about twice the diameter of the latter. All three openings are usually moderately notched laterally. The posterior opening is separated from the anterior aperture of the posttemporal by a short gap as is the anterior one from the posterior opening of the dermopterotic. Other members of the tribe follow closely the description of the redear sunfish, except the warmouth, L. humilis, L. symmetricus and L. punctatus. The description of the supratemporal elements fits very nicely the condition in Chaenobryttus and Lepomis symmetricus. Recalling this bone in Enneacanthus one is struck by the similarity of size in L. punctatus and L. humilis, although the bone does not quite attain proportions equal to the posttemporal in Enneacanthus.

Lateral Extrascapular

The whole bone is slightly tilted forward, usually touching the dorsoventral tip of the supratemporal-intertemporal (this bone is dovetailed into the upper end of the supratemporal-intertemporal in L. punctatus), and is moderately sigmoid in outline, except in L. symmetricus where it is shaped like a boomerang. In most of the species the ventral opening is slightly flared, so that the bone is wider ventrally than dorsally. The bone is mostly tubular in nature, but in L. gibbosus it is in the form of an open gutter and in L. auritus it is lateromesially flattened in the dorsal one-third. The upper and lower apertures are cleft ventrally.

Dermopterotic

The shape of this bone is like that of Micropterus and is mostly an open groove, over which thin transverse bony straps may occasionally be found. In. L. microlophus the canal is tubular posteriorly (except the "T" arms) but groovular anteriorly. It is almost entirely tubular in the green sunfish (Pl. V, Fig. 38). An additional unique feature in L. cyanellus is a thin lamina of bone extending laterally outward from the bone. Three species, L. macrochirus, L. microlophus and L. punctatus, have the bone so situated that the canal appears strongly depressed from the vertical. In L. punctatus, L. microlophus and L. humilis a thin strap of bone extends across the open groove near its anterior end and another just in front of the posterior end. In these areas the canal is slightly constricted, leaving a central, gently bulging segment. In the last three species the receiving end is in the form of a cup with a sulcus in its dorsal (to receive the lateral-line from the supratemporal-intertemporal) and ventral (to accommodate the upper end of the preopercle) walls. The anterior end of the inflated bone in the orangespotted sunfish is flared outward funnel-like. The dermopterotic of *Chaenobryttus* is similar to that of *Pomoxis*.

Preopercle

The general shape of the bone is essentially that of *Ambloplites*. The angle formed by the vertical and horizontal arms is about 90°, except in *L. symmetricus* where the angle is 110°to 115°. The posterior margin of the ascending arm and the lower margin of the horizontal one bear serrae in most of the species, but the number and size of the serrae are variable from species to species. In *L. auritus* (Pl. VII, Fig. 53) and *L. symmetricus* (Pl. VII, Fig. 61) the serrae are not striate above, whereas in the remaining species, including the warmouth, they are marked above by weak to strong striae. In *L. symmetricus*, *L. cyanellus* (Pl. VII, Fig. 60), *L. gibbosus* and *Chaenobryttus* the spines are restricted between an area slightly above to slightly below the preopercular angle. In *L. humilis* (Pl. VII, Fig. 56) the spines are localized in the area extending from the upper edge of the opening at the angle to the posterior margin of the anterior-most aperture of the preopercle. In the remaining species the denticulations usually occupy the lower half of the ascending and nearly the entire ventral length of the horizontal arm. In all of the species, the adult spination varies from mere undulations to a heavy saw-tooth condition. In the bluegill (Pl. VII, Fig. 55) there seems to be an alternation of patches of large serrae with patches of smaller, striate ones.

In the adult condition there are no long open gaps such as seen in *Ambloplites* and the modal aperture number is six, although specimens with five, because of failure of certain of the separating bars to develop, or seven pores, due to the subdivision of a normally single opening, are not uncommon in any of the species. Lepomis cyanellus (Pl. VII, Fig. 60) normally has seven pores, an extra bony tube being found near the dorsal tip of the bone. In only six specimens of 118 was this opening lacking. Lepomis humilis is variable for this character, the ratio between specimens with six and those with seven openings is about one to one.

With the exception of the lateral-line openings and the aberrant L. humilis, the preopercle is a completely tubular bone. The tubes of the horizontal arm are arranged in tandem, two at the angle and two directed anteriad (again, except L. Humilis). The anterior two openings are separated by a shallow longitudinal sulcus. In the orangespotted sunfish the canal is, like all others in this species, enormously enlarged and, except for very narrow straps of bone extending from the flat plate to the leading wall, the canal is a U-shaped groove (Pl. VII, Fig. 56). The last and next to the last two of these straps are usually sulcate and bifurcated at their insertion upon the plate. This bone, as well as others, may, in some populations, be found as a completely open gutter (Curd, 1959).

Articular

The angle of descent and shape of the lateral-line tube through this element is similar to that of Ambloplites. The canal passes almost straight through the bone in L. cyanellus, rather than diagonally, and in L. humilis it is little more than a hollow shell.

Dentary

As far as the dentary is concerned there are two series in the Lepomini, those with a long jaw and those with a short jaw. In the first group, comprised of Chaenobryttus, L. cyanellus (Pl. VI, Fig. 44) and L. humilis, the canal axis is nearly straight. In the remaining species, from the next to the last anterior opening to the terminal one, the canal is strongly deflected upward, as in L. macrochirus (Pl. VI, Fig. 43). The depth at the posterior end of the bone is equal, or nearly so, to the length of the dentary in the last group, but in the long-jawed forms the ratio of length to depth is about 1.75. Another difference between the two types of jaw bones is the relative size of the masseter muscle scar, which is quite extensive in the short-jawed species and considerably smaller in species like the green sunfish and rockbass. This is explainable by the physical laws of levers. A long lever, in this instance a dentary bone, if the fulcrum remains in a constant position, requires less force for movement than does a short one. Most of the shortening of the jaw has involved the lower ramus, from the posterior end to about the middle of its length. The upper ramus has become bent upward and forward to compensate for the loss of length in the lower.

TABLE III

COMPARISON OF AVERAGE DISTANCES BETWEEN LATERAL-LINE OPENINGS IN LONG AND SHORT DENTARY BONES OF LEPOMINI, EXPRESSED AS PARTS OF TOTAL DENTARY LENGTH

Lengths Compared	Long Jaw	Short Jaw
Posterior End to Aperture one	2.8	3.4
Posterior End to Aperture Two	1.4	2.0
Posterior End to Aperture Three	1.1	1.4

All species possess five lateral-line openings, which are disposed in positions shown in Figs. 43 and 44 (Pl. VI). Concomitant with the shortening of the lower ramus there has been a relative decrease in the distance between the posterior opening and the two apertures immediately in front of it (see Table III). These two last-mentioned openings are peculiarly formed by an arch of bone anteriorly and a U-shaped opening behind.

In the orangespotted sunfish the dentary canal occupies almost the entire width of the bone and the openings into it are very large. In some abnormal specimens the canal may appear as an open channel with undulating sides (Curd, 1959). Because of the extreme aperture size, the indices given in Table III will not hold for this species.

Suborbital Series

In the Lepomini the infraorbitals range from six to eight. L. microlophus possesses six of these small bones, all of which are usually tubes laterally notched at either end. These tubes are often dovetailed together to form a continuous line. The second ossicle behind the lachrymal (probably a fused element) is about twice the length of the others and occasionally bears a short ventrally-directed tube near its center. The jugal is a very small scale-like particle. In L. megalotis the number of suborbitals varies from six to seven (usually seven). The jugal and all of the elements posterior to it, except the dermosphenotic, are usually open grooves, but some bear a narrow bony strap near the center. Suborbitals three, four and five are often dovetailed together. Lepomis humilis, L. auritus and L. symmetricus also possess six suborbital bones, but the six remaining species in the tribe bear seven. In the last two species the dermosphenotic is of the usual shape and the others, except for thin straps near their middle, are mostly open V-shaped or U-shaped bones. The jugal, which is lacking in L. symmetricus, is always a minute bone similar to that of L. gibbosus. The middle members of the series are usually associated together like tile pipes.

The dermosphenotic of L. humilis is shaped like a funnel with the stem opened widely and, with the exception of the jugal, is the shortest in the series. The bones normally vary from shallow, open troughs to those with only a thin bony strip across the middle, as in Curd's (1959) anomalous specimens. The jugal is either completely lacking or represented by a minute particle of ossified material.

In species usually containing seven suborbitals, the jugal is always a very small, nontubular ossicle. Such a bone is illustrated for Lepomis gibbosus (Pl. VII, Fig. 59). The dermosphenotic and the two suborbitals immediately anterior to it are very often tubular in nature, but deeply cleft at their anterior and posterior ends. The others are mostly in the form of shallow gutters and the middle three are usually coupled as described above.

Lachrymal

Since there is considerable difference between all the members of the tribe Lepomini, this bone will be described briefly and compared with that of Ambloplites and with each species within the tribe. There are four openings in all of the species, as in all of the forms except Elassoma and Enneacanthus and Mesogonistius. There are several similarities between Ambloplites and the Lepomini. The upper and posterior margins of the bones are saddle-shaped in a facial view, except in L. symmetricus (Pl. VII,

Fig. 68), in which the posterior margin is nearly straight. Another similarity is seen in the serration, which, like that of the rockbass, is usually found at the anteroventral margin. These serrae may or may not be striated above. The length-width relationships of this bone in the various species are shown in Table IV.

TABLE IV

COMPARISON OF GREATEST LENGTH/GREATEST WIDTH OF THE LACHRYMAL BONE IN LEPOMINI. N = 25. SPECIMENS 75 mm. OR MORE IN STANDARD LENGTH

Species	Length/Width
Chaenobryttus	1.37
L. humilis	1.45
L. cyanellus	1.16
L. megalotis	1.03
L. macrochirus	1.28
L. marginatus	1.25
L. auritus	1.18
L. microlophus	1.24
L. symmetricus	1.81
L. punctatus	1.52

Chaenobryttus. The lachrymal of the warmouth is like that of Ambloplites and unlike those of other members of its own tribe, in bearing a notch posteroventrally at the point where the infraorbital canal enters the bone (Pl. VII, Fig. 63). At the posterodorsal and anterodorsal edges the bone bears some salient prong-like processes, the anterior one being narrow and sharp pointed. All of the openings are capacious and the upper one is surrounded by a shallow depression. The anterior branches are only slightly demarcated. Ectopic openings may occur anywhere in the lateral walls and the orbital edge of the bone is often crenulated. The spines are restricted to the anteroventral edge.

Lepomis humilis. In the orangespotted sunfish the lateral-line tube of the lachrymal is very large and the two anterior openings are more often confluent than not (Pl. VII, Fig. 75). These arms are usually not demarked at all, or if they are, it is only at their anterior extremities. The sharp prong at the dorsoanterior tip was illustrated by Curd (op. cit). The lateral walls may be partially or wholly lacking in any sample of specimens observed and, as seen in a population from the Verdigris River, Oklahoma, may involve a large percentage of the individuals. This may be a genetically variable characteristic in this species, but more work needs to be done before any generalization can be made. Spination varies from entirely lacking to 10 to 15 sharp serrae localized just in front of the lowest of the anterior pores. The ocular rim is usually smooth and the bone is widest in the dorsal third.

Lepomis cyanellus. The ventral aperture of the green sunfish lachrymal is in the form of an elongated slit (Pl. VII, Fig. 64), a character which is shared with *L. microlophus* and *L. auritus*. In shape, the bone is rather parallelogrammatic and not peltate as in *Ambloplites* and a few others. The dorsal and ventral parts of the canal seem to be pulled back toward the eye and the middle is pushed forward. All of the openings are flared, giving the canal the appearance of a series of pyramidal structures attached at their apices. Cancellate bone usually fills the spaces between the anterior branches, and the ocular rim is usually ragged. The serrae are restricted to a small area just in front of the anteroventral opening, or completely lacking, in specimens of 100 mm. or more in standard length. The lachrymal of young *L. cyanellus* is further discussed below.

Lepomis megalotis breviceps. The bone in this form, with some qualifications, is similar to that of the rockbass. The general contour of the canal is like that of L. cyanellus, but the dorsal-most pore is the smallest of the four openings and the bone is widest at its ventral end, where the anterior corner is prolonged. The few spines (six or seven) that are present are fairly large and are restricted to the small area in front of the more ventral of the two anterior openings. The longear sunfish, and three other species (L. macrochirus, L. marginatus and L. auritus), differ from other Lepomini in the arrangement of the anterior arms. The dorsal one is slightly depressed from the superior edge (Pl. VII, Fig. 73) whereas the ventral branch is angled directly toward the anteroventral corner. The ventral arm is nearly twice the length of the upper one. There is very little porous bone between the branches. Unlike any other member of the tribe, the opening communicating with the rest of the infraorbital canal is near the center of the ventral edge of the bone; in the other species this opening is normally found near the posterior corner. The ocular rim is usually smooth.

Lepomis macrochirus. As seen above, the ventral branch of the anterior two is considerably longer than the dorsal component and the spination is localized in the same general region. The ocular margin is usually smooth and the areas between branches are often filled in with osseous cement. The shape of the canal is not like that of the rockbass and the green sunfish. The lower two-thirds of the posterior edge of this ossicle is nearly straight and the upper end is deflected backward for a short distance before it terminates near the middle of the upper edge. The bluegill (100 specimens) possesses a large process from the upper posterior corner of the lachrymal (Pl. VII, Fig. 70) which seems to be peculiar to the species.

Lepomis marginatus. The general form of the lachrymal of *L. marginatus* recalls that of the longear sunfish. However, it is not as wide ventrally nor is the canal so capacious, nor is the ocular margin so strongly procurved. Cancellate bone between branches is scarce. The area of serration is restricted to the same region (Pl. VII, Fig. 66), but the spines are very few and nearly or sometimes completely obsolete.

Lepomis auritus. The yellowbelly sunfish possesses a most distinctive lachrymal. It is entirely aserrate, even in very young individuals, which is in itself peculiar. It is richly supplied with cancellate bone between the branches and is the only member of the Centrarchidae which has a large prong-like process, bearing a small keel near its center, at the posteroventral corner (Pl. VII, Fig. 72). The general shape of the canal is otherwise much as it is in *L. cyanellus*.

Lepomis microlophus. In canal and shape the lachrymal of the redear sunfish is most like that of *L. cyanellus*. The ventral-most of the anterior arms, however, is not directed toward the anteroventral corner, but slightly above this point and, in the adult, serration is usually reduced to a mere undulation, just below the ventral anterior opening. It is fairly well developed in specimens 25 to 30 mm. in standard length.

Lepomis symmetricus. The lachrymal is nearly two times longer than wide in this species (Table IV), being considerably wider dorsally than ventrally. The anterior arms open near the leading edge of the bone and the spination is restricted to about the same area as in the green sunfish.

Lepomis punctatus. The similarity in proportions between the redspotted sunfish and *L. symmetricus* is obvious from Table IV, the bone being about one and one-half times taller than wide. In this species the lachrymal is strongly parallelogrammatic, except for the posterior upper half, which curves backward (Pl. VII, Fig. 76). The two anterior branches, instead of opening near the leading edge, open near the center of the bone. A shallow sulcus extends from the ventral anterior opening to the anteroventral corner, where the moderately developed serrae are situated.

Frontal

The Lepomini are divided into two groups, those with four and those with five openings in the frontal bone. The first group is comprised of *Chaenobryttus*, *L. cyanellus*, *L. symmetricus* and *L. macrochirus*, which are usually like the rockbass. There were four apertures in 72 of 100 specimens of *L. symmetricus* and in four of 22 specimens of young *L. cyanellus* (22.0 to 25.6 mm. in standard length) possessed an additional opening. This fifth opening was not observed in any adult *L. cyanellus*.

The frontal bone is similarly shaped in most of the lepomine species, being more convex in species with short jaws and flatter in the long-jawed forms. The lateral-line canal is roughly Y-shaped, the anterior opening being largest, and the lateral arm about three times the length of the mesially-directed commissural arm. The latter arm is rather strongly curved mesiad and slightly anteriad. The four openings, in species with this arrangement, are disposed as follows: one at the anterior end of the bone, one about a third of the total canal length behind the first one, one at the coronal suture, near the posteromesial edge, and one near the posterolateral margin. In species with five openings, as in *L. auritus* (Pl. VI, Fig. 45) an additional pore is formed somewhere between the lateral one and the point where the commissural branch issues. In large specimens the edges of the canals are usually flanked by massive depositions of cancellous bone and a large transverse keel may be formed across the posterior arms. In some specimens a high boss overlies the canal adjacent to the mesial pore. In ten of 100 specimens of *L. symmetricus* an additional opening appeared immediately laterad to the usual mesial one, and in 14 of 100 fish there were one or two tiny ectopic openings in the crotch of the "Y".

The following species usually possess five openings into the frontal lateral-line canal: *L. auritus*, *L. marginatus*, *L. megalotis*, *L. gibbosus*, *L. humilis*, *L. punctatus* and *L. microlophus*. The fifth opening, as shown in *Lepomis auritus* (Pl. VI, Fig. 45), lies in the arm which communicates with the postocular sinus. Concerning this skeletal element, *L. marginatus* is reminiscent of the *L. auritus* condition, but one of nine specimens lacked the fifth aperture. In the pumpkinseed and longear sunfish, the sagittal suture is marked by an elevation of the bone in that region; this causes the commissural arm to appear considerably straighter than that of *Ambloplites* and *L. auritus*. In *L. microlophus* of 150.0 or more mm. in standard length the interorbital opening is often at the end of a very short bony tube, usually directed gently caudad, from the side of the mother canal. Although the redspotted sunfish has five frontal openings, the shape of the bone is more like that of *L. cyanellus*. As pointed out by Curd (1959) the frontal canals of *L. humilis* are huge in comparison with other members of the family. These canals occupy about two-thirds or more of the width of the frontal. The interorbital opening is twice the size of any other one and is nearly round in shape. The fifth opening was present in 75 per cent of the specimens observed, whereas, in the other 25 per cent, later deposition of aerolated bone had completely, or nearly, obliterated the pore. The fifth pore may have failed to develop in some of the specimens; but there is probably no way of verifying the latter statement. Curd's (op. cit.) normal specimens only had four apertures and many of the abnormal ones possessed roofing bone only from the anterior edge of the interorbital opening forward.

Nasal

The nasal bone is sigmoid (laterad anteriorly, mesiad posteriorly) in *L. auritus*, *L. gibbosus*, and *L. megalotis*, but straight posteriorly and gently curved laterad in the remaining forms of the tribe, thus corresponding to the condition of *Ambloplites*.

Remarks on Ontogeny of the Lateral-Line Ossicles of Lepomini

During the course of this study it was possible to take a few notes from a series of green sunfish ranging from 11.0 mm. to over 300.0 mm. in standard length. In a specimen of 11.0 mm. length all of the scales are of the cycloid type and none of the lateral-line bones bear serrae. The latter begin development sometime between the attainment of lengths of 15.0 to 25.0 mm. In the earliest stage observed the passageway of the supracleithrum is represented as a small round hole which becomes the posterior opening in the adult. The tube of this bone gradually begins formation from both sides, near the posterior edge of the bone, and gradually fills in the spaces until the tube is completed at about 30.0 mm. length.

At 11.0 mm. the posttemporal canal is completely uncovered, but, except for the dorsal canal, which never closes, it is covered by the time a length of 35.0 mm. is reached. In the 11.0 mm. fish both the supratemporal-intertemporal and the lateral extrascapular are small flat bones with the edges turned upward. These bones also attain the adult condition by 35.0 mm. The dermopterotic has been completed by 11.0 mm., except for the lateral walls which appear sometime before the 35.0 mm. stage. The preopercle of an 11.0 mm. fish is a simple folded bone, looking very much like the adult preopercle of Elassoma. This bone is one of the last to complete development and juvenile characteristics (lack of septa between apertures) were found in specimens of 100.0 to 125.0 mm. length. The articular and dentary canals appear much as they do in the larger specimens, but the openings are relatively larger. The lachrymal (Pl. VII, Fig. 67) of the 11.0 mm. specimen approaches the adult type, but it is nearly twice as high as wide. The septa which subdivide the original large orifices develop from the flat lachrymal plate and grow toward the roof of the canal to effectively cause the formation of the openings. One of these spicules of bone is seen in Fig. 67 (Pl. VII). At this stage the lachrymal looks like that of Lepomis symmetricus, but by the 35.0 mm. stage the canal attains the adult configuration. However, bone continues to accumulate at the dorsal, anterior and ventral edges, as well as between the anterior branches, until the fish is 300.0 mm. in length, and possibly longer. At 11.0 mm. the first three suborbitals are lacking and all of the others are open channels. By 35.0 mm. the only suborbital lacking is the jugal, but all of the bones, except the dermosphenotic, are still open laterally. By 48.0 mm. all of the ossicles are present and the two just anterior to the dermosphenotic have ossified while the others remain open. In a specimen 75.0 mm. long all of the suborbitals, except the jugal, which never assumes this form, are at least partially tubular (deeply notched at either end). In our smallest specimen the nasal bones, which assume their adult state sometime before 35.0 mm., are represented as open troughs. The frontals have already assumed their final configuration, but they are very smooth and the foamy-appearing bone is lacking along the edges of the canals. The anterior roof of the frontal has not yet contacted the roof of the canal posterior to the interorbital opening, which probably means that these two segments of the covering are developed from separate ossification centers. Judging from Curd's (1959) figures, which contrasted 22.0 mm. and 57.0 mm. specimens of L. humilis, this last statement should also apply in that species.

Elassominae

The genus Elassoma possesses so many osteological characters which are very dissimilar to the bones in the rest of the family, as now construed, that each bone will be briefly described. All three species are nearly unvaryingly alike in this regard.

Supracleithrum

Although the supracleithrum is in contact with the posttemporal, it is not penetrated by the lateral-line canal.

Posttemporal

The posttemporal element of the lateral-line (Pl. V, Fig. 39), is unlike any sunfish and is in two parts. The girdle element lies in the usual position, but the lateral-line element floats in the tissue over it. An occasional specimen of E. evergladei possesses a thin strap of bone over the middle part of the open trough.

Supratemporal-intertemporal

This bone is not T- or Y-shaped, as in all other centrarchids, but a simple grooviform bone which is slightly spatulate near its bese.

Lateral Extrascapular

Elassoma is the only member of the Centrarchidae which lacks this bone. It will be remembered that the supratemporal canal, in other centrarchids, occupies the two last-named bones.

Dermopterotic

This small bone is in the usual position and is an open groove. It slightly overlaps the posterodorsal margin of the sphenotic (not dermosphenotic) anteriorly.

Preopercle

The preopercle reminds one of a fish in very early ontogeny, for the entire length of the bone is a V-shaped groove (Pl. VII, Fig. 54), wholly unlike any true sunfish in nature.

Articular

Unlike any other centrarchids, there is no mandibular canal because the lateral-line does not penetrate the articular nor the dentary.

Suborbital Series

None of the suborbitals, including the dermosphenotic, are developed.

Lachrymal

The lachrymal seems very strange when compared with any of the other sunfishes (Pl. VIII, Fig. 74). It is a simple boat-shaped bone, situated in front of the eye with the open part directed anteriad.

Frontal

In *Elassoma okefenokee* (Pl. VI, Fig. 47) and *E. zonatum* the lateral line forms an L-shaped groove similar to Curd's (op. cit.) abnormal specimens of *L. humilis*. In *E. evergladei* a low wall often extends about one-third the length of the anterior half of the frontal bone between the coronal suture and the lateral-line groove. In one specimen the wall possessed a slight curvature toward the lateral wall.

Nasal

Like the other lateral-line bones, the nasal is an open groove. It is wider posteriorly than anteriorly and is only slightly shorter than the anterior part of the frontals.

CHAPTER VIII

COMPARISON OF CENTRARCHID OSTEOLOGICAL COMPONENTS WITH THOSE OF OTHER TAXA

Osteological studies carried out on the perciform skeleton have shown the osseous components of the lateral-line system to be very much as they are in the Centrarchidae. In the sciaenid, *Aplodinotus grunniens* Rafinesque, the lateral line (Green, 1940) courses through exactly the same skeletal parts as that of sunfishes, but the bones involved are very unlike the bones in centrarchids, although some of the ossicles superficially resemble those of *L. humilis*, as they are greatly inflated and the connective tissue tube is covered by mere struts of bone. Branson (in press) has pointed out some similarities and dissimilarities between serranids and cichlids and the centrarchids. The lateral-line system of many members of the Serranidae is easily identified with sunfishes, being especially similar to *Archoplites*, and such observations can be repeated in percids such as *Perca* (Allis, 1904) and *Stizostedion*. The most obvious evolutionary tendencies in all of these fishes, when compared with lower forms, is progressive degeneration in the amount of branching, the number of diverticula from the main canals (Tretyakov, 1944), and the widening of and reduction in length of some of the canals.

The generalized path of the lateral-line in non-perciform groups is also very similar to the one delimited for the Centrarchidae, but there are some important differences to be noted. The supratemporal canal, which in sunfishes occupies the lateral extrascapular and supratemporal-intertemporal, courses through the parietals in characids, cyprinids (Allis, 1904; Harrington, 1955) and some other ostariophysine fishes. The Salmonidae (Allis, 1884) and Umbridae (Dineen and Stokely, 1954; Chapman, 1934), however, follow the same plan as the sunfishes. The supratemporal canal becomes highly dendritic in the gar (Collinge, 1893) and involves some peculiar bones known as tabulars at the posterior part of the skull. Another difference between the percomorphs and other fishes is that the cephalic lateralis does not penetrate the supracleithrum in many members of the last group. The ostariophysine skeletal elements are otherwise much the same as in the Centrarchidae as far as lateral-line course is concerned (Harrington, 1955).

The preoperculomandibular canal penetrates the dentary bone, not through the articular as in most percids, but through the angular in such forms as _Amia_ and _Polypterus_ (Allis, 1889; 1904; Collinge, 1893). Furthermore, the mandibular canal is complete in several of the ancient forms, rather than ending near the mandibular symphysis.

The infraorbital canal of _Amia_ (Allis, 1889) and _Polypterus_ (Allis, 1904; Collinge, 1893) is quite distinct from the percomorph type in joining the supraorbital canal through the antorbital, or prefrontal (auct.), a bone which is without counterpart in the percids and their immediate congeners. Allis (1889) and Collinge (1893) pointed out another difference in _Amia_ and _P. bichir_, which is actually a character of the Selachii (Allis, 1904). In these fishes the infraorbital, after passing through the "antorbital," enters the ethmoid and anastomoses with the canal from the other side of the head.

The external canaliculi arise in most fishes as they do in the

Centrarchidae, from connective tissue sinuses between the ends of bones (Allis, 1904; Pollard, 1892).

The shape and arrangement of lateral-line bones varies considerably, as is to be expected, from one perciform taxon to another. The centrarchid bones are compared with several of these fishes.

Supracleithrum

The shape of this element varies from a simple blade-like ossicle in the Serranidae and Centrarchidae and *Pomatomus* (Allis, 1904) to a triradiate (in *Cottus*; Allis, 1904) or triangular structure (in *Cichlasoma*; Branson, in press), but in all of these forms the canal passes through the upper end of the bone.

Posttemporal

The posttemporal is heavily serrate in many of the true basses, similar to the condition seen in *Archoplites* and the Centrarchinae, but is smooth in some cichlids (Branson, in press), *Archosargus*, Percidae, *Cottus* and many others (Allis, 1904). In most of the forms, including the perches and cichlids, the bone is similar to that of sunfishes, i. e., in possessing two articulating prongs anteromesad. However, the cottid posttemporal (Allis, 1904) is reduced in this regard. The apertural arrangement of the Centrarchidae, in which there are two openings for external canaliculi, except in *Mesogonistius*, *Enneacanthus* and *Elassoma*, is very similar to the serranid and percid condition. In *Archosargus* there are two primary branches which often become bifurcated distally. Bifurcation is not known in the higher serranids, percids, centrarchids and cichlids. The single opening of the centrarchid forms mentioned above reminds one of the distal end of the posttemporal in some surfperches, cottids (Allis, 1904) and cichlids (Branson, in press).

Supratemporal-intertemporal

This small bone is Y-shaped in most teleost fishes (Harrington, 1955) but may be a simple, straight, or slightly flexed tube in some cottids (Allis, 1904). In the Centrarchidae the bone is very often an open gutter, as it is in several percids (Allis, 1904), although it is a closed tube in the greater number of species.

Lateral Extrascapular

The percids (Allis, 1904), Amia (Allis, 1889), serranids and cichlids (Branson, in press) and others have separate, tubular extrascapulars, as do the sunfishes, but some forms, i. e., Cottus, possess lateral extrascapulars (mesial extrascapular, auct.) which are fused to the parietals, and Archosargus, where the supratemporal canal is complete, has a third bone, on each side, in the series.

Dermopterotic

The Y-shape of the centrarchid dermopterotic (pterotic or squamosal, auct.) is of common occurrence in perchids (Allis, 1904), serranids and chiclids, but is just as often a straight tube with an opening at either end, as in Cottus, or with several apertures, as in Pomatomus or Archosargus. In many fishes there is no common sinus for the union of the preoperculo-mandibular, dermopterotic and supratemporal-intertemporal components, but independent arms and openings in the dermopterotic for communication with the other two bones, and in Cottus (Allis, 1904) there is an ossicle intercollated between the preopercle and dermopterotic.

Preopercle

Serranids, percids and sciaenids, as well as others, typically have a serrate preopercle similar to the ones herein illustrated for Archoplites, Centrarchinae and some Lepomis. In many groups, such as the Cichlidae, there are no serrae. Furthermore, the shape of the bone in perches and serranids, especially in the latter, is like that of the Ambloplitini, Centrarchini and some Lepomini. Comparatively, the preopercle becomes aberrantly shaped in such highly modified fishes as Cottus, in which it is triradiate. The arrangement of apertures on the bone is likewise variable. In Pomatomus, possessing two terminal and three side branches, all of the diverticula are restricted to the horizontal arm. Archosargus is peculiar in having as many as 17 apertures in this canal, and some of them are bifurcate. In all of the percomorphs the apertures into the preopercular canal open on the ventral side of the bone.

Articular

The articular vary rarely bears more than two lateral-line apertures and most often the canal passes through the bone as it does in nonmicropterine sunfishes. The shape is usually similar to that of sunfishes, especially in serranids, cichlids, sciaenids and percids. In Archosargus and its close relatives the bone is a rather wide element which has a much reduced anterior articular facet. The lateral-line canal usually possesses a third aperture somewhere between the terminal ones.

Dentary

In most percids and serranids this mandibular element is similar to that of most centrarchids, both in shape and in number of lateral-line openings. In retrospect, the primitive sunfishes have five apertures into the dentary canal, whereas some of the more advanced forms have only four, the latter being similar to *Cichlasoma*. Most of the Serranidae, many perches, such as *Perca fluviatilis* Linnaeus, *Pomatomus* (Allis, 1904) and others have five apertures, although Woolcott (1957) illustrated only four openings in American species of *Roccus* and *Morone*. Some of the more highly specialized forms, like the sheepsheads and sculpins, have a secondarily increased number (which also may be decreased) of openings into this lateral-line bone. In all of the fishes thus far referred to, the apertures open either directly into the canal or from its ventral margin, as they do in sunfishes.

Suborbital Series

The dermosphenotic lies in approximately the same position as it does in most percomorphs, but in some it is strongly fused with the underlying autosphenotic. In percids, cichlids and many others these elements are simple, pipe-like ossicles which, except for the lachrymal (discussed below), do not bear apertures in addition to the terminal ones. Flat plates of bone, mesad to the lateral-line tube, and arranged parallel to the side of the head, are commonly observed in all percomorphs. In some peculiar forms, *Cottus* and *Archosargus*, the suborbitals are very dissimilar to those of sunfishes, serranids and cichlids. In the sheepshead and other sparids there is progressive enlargement of the suborbitals from the dermosphenotic anteriad. In this fish suborbitals four and five are very similar to the lachrymal in shape and in number of side branches, all of them having four anterior apertures. Some of these apertures are at the ends of tertiary branches formed by bifurcation of secondary diverticula. This is considered as a specialization and is not seen in any of the fishes most closely related to the Centrarchidae, although fusion of some suborbitals may induce the formation of single side branches as described in _Micropterus coosae_ and in _Cichlasoma cyanoguttatum_ (Branson, in press).

Reduction in number of suborbitals, although not carried to the extreme of _Elassoma_ and the Enneacanthini, is a common phenomenon in percids. This comes about either through a loss of elements or through fusion of two, or more preexisting ones. In the cottoids and Gasterosteiformes (Berg, 1946) one of the infraorbitals is usually united with the peropercle and fusion of several suborbitals takes place in _Trigla_ (Allis, 1909) to form a single large plate anteriorly. The third suborbital of _Cottus octodecimospinosus_ is the ossicle which is involved in the suborbital-preopercular union and the first two bones, in this series, posterior to the lachrymal are nearly identical to the lachrymal in having a side branch like that of the jugal-suborbital fusion of _Micropterus_. In most percids and serranids five or six suborbitals are generally present, excluding the lachrymal.

Lachrymal

The peltate shape is retained in most percomorph fishes, even when the other suborbitals become highly aberrant. This bone is nearly always present, often being "normal" in shape (compared within the matrix of the group of fishes to which a given species belongs) when the rest of the suborbitals have disappeared or become otherwise modified. The centrarchid arrangement, e. g., the lachrymal situated in an almost vertical position before the eye is similar to serranids and _Perca_, but unlike the situation in Cichlasoma and Cottus, where the bone lies in a nearly vertical plane. In other perciformes the morphology of the lachrymal lateral-line canal is essentially like that seen in the Centrarchidae. The four openings, two terminal and two at the ends of anteriorly-directed branches, is repeated again and again in sciaenids, percids, cottids and cichlids. In sparids, where the anterior branches often bifurcate, the pore number is sometimes six or more; however, if the bifurcations are ignored, the number of branches is reduced to two, except in Archosargus (Allis, 1904), where there are five. Some cottoids, like the Enneacanthini, possess only three apertures, and some surfperches have five unbranched apertures.

Preopercular serration is common in the percomorphs, but is not universal. Whole families and sections of families lack these spines, but most of the drums and serranids bear very numerous serrae on this bone. The serranid lachrymal, as in Roccus chrysops, is markedly similar to Archoplites in this regard.

Frontal

The usual apertural number for the frontal lateral-line canal of cottids, percids, sparids (Allis, 1904), and serranids is four. The canal of this bone, the largest of all lateral-line elements, is usually quite superficially placed, as it is in the Centrarchidae. However, in the cichlids (Branson, in press) the canal is very deeply imbedded in bone and there is an additional aperture, at the end of a raised tube, between the interorbital opening and the posterior nostril aperture, a condition seldom observed in any perciform. Another difference and peculiarity noted in the cichlids is that of the coronal suturing mechanism and mode of formation of the supraorbital commissural canal. In the Centrarchidae this last canal is a simple branch from the mother supraorbital canal which opens near the midline on each side near the posterior margin of the frontal bone. In Cichlasoma, Tilapia and other cichlids the commissural arm burrows deeply into the frontal to an opening near the basal part of the bone near the coronal suture. A high crest extends almost the entire length of the suture, being involved in the suture for its total depth, and a half-tube is formed in the crest (on each side) which is nearly as long as the supraorbital canal. This is possibly a characteristic not found elsewhere in percomorph fishes.

Nasal

The percid and serranid nasal resembles its counterpart in the Centrarchidae, but the same bone is dissimilar to that of fishes in some other taxa. According to Allis' (1904) figure these bones may become annexed by the ethmoid to form a complex structure not seen in most of the higher forms. In the Cichlidae the bone is very solidly constructed and is positively curved in two directions, convex upward and both ends deflected laterad.

Elassoma

The greatly reduced lateral-line system and other unusual characters, discussed below, of the pygmy sunfishes pose a very annoying problem. Although lateral-line systems are commonly reduced, Elassoma presents a reduction so extensive as to be nearly unique. Bertin (1942) made some observations on the osteology of Avoceltinops resulting in the discovery of a moderate degree of disossification, which was considered to be morphological indication of neoteny, a position upheld by Myers (1958). The latter worker, reasoning along the same lines, considered a reduction or suppression of the lateral line and/or simplification of the supraorbital crest to be of a neotenic nature. Furthermore, he considered a small species, belonging to a taxon which contains predominantly moderate to large forms, to be additional indicative evidence for neoteny. Eaton (1956), therefore concluded that the peculiarities of Elassoma could be regarded as evidence of neoteny.

CHAPTER IX

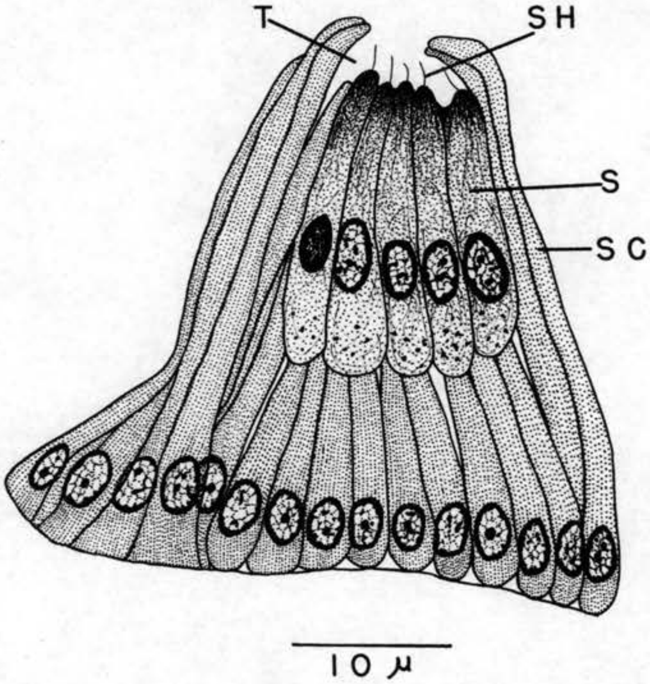
HISTOLOGICAL OBSERVATIONS

External Neuromasts

External neuromasts are relatively scarce in most adult sunfishes and when present are often absent from the lachrymal region except in *Elassoma*. For this reason it has been possible to observe the histology of these organs in only a few species. Since *Elassoma* is the only member of the family with well-developed neuromast lines, almost every section having at least one organ, one of its neuromasts will be described and compared with the data that are available for other forms. However, it must not be concluded that the external organs of the pygmy sunfishes are typical of the whole family.

Elassoma

The distribution of these organs has already been discussed. All of the external neuromasts of these tiny fishes are more or less sunken into pits or crypts, from which the distal end of the organ protrudes. In all three species the organs are bell-shaped, ranging from 31.0 to 44.3 microns (average 37.8) in diameter at the base, 11.0 to 25.1 microns (average 14.6) at the apex and from 27.0 to 45.0 microns (average 37.2) in depth. Text Fig. 6 shows that the neuromasts consist of two kinds of cellular elements, sustentacular and receptive or sensory cells. The figure, which is a camera lucida drawing from a facial section, shows the latter cells couched among some supporting cells. Such an illustration may be misleading, for the supporting cells of an intact organ actually completely surround the sense cells. Furthermore, although many authors have thought otherwise, the central supporting elements do not end at the proximal ends of the sensory elements but penetrate upward, as slender processes, between the latter cells. In the region of the distal (outer) sustentacular cells, the outer supporting elements extend beyone the tips of the sense cells and curve toward the center of the organ (Text Fig. 6). The supporting cells thus form a cavity around the receptive ends of the sensory cells herein called the tremognostic chamber. This cavity measures 2.3 to 4.4 (3.5) microns in depth and 9.5 to 11.9 (10.8) microns in diameter,



Text Figure 6. External Neuromast of *E. zonatum*. S, sense cell; SC, supporting cell; SH, sensory hair; T, tremognostic cavity.

the last figures corresponding closely to the area circumscribed by the sensory surface of the organ. As far as known, the only other species in which the neuromasts are so modified are those of the Enneacanthini. In situ, the neuromasts are depressed into their crypts to the level of the upper ends of the sense cells, the rest of the organ extending freely from the surface of the skin. In a surface view one observes an organ, surrounded by a moat, which is penetrated by a smaller opening, the tremognostic aperture.

Sustentacular Cells

The supporting cells of the external neuromasts are attenuate-rhopaloid or club-shaped, a generality in all fishes. They measure 23.0 to 36.7 (32.1) microns in length and average 1.2 (0.8 - 1.5) microns in apical diameter. The nucleus nearly fills the basal extremity of the cell and it is nearly impossible to measure the diameter of these oval bodies without also measuring the diameter of the cells in that region. Consequently, these two diameters are herein used interchangeably. This diameter was found to be 1.8 to 3.1 (average for all three species, 2.5) microns. However, in _E_. _okefenokee_ the average nuclear diameter was 3.1 (2.8 - 3.1) microns, whereas in the others it was 2.1 to 2.3 (1.8 to 2.3) microns. This discrepancy may be the result of formalin fixation which has a tendency to cause hypertrophy of some cellular elements if the formalin is not buffered. Since the specimens of _E_. _zonatum_ were fixed in two different cytological fixatives, and since there is general agreement between the last species and _E_. _evergladei_, the nuclear diameter of the supporting cells of _Elassoma_ is thought to lie somewhere between 2.1 and 2.3 microns, the range of averages for the last two species. The supporting cells rest upon a thin basement membrane (2.0 to 5.0 microns thickness) which stains pale blue with Mallory's triple connective tissue stain and intensly purplish-black with iron hematoxylin. This membrane marks the outer limits of the corium. The cytoplasm of the sustentacular cells is of a homogeneous nature and stains bluish-gray with hematoxylin and light red with Mallory's (Mallory's will henceforth be used for Mallory's triple connective tissue stain and "hematoxylin" for Heidenhain's iron hematoxylin). There are no inclusions nor the slightest indication of intracellular fibers. These cells do seem to have a thin intercellular cement between them which recalls the substance between the epithelial cells of mammals. No tonofibrilles or intercellular bridges were noted.

The oval-shaped supporting cell mucleus, as mentioned above, is basally located (Text Fig. 6). In staining reactions these bodies exhibit both acidophilic and basophilic properties. The membrane, which is thickly clumped with basochromatic susbtance, presumedly chromatin, stains very darkly with hematoxylin and Mallory's. Some centrally-placed endosomes are connected to the thickened membrane by thin strands and all of them stain with the same intensity as the material found on the nuclear membrane. These bodies average 0.8 (0.5 - 0.9) microns in diameter, and the vesicular nuclear sap in which they are embedded stains very faintly. Some tiny acidophilic granules may also be seen in the nuclear sap.

Sensory Cells

The receptive cells, in a frontal section, are few in number (five or six) and, unlike the supporting elements, are strongly polarized. The distal end bears a single hair-like structure, usually termed a "sense hair," averaging 1.9 (1.6 - 2.3) microns in length. This "hair" extends from the tip of the setiferous cell into the tremognostic chamber, which may or may not be ensconced by cupular substance in life. The latter structures, although common over lateral-line organs, were not observed in the external neuromasts. The sensory cells are tenpin-shaped, taking more stain distally and progressively less basally. Critical observation reveals a tiny blepharoplast-like body just below the insertion of the hair into the cell. Since the upper end of the cell and this small body both take stains deeply, it was not possible to obtain enough resolution to determine whether a connection exists between the sense hair and the granule. The cell appeared to be striated (fibers) below the upper membrane, and the cytoplast, in areas which stain less intensely, appears to possess some very fine fibrils, especially near the nucleus. Near the base of the cell a few irregular, dark-staining bodies of less than 0.5 microns were seen. The sensory cells measure 1.8 (1.6 - 2.3) microns apically, 3.4 (2.9 - 5.0) microns at the base and 17.3 (15.0 - 19.0) microns in length.

The nearly round sensory nucleus is almost in a central position and somewhat larger, 3.2 (2.4 - 4.1) microns in diameter, than the supporting nuclei below. Like the sustentacular cell nuclei, their membranes are thickened by dark-staining chromatin and some endosomes of a size equal to the ones measured in the supporting cells are seen in the vesicular nuclear sap.

In the Rio Grande perch, Branson (in press) described some terminal bars between the sensory cells. Similar structures again were encountered in studying the sensory elements of Elassoma and, to this writer's knowledge, these elements have not been alluded to elsewhere.

Comparison of Elassoma with Other Centrarchidae

According to Herrick (1901) there are two kinds of external neuromasts, large ones and small ones, the distinction being that the former are observable with the unaided eye. Using this criterion, all of the centrarchid external neuromasts are of the small type. Herrick further distinguished between external organs as "naked" or "sunken," according to whether they were depressed into pits or situated free on the skin. The sunken variety are termed pit organs by most recent workers, although Sâto (1955a) has shown these two types to be nothing more than developmental stages of the same organ, the raised variety being the initial stage. All of the organs in sunfish are pit organs, but in very young specimens the neuromasts are probably of the naked type.

Centrarchinae

There were no histological observations made, but the shape of the external sense organs are like those in Lepomis and Micropterus.

Lepominae - Enneacanthini

Although the neuromasts are of slightly different shape and proportions, there is an immediately recognizable resemblance between the species in this tribe and those of the genus Elassoma in this regard (Pl. X, Fig. 114). One tremognostic chamber of E. gloriosus measured 5.9 microns in depth and 11.8 microns in diameter, being slightly deeper than those described in the pygmy sunfishes. The entire organ was also larger, measuring 41.5 microns at the base, 18.2 apically and 41.5 microns in length. The cellular elements, while being comparable, differed in their proportions. The sensory cell was found to average 18.8 (17.6 - 20.2) microns in length, 2.8 (2.6 - 2.9) microns apically and 4.4 (4.1 - 5.1) microns at the base. Their nuclei, reacting identically to the stains, were 3.4 (3.2 - 3.6) microns in diameter and bore endosomes of about the same dimensions as those in Elassoma. The single sense hairs averaged 3.1 microns in length.

The only observable difference between the sustentacular cells of Elassoma and Enneacanthus, or for that matter, any of the Centrarchidae, is one of relative measurements. These cells in E. gloriosus averaged 34.9 (33.0 - 36.7) microns in length, thus broadly overlapping the mensurable characteristics of Elassoma. The same is true of the apical diameter, 1.4 (1.3 - 1.5) microns, but the nucleus averages somewhat larger, being 2.6 to 3.4 (3.0) microns in diameter. The nuclear endosomes are like those of Elassoma.

Lepominae - Micropterini

The external neuromasts of the black basses are not like those of the Enneacanthini and Elassoma, either in shape or arrangement in the skin. In this tribe the organ is rather cigar-shaped (Pl. IX, Fig. 93; Pl. X, Fig. 105) and is sunken very deeply into the skin, with no part of the neuromasts extending above the surface. As seen in the figure a narrow tremognostic canal extends downward to the distal end of the neuromast. Comparing the organ with those briefly discussed above, it is found to measure only 26.5 microns proximally and 10.2 microns apically, considerably smaller than either of the others. The total length of the neuromast was found to be 32.6 microns, also less than the others, but the length of the cellular elements was not unlike those already discussed. The sustentacular elements are 31.7 (30.8 - 32.5) microns long, whereas the sensory ones measured 18.6 microns. The apices measure 1.9 (1.8 - 2.0) and 2.6 (2.3 - 2.9) microns respectively for the supporting and sensory cells, being longer than those parts in the other measured species. The sensory cell base was found to be of intermediate size between those of *Enneacanthus* and *Elassoma*, measuring 3.8 (3.5 - 4.3) microns. The sustentacular nucleus, and thus the proximal end of the cells, is much larger in the basses than in either of the other two tribes, 3.7 (3.1 - 4.0) microns, but its endosomes are similar in being 0.6 to 0.9 (0.8) microns in diameter. The sensory nucleus, endosomes and general cytoplasm are very similar to those cited for *Elassoma* and *Enneacanthus*, but the nucleus is slightly smaller in the last-named form, averaging 3.0 (2.7 - 3.1) microns. The sensory hairs in the Micropterini are nearly twice as long as those of compared species, 2.8 microns in average length.

Lepominae - Lepomini

If Moore's (1956) figure is representative of all of the species in this tribe, then the external neuromasts of *Lepomis* and *Chaenobryttus* are very similar to those in *Micropterus*. No histological data are available at this time.

CHAPTER X

COMPARISON OF CENTRARCHID EXTERNAL NEUROMASTS WITH THOSE OF OTHER TAXA

Most fishes possess external neuromasts (Dijkgraaf, 1952) which present some variation of the bell-shaped structure seen in *Elassoma*. However, the peculiar tremognostic chamber seems to be rather uncommon as a search of the literature has failed to disclose records of it. Many authors have described the neuromast as occupying pits or moats. Satô (1955a) illustrated the neuromasts of several fishes, and in *Oncorhynchus*, *Oryzias* and some cyprinids the distal surface of the organ is nearly flush with the skin, extending slightly above it as in *Elassoma*, but in the catfish *Parasilurus asotus* Linnaeus the organ is depressed into the dermis so that a wide to narrow tremognostic canal ("pit cavity," Moore, 1950) is formed. These organs, although similar to the Micropterini and Lepomini in possessing the short canal to the exterior, are differently formed; they are about as wide as long and the sensory surface is nearly flat. The pit organs of soleids (*Symphurus* and *Cynoglossus*) are also similar to many sunfishes in this respect (Tirelli, 1958); but, instead of having single organs at the bottom of the canal, there is one large external opening which immediately branches within to form two tubes leading to a pair of organs. Further examples for comparative purposes are found in *Fundulus heteroclitus* (Denny, 1937) and *Hybopsis aestivalis* (Moore, 1950), the organs of which are found surrounded by shallow moats but with the sensory surface exposed to the surrounding water.

The cupular material was first observed by Emery (1880) in a teleost collected near Naples and has since been observed in a host of other fishes (Moore, 1950; Denny, 1937; Dijkgraaf, 1952; Curd, 1959; and many others). Although this object was not observed in the external neuromasts discussed herein, it may be present in life, for as Denny (1937) has pointed out, the cupulae are fragile and easily disrupted during fixation and handling.

In histological studies it is usually stated that the supporting cells are long and distally attenuate, their nuclei occupying a proximal bulge (Sâto, 1955a) or they are so illustrated (Moore, 1950). Nevertheless, little work has been done on their cytological make-up, and measurements of them are very scarce. In Fundulus the supporting elements are much more numerous than the sensory cells, there being a ratio of about 80 or 90 to three or five, and some well-defined terminal bars are present between them. In the Centrarchidae the degree of discrepancy between the number of sensory and supporting cells is not so great and terminal bars were not observed between the supporting cells of external organs.

As with the supporting elements of the external neuromasts there is a dearth of data concerning the sensory cells. These cells are tempin- or pear-shaped in all fishes and dark-staining granules near the base, similar to those in Elassoma, apparently occur in the canal organs of most fishes. However, because of the lack of close attention, the cells of external organs have not often been described. The nucleus, described here as being vesicular with a darkly stainable, confluxed membrane, is quite similar to those of most osteichthine fishes. Moore (1950), Moore and Burris (1956) depicted the bodies as being round and dark-staining, which is apparently the usual case. Denny (1937) is one of the few workers who have given any details concerning the nuclei. In Fundulus the karyosome is located in the proximal half of the sense cell, as it is in sunfishes, and its affinities for stains are similar to the ones already described. Two or three endosomes (nucleoli) were observed, but apparently were not found to be connected with the nuclear membrane. The general sensory cytoplasm of this cyprinodont included some vary fine fibrils, termed epitheliofibrillae by Denny (1937), that are doubtless homologous to those observed in Elassoma and other centrarchids. Miss Denny also mentioned the presence of some rod-shaped mitochondria, parallel to the long axis of the cell, which may be collatives of the dark subnuclear granules found in sunfishes. However, it is unwise to call these aggregates mitochondria until they have been studied by means of ribophillic stains or electromicroscopy. The strongly polarized condition of the cells has either been remarked upon or demonstrated in illustrations by almost every investigator interested in the study of lateral-line systems. The point of origin of the sense hair stains very heavily, even darker than the nucleus (Bunker, 1897) in most species of Ictalurus, but the blepharoplast-like granules at the base of the hair have seldom been recorded in the literature. Denny (1937) described them as being rod-shaped in the mummichog and Speidel (1947), working with tadpoles, illustrated them as small grains at the bases of sense hairs.

CHAPTER XI

HISTOLOGY OF CANALS AND CANAL NEUROMASTS

the neuromasts contained in well-defined canals are structurally similar to the external organs, but are generally of larger size. Once they have attained their adult size cellular accretion ceases. In the thousands of organs observed not a single mitotic figure was observed, so, this final state is attained very early in life. Before discussing the histological nature of the canals and their contained organs a brief statement concerning the distribution of the neuromasts will be given.

In those species with lateralis canals each tube-bearing scale possesses a single organ near the center of the tube (Pl. IV, Fig. 27).

The distribution of canal organs can be roughly estimated by observation of the gross external morphology of the canal system as there is generally one neuromast between each two side branches. However, in a few areas this leads to error. There is one organ near the center of each of the following bones: nasal, supratemporal-intertemporal, lateral extrascapular (except in Elassoma, where this element is missing), dermopterotic, dermosphenotic, each of the suborbitals (except the lachrymal) and the articular. There are four neuromasts located in the preopercles of the Enneacanthini, five in the other Lepomini and in the Centrarchini, and six in the three genera of the Amblopitini. The dentary component of the preoperculomandibular canal contains three organs in the Enneacanthini and four in all of the others except Elassoma (discussed below).

A single organ is found in all centrarchids in the commissural canal of the frontal complex. Two others, one in the branch which connects with the postocular sinus and one between the interorbital opening and the posterior nostril pore complete the complement in this bone. Two neuromasts are found in the lachrymal canal in all species except *Enneacanthus*, *Mesogonistius* and *Elassoma*, which have a single organ. *Elassoma*, with only 20, possesses fewer canal organs than any other sunfish. Three of these (Text Fig. 2) are found in the preopercle, one each in the posttemporal, supratemporal-intertemporal, dermopterotic and nasal, and three in the frontal (Text Fig. 3).

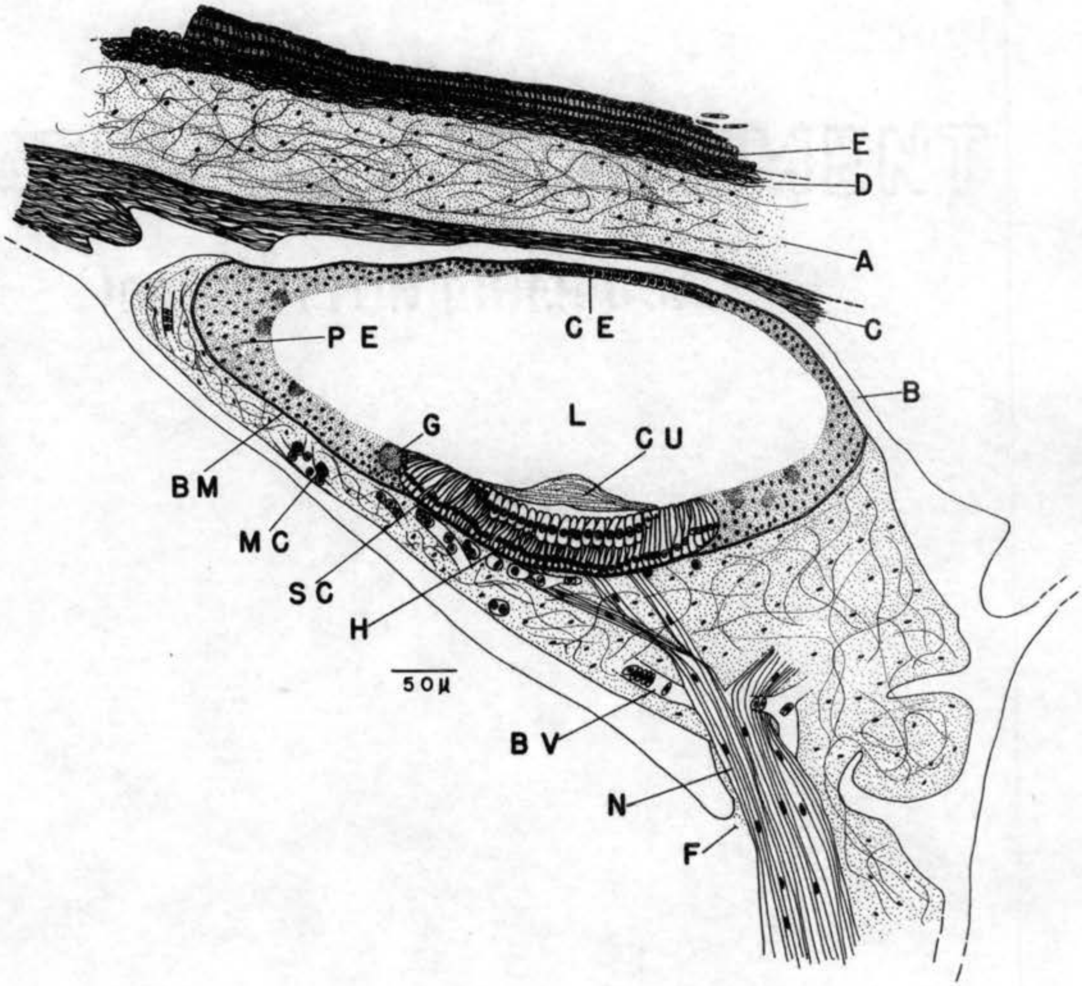
In all of the species the organ is implanted on the floor, or proximal wall of the canals, according to the position of a given canal.

As with other aspects of the system one species, *Lepomis symmetricus*, will be described in detail and compared with the rest of the family.

Lepomis symmetricus

The lateral-line canal has a continuous lumen, except at points where it becomes interrupted. This canal is composed of the basement membrane of the cellular elements of the system and averages 1.7 (1.5 - 1.9) microns in thickness (Table V). The tube thus formed occupies a passageway through various bones, the one in the lachrymal averaging 316.5 (273.0 - 424.5) microns in diameter (Table V). As seen in Text Fig. 7, the connective tissue tube formed by the basement membrane is not round, but ovoid in shape; its diameter is 233.3 (209.5 - 258.8) microns. Throughout its length the canal is lined by simple cuboidal epithelium of a rather low type which nearly completely lacks mucous cells. However, as an organ is approached the cuboidal nature of the lining rapidly becomes pseudostratified (Text Fig. 7) and in the proximity of the neuromast numerous goblet cells are encountered. The pseudostratified cells become very deep and completely surround the neuromast peripherally. The cuboidal epithelium merges with the stratified squamous cells of the normal skin in regions where the canal system opens to the exterior, as illustrated in Pomoxis (Pl. X, Fig. 115). The peculiar septum-like thickenings of the canal lining opposite the canal organ, described by Moore (1956) in Lepomis humilis and L. cyanellus, are not present in the lacyrymal or suborbital canals of any centrarchid, but are easily observed in stained skins, in many of the other canals. The connective-tissue canal is suspended in the bony passages by a rather common-appearing areolar connective tissue. Just below the region of the neuromast many blood capillaries are seen and quite often some large cellular elements which may represent mast cells (Text Fig. 7) are located near these vessels. It is in this general area that the lateral-line nerve, after passing through a foramen in the bone, penetrates the basement membrane, loses its myelenation, and splays out under the sensory cells.

A typical canal neuromast is lozenge-shaped, except for the base, which, of course, fits the curvature of a given canal, and in sectional view they assume the shape of a quarter sphere. Including the basement membrane, the two organs in the lachrymal canal measured 36.6 (34.9 - 38.8) microns in depth and 305.0 (224.3 - 513.1) microns in diameter (Table VI). As illustrated, the sensory cells are localized near the center of the organ, their surface area being about 187.2 (162.2 - 229.6) microns in diameter, or 66.7 per cent of the total organ diameter (Graph II). The organ depth may also be expressed as 13.6 per cent of the total diameter of the neuromast (Graph I). From the above measurements it is obvious



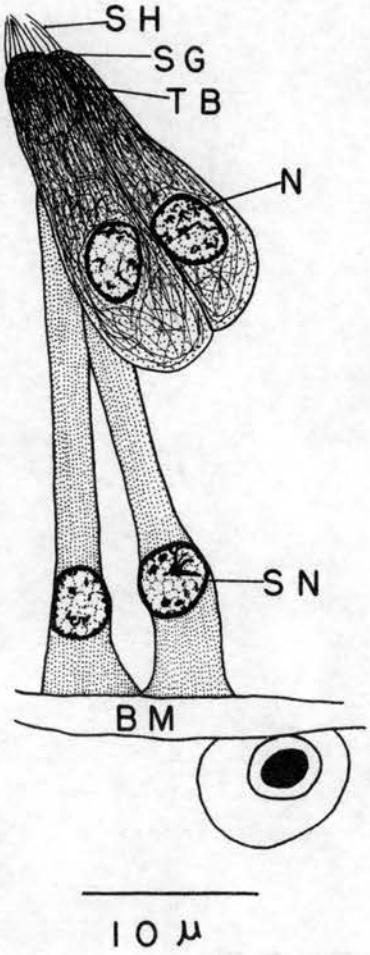
Text Figure 7. Transverse Section of Lachrymal Bone in Lepomis symmetricus. A, areolar connective tissue; B, lachrymal bone; BM, basement membrane; BV, blood vessel; C, collagenous connective tissue; CE, cuboidal epithelium; CU, cupula (shrunken); D, dense connective tissue; E, stratified squamous epithelium; F, foramen; G, goblet cell; H, sense cells; L, lumen; MC, mast cell; N, nerve; PE, pseudostratified epithelium; SC, sustentacular cells.

that the canal organs, although being morphologically homologous, are much larger than the external organs. Such an increase in size has come about mainly by simple multiplication of the total number of cells, but, as will be pointed out below, there has not always been a corresponding increase in both types of elements in some of the other species.

In text Fig. 7 a cupula covers the distal tips of the sensory cells, however, this is probably a very shrunken, misshapen structure, as the space between the sense hairs and lower surface of the cupula would indicate. This enscouncement stains pale blue with Mallory's and dark purple with hematoxylin. Since the cupula was so badly fixed, any measurements of it would be meaningless.

The elements which make up the neuromasts found in canals are essentially the same as those in the unprotected organs. The supporting cells are again found to be attenuate-rhopaloid in shape (Text Figs. 7 and 8) and average 2.2 (1.7 - 2.8) microns apically and 35.1 (31.0 - 41.8) microns in length (Table VII). Their cytoplasm is of the same homogeneous nature referred to earlier and well-marked terminal bars are present between them distally or between the supporting cell apices and the apices of the sensory cells, where the latter are contacted. The extreme apex of these attenuate cells seems to be faintly striate in most preparations and the nuclei, being about 3.9 (2.8 - 4.7) microns in diameter, stain about like those already discussed. There are one to seven or more endosomes, several of which are usually attached to the nuclear membrane by thin strands of chromatin, averaging 0.9 (0.7 - 1.1) microns in diameter. In 39 organs there was usually an average of 76 cells per cross section.

The sensory cells are also similar to those observed in external neuromasts in being tenpin-shaped. Since the organ is convexly curved in all directions one must guard against being deceived by the appearance of the cells located on the very periphery of a neuromast (Text Fig. 7). In contrast to the supporting cells there are usually only about 32 sensory elements per section. Cellular differentiation is apparent among the sense cells, as they are not all alike. For convenience' sake, the sensory cells in each observed neuromast were divided into three regions, central, lateral and marginal, the marginal area being exclusive of the unevenly sectioned ones. These three regions are compared in Table VIII, where it is easily seen that the cells located just laterad to the central area are larger, 6.5 (5.2 - 8.3) microns in basal diameter, than

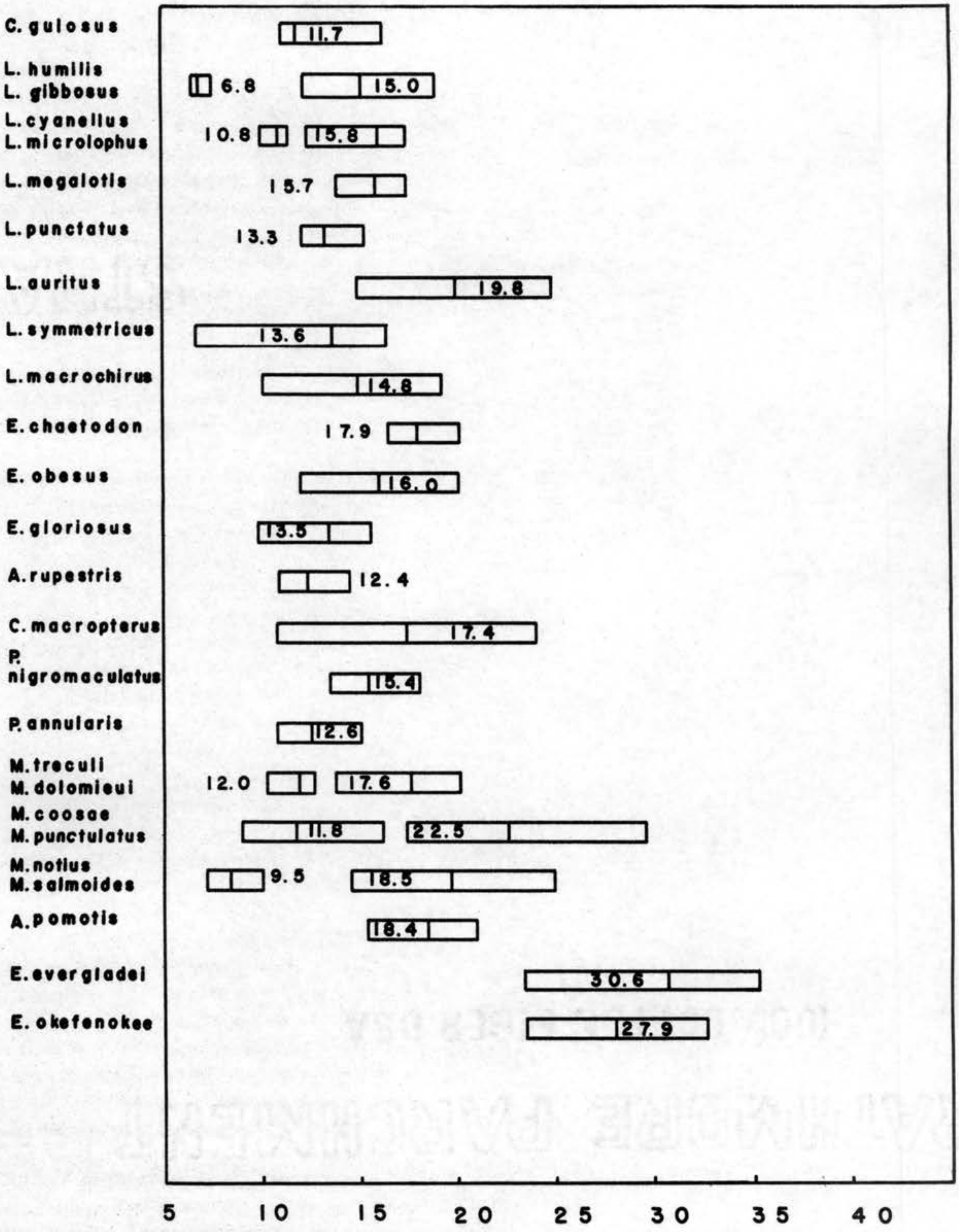


Text Figure 8. **Selected Sense and Supporting** Cells from Lachrymal Neuromast of L. symmetricus. BM, basement membrane; N, sense cell nucleus; SG, sense-hair granule; SH, sense hair; SN, sustentacular cell nucleus, TB, terminal bar.

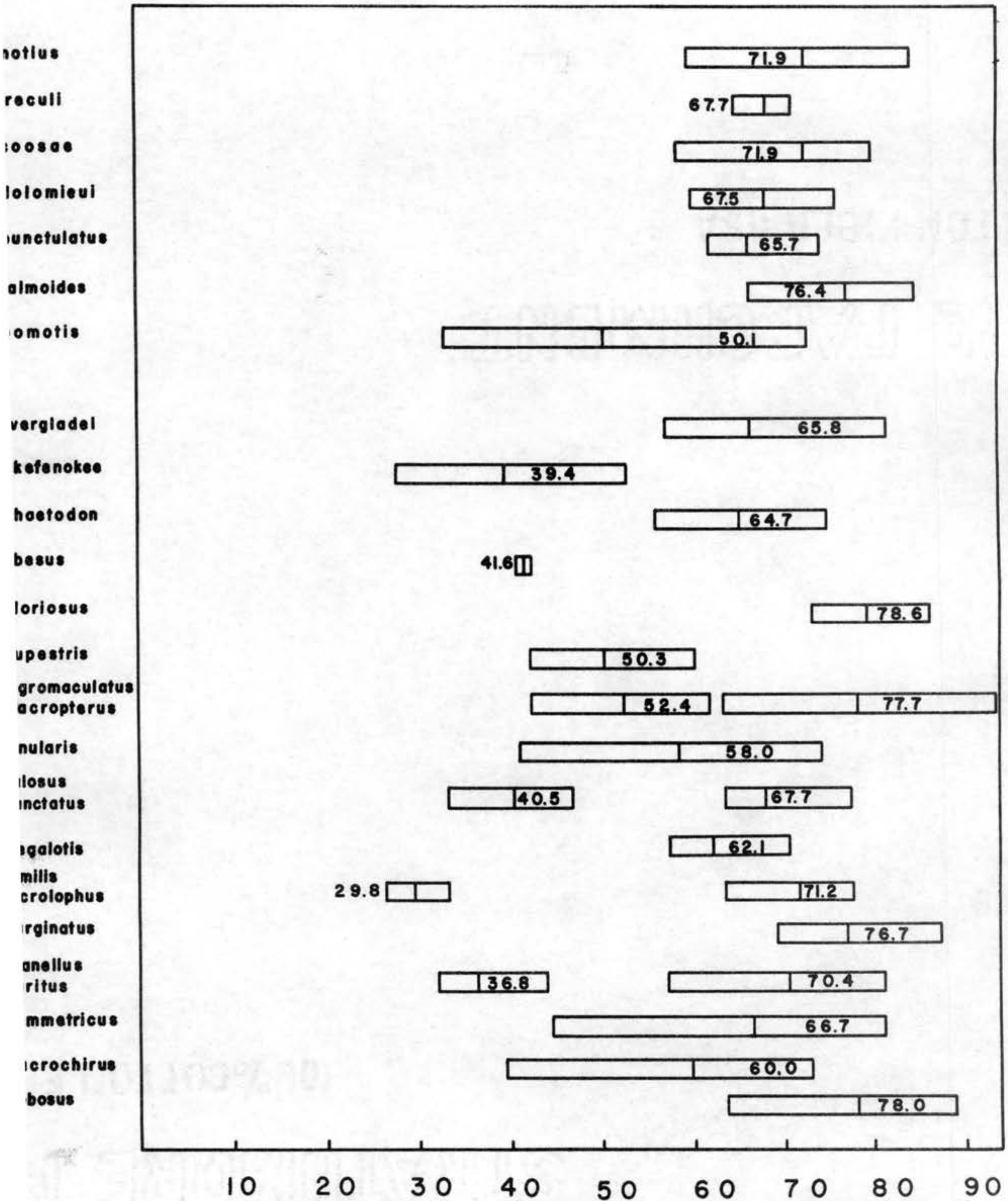
those of the other two regions where the diameters were found to be 5.8 (4.8 - 6.3) and 5.7 (4.3 - 6.6) in central and marginal regions respectively. Actually, L. symmetricus is the only species of Lepomis which demonstrates this characteristic to any marked degree. However, in some other tribes there is a very obvious difference between the cells of the three categories. The apical diameters of cells from each region also show some discrepancy between areas (Table IX: central, 3.6 (2.7 - 4.9); lateral, 4.5 (3.3 - 6.8); marginal, 4.2 (2.6 - 5.5). However, there is little to distinguish the nuclei, as far as size is concerned (Table X). Furthermore, the endosomes are all practically the same size from one cell to the next (Table XII). Comparing the lengths, the central cells are the longest, 16.6 (16.0 - 17.6) microns, whereas in the lateral and marginal regions the cells average 11.5 to 11.6 microns (Table XI). In addition to those of a mensurable nature there are some other visual differences. The general appearance of these cells is one of paleness, including the nucleus, which is considerably lighter in staining affinities than that of the central and marginal cells. There are usually only two or three of these cells per section.

The more numerous cells (Text Fig. 8) possess nuclei which are very similar to those described for external neuromasts except that the epithiliofibrillae are usually slightly more evident. No subnuclear granules were noted.

A striking difference was noted between the interior sense cells and those located in the external neuromasts. The sense hairs are not single, but as many as five per cell were counted; correlated with this observation were similar counts of the granules located at the base of the hairs (Text Fig. 8). These cells call to mind the morphology of the ciliated



GRAPH I. COMPARISON OF ORGAN DEPTH EXPRESSED AS PERCENTAGE OF ORGAN DIAMETER IN CENTRARCHIDAE. BOX ENDS ARE LOWER AND UPPER EXTREMES; THE BAR IS MEAN PERCENTAGE. WHERE TWO SPECIES ARE ARRANGED ON THE SAME LINE, THE UPPER NAME OF A PAIR CORRESPONDS TO THE BOX NEAREST LEFT MARGIN. N = 39 EXCEPT IN *E. OBESUS* WHERE IT IS 7.



GRAPH II. COMPARISON OF NEUROMAST SENSORY-AREA DIAMETER EXPRESSED AS PERCENTAGE OF ORGAN DIAMETER IN CENTRARCHIDAE. BOX ENDS ARE LOWER AND UPPER EXTREMES: THE BAR IS MEAN PERCENTAGE. WHERE TWO SPECIES ARE ARRANGED ON THE SAME LINE, THE UPPER NAME OF A PAIR CORRESPONDS TO BOX NEAREST LEFT MARGIN. N = 39 EXCEPT IN E. OBESUS WHERE IT IS 7.

ependymal cells from the tuberculum acusticum in the cat (Maximow and Bloom, 1944) which bear five to ten or more hair-like structures associated with as many blepharoplast-like bodies. In the fish neuromast there does not seem to be any difference in the lengths of hairs from one cell to the next. Under high dry magnification and, to a lesser extent, under oil immersion, the hairs cause refringence of light rays which creates the allusion of a triangular structure located on the apex of the sense cell. However, critical examination reveals the multiple nature of the sensory hairs. As far as this writer knows, such a condition has only been recorded in one other fish, Cichlasoma cyanoguttatum (Branson, in press).

The continuous nature of the lateral-line canals referred to in the discussion of L. symmetricus is the usual condition in all fishes. Furthermore, the elements constituting the cellular or fibrous parts of the system are very similar in all centrarchid species.

Centrarchinae--Ambloplitini

The general canal interior is not much different than that of Lepomis symmetricus, with the possible exception of a few more mucous cells being present in the rockbass. In Acantharchus the canal is nearly round in section (Pl. X, Fig. 113), rather than elliptical, and measures 191.9 (106.0 - 227.5) microns in diameter. Its bony passage in the lachrymal averages, in our few specimens, 264.1 (189.8 - 300.5) microns, whereas these same measurements in Ambloplites are 258.7 (227.5 - 333.5) and 366.5 (306.8 - 433.3) respectively. However, the differences here are mainly ones of an overall discrepancy in size between the two species. Measurements for Archoplites do not appear in the various tables because the specimens were improperly fixed for cytological and histological measurements. In general it may be said that, comparatively speaking, members of the Centrarchinae have the most capacious lateral-line canals in the family, and, as seen in Table V, these fishes, with the exception of Elassoma, also possess the thickest basement membrane in the Centrarchidae.

The neuromast of the tribe Ambloplitini is not particularly distinctive in size (Table VI). The organ depth represents 12.4 and 18.4 per cent of the organ diameter in Ambloplites and Acantharchus respectively. The former is comparable to the same index in L. symmetricus, but in Acantharchus, the organ being deeper in proportion to its diameter, the percentage index being greater than that of many of the other sunfishes. The sensory cells are, as usual, located near the center of the organ (Pl. X, Fig. 113), but the area occupied by the cells is only about 50 per cent (Graph II) of the total diameter. These and other percentages represent arithmetic means; the ranges are given in Graphs I and II, as all species are variable for these characters, Acantharchus being the most variable of all the species observed. The mud sunfish averaged 59 supporting and 14 sensory cells per section whereas Ambloplites had 90 sustentacular elements and 76 sense cells. Cupulae were not observed in the few specimens of the mud sunfish, but almost every organ of the rock bass possessed the shrunken remains of one of these structures (Pl. XI, Fig. 122).

In general appearance the supporting cells are much like other similar elements (see Pl. VIII, Figs. 80, 83 and 84). Those of Acantharchus are more like those of Lepomis in comparative measurements, being 2.0 (1.2 - 3.1) microns at the apex, 3.4 (2.3 - 4.5) basally and 33.2 (30.8 - 37.3) microns in length, whereas those of Ambloplites are 2.3 (1.5 - 3.2), 4.4 (3.4 - 5.6) and 54.2 (44.0 - 74.8) microns. With the exception of *Lepomis cyanellus* and *Chaenobryttus*, *Ambloplites* has the longest supporting cells in the family. The supporting cell nuclei of *Acantharchus* differ slightly in possessing only single endosomes.

TABLE V

COMPARISON OF DIAMETERS OF LATERAL-LINE TUBES, BONY CANALS AND BASEMENT MEMBRANE THICKNESS IN THE CENTRARCHIDAE. SCALE IN MICRONS. N = 39, EXCEPT IN *E. OBESUS* WHERE IT IS 7, FIGURES IN PARENTHESES ARE RANGES

Species	Lateral-Line Tube	Bony Tube	Membrane
C. gulosus	299.6 (209.7—364.0)	541.0 (437.0—637.0)	2.0 (1.6—2.0)
L. gibbosus	197.1 (172.9—210.8)	276.0 (229.9—323.3)	2.0 (1.8—2.2)
L. cyanellus	330.1 (318.5—347.3)	659.4 (637.0—678.3)	1.5 (0.8—2.9)
L. humilis	327.1 (246.7—412.8)	658.9 (583.5—734.3)	2.1 (1.2—2.9)
L. microlophus	190.6 (182.0—202.0)	383.0 (310.5—448.3)	1.6 (0.9—2.6)
L. megalotis	199.2 (183.0—215.8)	304.0 (241.3—367.3)	1.6 (1.0—2.2)
L. auritus	222.0 (189.0—268.3)	354.6 (324.3—395.3)	2.3 (1.3—2.9)
L. punctatus	227.2 (167.8—260.0)	442.2 (332.3—550.5)	1.7 (1.3—2.4)
L. marginatus	232.2 (187.4—253.0)	329.3 (313.0—353.5)	2.0 (1.5—2.7)
L. macrochirus	292.4 (257.5—314.3)	434.9 (324.8—505.0)	0.9 (0.9—1.0)
L. symmetricus	233.3 (209.5—258.8)	316.5 (273.0—424.5)	1.7 (1.5—1.9)
P. nigromaculatus	289.2 (203.3—327.3)	465.2 (295.5—557.3)	2.7 (1.5—4.3)
P. annularis	323.8 (299.3—343.5)	481.9 (455.0—513.0)	2.5 (1.9—3.2)
C. macropterus	185.0 (155.3—212.3)	299.9 (224.8—326.0)	1.5 (1.1—1.9)
A. rupestris	258.7 (277.5—333.5)	366.5 (306.8—433.3)	2.5 (1.3—3.3)
E. obesus	224.3 (200.8—246.3)	286.3 (245.3—301.4)	1.9 (1.8—1.9)
E. gloriosus	198.7 (171.3—210.8)	318.8 (273.8—358.5)	1.2 (0.5—2.0)
M. chaetodon	197.3 (186.5—205,8)	311.9 (281.3—346.5)	1.5 (1.2—2.0)
M. salmoides	128.5 (102.3—141.8)	233.3 (203.3—265.0)	1.7 (1.4—2.0)
M. punctulatus	152.0 (136.5—182.9)	200.8 (155.3—263.8)	1.6 (1.4—2.0)
M. dolomieui	185.7 (167.8—220.8)	251.7 (227.5—273.0)	1.3 (0.9—1.9)
M. coosae	274.5 (227.5—318.5)	494.9 (409.5—627.5)	2.4 (1.5—4.0)
M. treculi	151.1 (136.5—182.8)	216.2 (166.5—251.3)	1.7 (1.0—2.0)
M. notius	326.1 (310.5—343.5)	418.5 (364.0—465.5)	1.6 (1.1—2.4)
A. pomotis	191.9 (106.0—227.5)	264.1 (189.8—300.5)	2.9 (2.6—3.3)
E. evergladei	110.0 (89.4—137.8)	161.4 (129.4—184.0)	2.4 (2.2—2.9)
E. okefenokee	129.2 (128.5—129.8)	154.7 (150.3—159.0)	3.2 (2.5—3.6)

TABLE VI

COMPARISON OF ORGAN DEPTH, ORGAN DIAMETER AND DIAMETER OF THE SENSORY AREA IN CENTRARCHIDS. SCALE IN MICRONS. N = 39, EXCEPT IN *E. OBESUS* WHERE IT IS 7.

Species	Depth	Diameter	Diameter Sense Area
C. gulosus	68.7 (51.8--81.0)	599.1 (455.0--731.3)	251.4 (180.3--333.7)
L. gibbosus	37.8 (34.1--44.6)	254.1 (238.0--286.2)	197.1 (182.8--216.0)
L. cyanellus	57.0 (51.9--63.6)	532.5 (455.0--614.8)	192.3 (182.0--200.3)
L. humilis	45.8 (38.2--55.0)	658.5 (562.3--741.8)	172.6 (159.0--186.1)
L. microlophus	47.5 (46.8--48.8)	303.4 (273.0--384.0)	196.3 (148.8--243.8)
L. megalotis	28.8 (23.8--31.8)	172.3 (118.2--212.0)	118.5 (85.9--149.7)
L. auritus	44.3 (42.4--48.6)	264.6 (216.8--291.9)	187.0 (137.8--232.2)
L. marginatus	47.2 (40.6--53.0)	242.4 (217.4--273.0)	185.3 (164.3--204.3)
L. punctatus	50.3 (48.3--53.0)	382.2 (318.5--409.5)	260.3 (194.3--315.5)
L. macrochirus	30.9 (26.3--37.7)	220.6 (150.4--261.3)	139.6 (59.6--190.8)
L. symmetricus	36.6 (34.9--38.8)	305.0 (224.3--513.1)	187.2 (162.2--229.6)
P. nigromaculatus	51.5 (43.9--60.3)	335.3 (275.6--368.5)	174.4 (116.6--226.3)
P. annularis	52.1 (41.3--66.5)	429.5 (275.6--598.5)	233.1 (203.6--265.1)
C. macropterus	50.0 (34.4--60.9)	299.1 (230.8--329.4)	232.3 (181.5--294.8)
A. rupestris	49.0 (45.5--59.3)	394.8 (351.0--409.5)	197.3 (174.4--246.3)
E. obesus	29.2 (24.3--34.2)	186.5 (171.6--201.4)	77.6 (70.4-- 84.8)
E. gloriosus	31.1 (28.9--32.0)	236.5 (205.8--293.3)	170.8 (159.0--178.0)
M. chaetodon	25.8 (24.5--26.7)	144.5 (133.4--151.7)	93.0 (84.8-- 98.7)
M. salmoides	34.3 (28.2--41.3)	178.0 (156.5--195.8)	134.2 (119.5--164.0)
M. punctulatus	36.4 (31.8--46.6)	171.0 (109.5--243.8)	114.4 (69.1--179.0)
M. dolomieui	43.5 (40.4--45.5)	250.3 (227.5--293.0)	169.4 (142.4--207.0)
M. coosae	42.0 (40.9--44.3)	377.0 (275.0--455.8)	274.9 (159.4--357.7)
M. treculi	28.6 (27.8--30.4)	240.6 (201.4--251.3)	162.7 (140.9--166.5)
M. notius	32.9 (28.3--37.8)	388.7 (379.0--407.8)	280.3 (224.6--341.0)
A. pomotis	36.3 (33.8--38.6)	201.0 (176.5--250.2)	105.3 (58.1--180.2)
E. zonatum	28.0 (24.0--32.0)	123.0 (-- --)	-- (-- --)
E. evergladei	27.7 (24.5--35.5)	91.9 (69.8--170.5)	59.3 (53.0-- 66.9)
E. okefenokee	30.6 (28.7--32.7)	111.3 (95.4--127.2)	43.0 (35.3-- 53.0)

There is considerable contrast between the sensory cells of this tribe and those of *L. symmetricus*. The most obvious visual difference between the two groups is that the receptive ends of the cells are flattened in the Ambloplitini (Pl. VIII, Figs. 83 and 84), forming a disk for the insertion of sense hairs. In *L. symmetricus* the distal end of the sense cells are slightly convex. The cells of the rockbass and of *Acantharchus* take up less stain than those in Lepomis and, as shown in Fig. 83 (Pl. VIII), there is a rather large accumulation of subnuclear granules in Ambloplites, but very few in Acantharchus (Pl. VIII, Fig. 84). As described in L. symmetricus, there is a definite heteromorphism found in the sensory cells of the Ambloplitini. In the mud sunfish the large pale cells, 10.1 (5.5 - 22.0) microns in A. pomotis and 8.4 (6.5 - 10.4) microns in Ambloplites, are in the same region as those delineated for Lepomis. Ambloplites differs in this respect, for the big cells are not found in the lateral area but in the marginal cells. It will be noticed in Table VIII that all of the sense cells of the rockbass are larger than any of those in L. symmetricus, as are most of those in Acantharchus. The heteromorphic cells of the last-named form are larger on the average than those in any other sunfish. The apical diameters of the sensory elements vary little (Table IX) in the whole family. Ambloplites rupestris possesses the largest sense cells of any member of the Centrarchidae (Table VIII), but those of Acantharchus are comparable to those described for L. symmetricus.

The sensory nuclei of the Ambloplitini are considerably larger than those of L. symmetricus (Table X) but the staining properties are the same. As mentioned in the discussion of the last form, there is little variation in size of the nuclei between the large and normal-sized cells in the rockbass, but in Acantharchus the karyosomes in these elements are very large. The endosomes are about the same in all of the centrarchids, but there is one remarkable difference in Ambloplites. The endosomes in most of the sensory cells of this species are about half again as large as those in the sustentacular cells (Table XII).

The sense hairs and blepharoplast bodies are similar to those described above but those of Ambloplites (Table XII) measure 2.6 (1.5 - 3.3)

TABLE VII

COMPARISON OF THE NUCLEAR AND APICAL DIAMETER AND LENGTHS OF SUSTENTACULAR CELLS FROM CANAL ORGANS OF CENTRARCHID FISHES.
N = 39, EXCEPT IN *E. ZONATUM* WHERE IT IS 150

Species	Apical	Nuclear	Length
C. gulosus	2.5 (1.5--5.3)	4.5 (3.4--5.6)	59.0 (42.7--79.7)
P. nigromaculatus	2.3 (1.3--3.3)	5.4 (3.4--5.4)	46.5 (37.4--57.1)
P. annularis	2.4 (1.8--3.0)	4.3 (3.4--5.0)	35.0 (21.5--56.2)
C. macropterus	2.3 (1.4--3.0)	3.5 (2.9--4.5)	33.9 (17.6--48.8)
E. gloriosus	1.9 (1.3--2.6)	3.2 (2.6--4.1)	28.8 (26.0--30.4)
E. obesus	1.6 (1.2--2.3)	3.1 (2.2--4.0)	32.6 (19.5--41.0)
M. chaetodon	1.8 (1.2--2.5)	3.0 (2.5--3.7)	27.0 (24.7--30.8)
A. rupestris	2.3 (1.5--3.2)	4.4 (3.4--5.6)	54.2 (44.0--74.8)
M. salmoides	1.7 (1.3--2.3)	3.1 (2.6--3.8)	28.7 (24.4--32.6)
M. punctulatus	1.8 (1.3--2.4)	3.3 (2.8--4.5)	32.9 (26.4--46.4)
M. dolomieui	1.9 (1.2--3.0)	3.9 (3.3--6.5)	41.1 (35.2--45.8)
M. coosae	2.1 (1.4--2.4)	3.6 (3.0--4.6)	42.9 (37.9--48.4)
M. treculi	2.0 (1.3--3.4)	3.5 (2.9--4.3)	28.4 (25.5--31.9)
M. notius	2.0 (1.7--2.4)	3.5 (3.0--4.1)	31.5 (25.1--37.1)
E. zonatum	2.0 (1.6--2.3)	3.2 (2.4--3.6)	26.0 (23.0--26.0)
E. evergladei	1.5 (1.0--2.5)	2.8 (2.2--3.4)	23.9 (17.6--26.4)
E. okefenokee	1.4 (1.0--2.1)	3.1 (2.4--4.3)	24.9 (19.4--30.8)
L. gibbosus	1.8 (1.1--2.5)	3.9 (3.0--4.5)	37.7 (32.8--48.4)
L. cyanellus	2.3 (1.6--3.2)	4.2 (3.6--4.7)	59.4 (42.4--72.2)
L. humilis	2.3 (1.5--3.4)	4.2 (3.1--4.8)	39.0 (33.8--44.5)
L. microlophus	1.9 (1.4--3.0)	3.7 (3.1--4.1)	47.4 (40.9--52.8)
L. megalotis	2.3 (1.3--3.4)	3.9 (3.1--5.5)	24.7 (17.3--31.4)
L. auritus	2.3 (1.7--3.2)	4.1 (3.4--4.9)	45.8 (41.6--52.8)
L. punctatus	2.1 (1.2--3.2)	4.6 (3.8--5.6)	49.5 (45.8--55.2)
L. marginatus	2.1 (1.2--2.8)	3.7 (2.6--4.7)	38.2 (24.4--49.4)
L. macrochirus	1.7 (1.4--2.3)	3.5 (2.8--3.9)	29.3 (22.8--36.5)
L. symmetricus	2.2 (1.7--2.8)	3.9 (2.8--4.7)	35.7 (31.0--41.8)
A. pomotis	2.0 (1.2--3.1)	3.4 (2.3--4.5)	33.2 (30.8--37.3)

microns in length.

Acantharchus pomotis shares one sensory-cell characteristic with *Chaenobryttus* that was not observed elsewhere in the family. A granular, relatively dark-staining, round body, located just above the nucleus, was observed in a very few sensory cells. This body, which averaged 0.8 microns in diameter, has no other distinctive characteristics.

TABLE VIII

COMPARISON OF THE BASAL DIAMETER OF SENSE CELLS FROM CANAL NEUROMASTS IN CENTRARCHIDAE. N = 39

Species	Central	Lateral	Marginal
C. gulosus	6.1 (4.7--7.4)	8.7 (4.9-10.7)	5.6 (4.2--6.2)
P. nigromaculatus	8.4 (5.9-10.0)	9.6 (7.9-13.4)	9.8 (9.0-10.9)
P. annularis	6.6 (4.8--8.8)	8.7 (8.0--9.3)	5.4 (4.5--7.0)
A. pomotis	7.3 (5.7-10.1)	10.1 (5.5-22.0)	6.2 (4.9--7.0)
C. macropterus	7.0 (5.8--7.9)	7.9 (4.9--9.2)	6.2 (4.0--7.9)
E. gloriosus	6.2 (5.0--7.7)	6.1 (5.0--7.1)	6.3 (5.2--7.2)
E. obesus	4.6 (4.2--4.8)	4.9 (4.0--5.6)	4.2 (3.1--4.7)
M. chaetodon	5.2 (4.8--5.8)	5.1 (3.8--6.0)	5.0 (3.9--6.9)
A. rupestris	7.4 (6.0--8.2)	7.1 (5.9--7.2)	8.4 (6.5-10.4)
M. salmoides	5.9 (4.5--7.3)	5.5 (4.5--6.3)	6.3 (5.4--7.4)
M. punctulatus	5.4 (4.3--6.9)	5.5 (4.3--6.6)	4.5 (4.2--6.9)
M. dolomieui	5.7 (4.7--6.8)	5.9 (5.0--7.8)	6.1 (4.8--7.5)
M. coosae	6.0 (5.3--6.8)	5.8 (5.3--6.7)	6.1 (4.9--7.4)
M. treculi	5.5 (4.5--6.4)	5.5 (5.1--6.1)	5.2 (4.5--5.9)
M. notius	5.7 (5.1--6.5)	5.8 (4.7--6.5)	5.6 (4.7--6.5)
E. evergladei	4.3 (3.4--4.9)	4.3 (3.7--5.2)	3.9 (3.4--5.0)
E. Okefenokee	4.3 (3.6--5.1)	4.8 (4.3--5.6)	4.6 (3.8--5.4)
L. gibbosus	6.9 (5.9--8.3)	6.6 (5.4--7.5)	6.6 (5.4--7.6)
L. cyanellus	6.8 (6.0--7.5)	6.7 (6.0--7.6)	6.7 (6.0--7.5)
L. humilis	6.8 (5.8--7.7)	6.7 (5.7--7.3)	6.9 (6.0--8.0)
L. microlophus	6.8 (6.1--8.1)	6.8 (6.0--7.7)	6.7 (5.2--7.5)
L. megalotis	5.7 (4.8--6.8)	5.2 (4.6--6.0)	5.2 (4.4--6.2)
L. auritus	6.9 (5.1--7.8)	6.7 (5.8--8.0)	6.7 (5.9--7.7)
L. punctatus	6.5 (7.3--7.9)	6.8 (6.6--7.1)	7.1 (5.3--7.7)
L. marginatus	6.7 (5.2--7.7)	6.3 (5.2--7.3)	5.8 (5.0--7.3)
L. macrochirus	5.5 (4.9--6.4)	5.7 (5.2--6.4)	5.9 (4.7--7.5)
L. symmetricus	5.8 (4.8--6.3)	6.5 (5.2--8.3)	5.7 (4.3--6.6)

Centrarchinae--Centrarchini

Absolute measurements, in many instances, will show very little difference between forms when large species are compared with small ones. This is especially true with such data as is derived from measurements of canal size. Nonetheless the lachrymal lateral-line canal in the flyer is only moderately smaller than that of L. symmetricus and is equal to or larger than those of much larger fishes (Table V). The same canal in Pomoxis is nearly as large or larger than in species near the upper end of the scale. The basement membrane of Centrarchus measured 1.5 (1.1 - 1.9) microns, which is near the figures given for L. symmetricus, but it measured almost twice this thickness in both species of Pomoxis.

As with the species of Amblopliteni, it is more informative if the measurements of the intact organ are compared as percentages of one another. The data for these comparisons are listed in Table VI. Graph I demonstrates neuromast depth as a percentage of the total organ diameter, 17.4, 12.6 and 15.4 for Centrarchus, P. annularis and P. nigromaculatus in that order, all of which lie near the middle of the range when compared with the whole family. The discrepancy seen in the species of Pomoxis is probably explainable on the basis of sampling error. The values, 77.7, 58.0 and 52.4 (arranged as above), show that the sensory area of the neuromasts in Pomoxis (Pls. X and XI, Figs. 115 and 130) are not unlike many other centrarchids, but that of Centrarchus (Pl. VIII, Fig. 82) shares with Lepomis gibbosus, Enneacanthus gloriosus and Micropterus punctulatus the position of having more of the neuromast surface area occupied with sense cells than most other forms. The lachrymal neuromast of Pomoxis is located very near the opening of the dorsal-most anterior arm of that bone and is of a different shape and size than the lower one (compare Figs. 115 and 130). Cupulae were noted on several organs in all three species. The ratio of supporting cells to sensory cells was found to be: P. nigromaculatus, 62/39; P. annularis, 123/62; and Centrarchus, 70/43 (Table XIII). It is thus easily seen that P. nigromaculatus is more like Centrarchus, both of which resemble L. symmetricus in this respect, than like P. annularis. Furthermore, the supporting cells of P. annularis

TABLE IX

COMPARISON OF THE APICAL DIAMETER OF SENSE CELLS FROM CANAL NEUROMASTS IN CENTRARCHIDAE. N = 39

Species	Central	Lateral	Marginal
C. gulosus	3.0 (2.1--4.1)	5.6 (4.5--7.7)	3.6 (2.3--4.9)
P. nigromaculatus	5.5 (4.0--8.9)	7.5 (5.7--9.8)	6.7 (5.2--8.9)
P. annularis	3.8 (3.4--4.7)	6.1 (4.3--7.7)	4.2 (2.7--5.0)
C. macropterus	4.3 (3.0--5.6)	5.2 (3.0--7.0)	4.2 (4.1--5.6)
A. pomotis	5.0 (4.3--6.0)	5.6 (4.3--6.2)	4.4 (4.0--5.3)
E. gloriosus	4.0 (3.0--4.9)	4.1 (3.4--5.9)	4.2 (3.5--4.9)
E. obesus	2.9 (2.1--3.7)	2.9 (2.6--3.4)	2.9 (2.4--3.4)
M. chaetodon	3.1 (2.5--3.7)	3.3 (2.5--4.0)	3.0 (2.3--3.5)
A. rupestris	3.9 (3.5--4.0)	3.6 (3.0--4.3)	3.4 (3.4--5.1)
M. salmoides	3.4 (2.8--4.0)	3.2 (2.8--3.7)	3.7 (3.0--5.3)
M. punctulatus	3.4 (2.6--5.1)	3.5 (2.9--4.1)	3.6 (2.5--5.5)
M. dolomieui	3.7 (3.0--4.4)	3.5 (2.5--4.9)	3.9 (3.3--4.9)
M. coosae	4.0 (3.2--5.0)	3.9 (3.4--4.5)	4.1 (3.4--4.4)
M. treculi	3.3 (2.9--3.7)	3.6 (3.2--4.3)	3.4 (3.1--3.7)
M. notius	4.1 (3.3--5.2)	3.9 (3.4--4.4)	3.7 (3.0--4.7)
E. evergladei	2.6 (1.8--3.5)	2.8 (2.2--3.3)	2.6 (1.9--3.2)
E. okefenokee	2.9 (2.2--3.7)	2.7 (2.1--3.7)	2.6 (2.2--3.2)
L. gibbosus	5.2 (4.0--6.5)	4.7 (3.7--5.8)	4.7 (3.3--5.4)
L. cyanellus	4.7 (4.0--5.5)	4.6 (4.0--5.6)	4.7 (3.8--5.7)
L. humilis	3.9 (3.2--4.7)	3.9 (2.7--4.8)	4.0 (2.7--5.2)
L. microlophus	5.0 (4.2--6.5)	4.8 (3.8--5.2)	4.6 (3.8--5.5)
L. megalotis	3.3 (2.5--3.9)	3.5 (2.4--4.4)	3.6 (2.8--5.3)
L. auritus	5.0 (3.9--6.4)	5.3 (4.1--6.2)	5.2 (4.2--5.9)
L. punctatus	4.4 (3.8--4.9)	4.4 (3.6--5.6)	4.5 (3.7--5.6)
L. marginatus	4.7 (3.9--6.1)	4.5 (3.7--5.5)	4.2 (3.2--5.2)
L. macrochirus	3.1 (2.3--3.6)	2.9 (2.3--3.4)	3.7 (3.7--4.5)
L. symmetricus	3.6 (2.7--4.9)	4.5 (3.3--6.8)	4.2 (2.6--5.5)

are more similar to Centrarchus in mensurable details than they are to P. nigromaculatus (Table VII). Further perusal of this table will reveal that the Centrarchinae, with the exception of Acantharchus, L. punctatus, L. auritus, L. cyanellus and L. humilis, have the largest supporting nuclei in the family. In Pomoxis the supporting cell nuclei are extremely visiculated and very seldom have endosomes. In referring to Figures 85 and 88 (Pl. VIII) it is readily seen that the supporting cells actually extend upward between the sensory elements. One such sustentacular element is illustrated in _P_. _nigromaculatus_ to show the distal attenuation that occurs at the point where the cell enters the raft of sensory cells.

Figures 85, 87 and 88 (Pl. VIII) illustrate some of the differences observed in the heteromorphy of the sensory cells of the Centrarchini. In _Centrarchus_ the differences between the two kinds of cells are very slight and measurements given for the different cells in Tables VIII, IX, X and XI actually do not tell us very much in this species. The situation is quite different in _Pomoxis_ where there are some very distinct differences. The large cells of _P_. _nigromaculatus_ are found in both the lateral and marginal areas, whereas they are generally localized in the lateral region in _P_. _annularis_. In this group of fishes the large cells are often shorter than the normal ones (Table XI). The sense hairs of the heteromorphic elements are seldom associated in a triangular arrangement as they are in the others (Pl. VIII, Figs. 85, 87 and 88) and these structures are very short in _Centrarchus_ (average 1.4 microns) when compared with many of the other sunfishes (Table XI).

The sensory cells of the Centrarchini are more similar to _Lepomis symmetricus_ than to those of the Ambloplitini in having a convex sensory surface rather than the flat, plate-like surface observed in the latter group.

Lepominae--Enneacanthini

These small fishes have very large lateral-line canals (Table V) which, if their small proportions are considered, are equal to species like _Ambloplites_ _rupestris_. _Mesogonistius_ possesses smaller neuromasts than either of the _Enneacanthus_, but the proportions of depth to diameter

TABLE X

COMPARISON OF THE NUCLEAR DIAMETER OF SENSE CELLS FROM CANAL NEUROMASTS IN CENTRARCHIDAE

Species	Central	Lateral	Marginal
C. gulosus	5.2 (3.6--5.9)	5.5 (4.5--6.7)	5.0 (3.9--5.8)
P. nigromaculatus	5.4 (4.8--6.5)	6.0 (5.6--6.6)	4.9 (3.5--6.0)
P. annularis	4.9 (4.2--5.3)	5.4 (5.0--5.7)	3.4 (2.9--4.3)
A. pomotis	5.1 (4.2--5.9)	6.6 (5.1-12.2)	4.8 (3.8--6.1)
C. macropterus	4.8 (4.1--5.6)	5.2 (4.5--5.8)	4.2 (2.9--5.6)
E. gloriosus	4.5 (3.9--5.4)	4.2 (3.4--4.9)	4.3 (3.6--4.9)
E. obesus	3.2 (2.6--4.2)	3.3 (2.4--4.2)	3.1 (2.4--4.1)
M. chaetodon	3.7 (3.4--4.2)	3.7 (3.0--4.4)	3.5 (3.1--4.7)
A. rupestris	5.8 (5.3--6.2)	5.3 (4.6--6.0)	6.0 (5.5--6.5)
M. salmoides	4.1 (3.1--4.9)	4.0 (3.3--5.2)	4.4 (4.0--5.5)
M. punctulatus	3.8 (3.0--5.0)	4.2 (3.2--5.2)	4.2 (3.6--5.2)
M. dolomieui	4.1 (3.7--4.8)	4.1 (3.6--4.9)	4.4 (3.7--5.7)
M. coosae	4.4 (3.8--5.0)	4.3 (3.9--5.1)	4.7 (4.2--5.4)
M. treculi	3.9 (3.6--4.5)	4.0 (3.7--4.3)	4.2 (3.5--4.5)
M. notius	4.4 (3.8--5.0)	4.5 (3.4--4.4)	4.5 (3.0--4.7)
E. evergladei	3.2 (2.5--4.0)	3.2 (2.4--3.8)	3.0 (2.5--3.5)
E. okefenokee	3.1 (2.4--4.4)	3.3 (2.7--4.3)	3.3 (2.6--4.5)
L. gibbosus	4.8 (4.1--5.1)	4.8 (4.0--5.5)	4.3 (4.1--5.1)
L. cyanellus	5.1 (4.4--5.8)	4.8 (4.2--5.5)	4.7 (4.3--5.6)
L. humilis	4.8 (3.9--5.7)	4.5 (3.3--5.3)	4.6 (3.3--6.3)
L. microlophus	4.9 (4.1--5.6)	4.9 (4.3--5.7)	4.8 (4.3--5.3)
L. megalotis	4.5 (3.7--4.9)	4.1 (3.8--4.5)	4.2 (3.3--5.0)
L. auritus	4.7 (4.2--5.2)	4.8 (3.8--5.8)	4.5 (3.7--5.1)
L. punctatus	5.1 (4.4--6.8)	5.0 (4.4--6.3)	5.6 (4.7--6.5)
L. marginatus	4.7 (3.8--5.2)	4.3 (3.7--4.7)	4.7 (3.7--4.8)
L. macrochirus	4.4 (3.5--5.0)	4.1 (3.8--4.5)	4.7 (3.7--4.8)
L. symmetricus	4.6 (4.1--5.5)	4.8 (4.1--5.5)	4.2 (2.8--5.0)

and of sensory area to total organ diameter are similar in all three species (Pls. X and XI, Figs. 104, 114 and 119). With the exception of those found in *Elassoma*, the organs of *M. chaetodon* are the smallest in the family (Table VI). Because of a decrease in depth, this component in *Mesogonistius* represents a greater percentage than it does in *E. gloriosus* and *E. obesus* (Graph I). Only four species, *L. humilis*,

TABLE XI

COMPARISON OF THE LENGTHS OF SENSE CELLS IN THE CENTRARCHIDAE. N = 39

Species	Central	Lateral	Marginal
C. gulosus	15.4 (13.2--17.6)	14.5 (11.0--17.6)	17.1 (13.2--19.0)
P. nigromaculatus	15.3 (13.2--17.6)	13.9 (12.1--16.3)	13.2 (13.2--13.2)
P. annularis	14.2 (11.3--17.6)	11.6 (9.9--14.2)	13.1 (8.8--17.1)
A. pomotis	15.3 (13.9--17.8)	16.6 (14.8--17.6)	16.0 (11.3--18.8)
C. macropterus	14.4 (13.2--17.6)	13.9 (10.8--17.4)	14.1 (10.3--17.6)
E. gloriosus	16.6 (15.5--17.6)	17.1 (15.9--18.2)	17.5 (17.3--17.6)
E. obesus	15.8 (15.0--16.5)	15.2 (15.1--15.2)	15.5 (14.3--16.6)
M. chaetodon	13.0 (11.1--15.0)	14.2 (13.2--14.8)	13.0 (11.6--14.2)
A. rupestris	21.9 (19.0--24.6)	23.0 (22.0--24.1)	21.4 (15.4--23.9)
M. salmoides	15.7 (14.3--16.6)	15.3 (14.7--16.3)	14.1 (12.6--15.7)
M. punctulatus	16.9 (16.0--20.3)	17.4 (16.0--19.9)	16.5 (14.5--20.6)
M. dolomieui	19.5 (18.2--20.4)	20.1 (17.6--22.0)	20.3 (18.7--22.0)
M. coosae	16.8 (16.3--17.6)	16.6 (16.9--18.5)	15.8 (14.9--16.9)
M. treculi	16.0 (14.9--17.6)	16.0 (15.4--16.6)	15.2 (14.1--16.1)
M. notius	16.1 (15.1--17.6)	16.9 (16.3--17.6)	16.8 (15.7--17.6)
E. evergladei	13.0 (12.4--13.2)	14.1 (12.3--15.7)	13.7 (12.8--15.5)
E. okefenokee	15.3 (14.8--16.3)	17.4 (15.6--17.6)	14.8 (14.1--15.1)
L. gibbosus	17.3 (16.1--22.0)	16.9 (15.2--20.0)	14.7 (13.2--16.6)
L. cyanellus	18.1 (17.6--19.7)	17.0 (16.1--17.6)	16.7 (15.1--17.6)
L. humilis	17.8 (16.0--18.7)	18.2 (16.9--19.7)	15.8 (11.3--21.1)
L. microlophus	18.3 (16.4--20.8)	17.4 (16.8--17.6)	17.7 (14.2--20.0)
L. megalotis	15.0 (13.2--17.4)	11.8 (11.6--14.4)	12.4 (9.0--16.1)
L. auritus	15.9 (14.1--17.4)	15.9 (14.1--17.6)	14.6 (13.2--16.6)
L. punctatus	19.2 (17.6--20.2)	19.1 (17.0--20.1)	19.1 (17.6--22.0)
L. marginatus	19.0 (17.6--22.0)	18.8 (17.1--21.2)	18.4 (13.2--19.2)
L. macrochirus	13.9 (11.8--15.0)	14.0 (12.6--14.8)	11.1 (8.8--12.1)
L. symmetricus	16.6 (16.0--17.6)	11.6 (9.6--13.5)	11.5 (8.8--12.8)

L. cyanellus, Chaenobryttus and Elassoma okefenokee, possess sense cells which occupy less of the total area of the canal neuromast than they do in E. obesus (Graph II). With regard to this last index, Enneacanthus gloriosus and M. chaetodon are very similar to the other centrarchids. The following cell counts, showing the ratio of the average number of supporting cells to average number of sense cells, indicates the same relationships as Graph II:

TABLE XII

COMPARISON OF THE DIAMETERS OF NUCLEAR ENDOSOMES IN SENSE CELLS AND SUSTENTACULAR CELLS AND THE LENGTHS OF SENSE HAIRS IN CENTRARCHIDAE. N = 39

Species	Sense Cells	Sustentacular Cells	Sense Hairs
C. gulosis	1.0 (0.7--1.3)	1.0 (0.8--1.3)	1.8 (0.7--4.3)
P. nigromaculatus	0.9 (0.6--1.0)	0.8 (0.6--1.1)	2.0 (1.2--2.8)
P. annularis	0.9 (0.5--1.1)	1.0 (0.8--1.2)	1.6 (1.3--2.1)
A. pomotis	0.9 (0.6--1.8)	0.9 (0.6--1.2)	1.8 (1.1--3.0)
C. macropterus	0.8 (0.5--1.1)	0.8 (0.6--1.2)	1.4 (0.9--1.8)
E. Gloriosus	0.8 (0.6--1.2)	0.7 (0.4--1.0)	2.0 (1.5--2.4)
E. obesus	0.6 (0.4--1.0)	0.8 (0.4--1.1)	2.4 (1.6--3.0)
M. chaetodon	0.7 (0.4--1.1)	0.7 (0.5--1.1)	1.7 (1.1--2.3)
A. rupestris	1.0 (0.6--1.5)	0.7 (0.5--1.0)	2.6 (1.5--3.3)
M. salmoides	0.7 (0.5--1.0)	0.7 (0.4--0.9)	2.6 (1.5--3.3)
M. punctulatus	0.8 (0.5--1.2)	0.8 (0.4--1.2)	2.8 (1.6--3.8)
M. dolomieui	0.9 (0.6--1.2)	1.1 (0.6--1.5)	2.9 (1.8--4.3)
M. coosae	0.8 (0.5--1.1)	0.7 (0.5--1.1)	-- -- --
M. treculi	0.7 (0.5--1.0)	0.8 (0.6--1.3)	5.1 (3.2--7.2)
M. notius	0.8 (0.5--1.0)	0.8 (0.5--1.0)	-- -- --
E. evergladei	0.7 (0.4--1.0)	0.7 (0.5--1.1)	2.8 (2.0--3.7)
E. okefenokee	0.7 (0.4--1.0)	0.7 (0.3--1.0)	2.5 (1.4--4.1)
L. gibbosus	0.9 (0.7--1.3)	0.9 (0.7--1.3)	3.0 (2.0--3.8)
L. cyanellus	0.9 (0.6--1.1)	1.0 (0.7--1.3)	2.2 (1.5--2.7)
L. humilis	0.8 (0.5--1.1)	0.8 (0.5--1.2)	3.2 (2.2--3.9)
L. microlophus	0.8 (0.4--1.1)	0.8 (0.5--1.1)	2.1 (1.1--2.6)
L. megalotis	0.9 (0.6--1.2)	0.8 (0.6--1.2)	1.4 (0.9--2.3)
L. auritus	0.9 (0.6--1.2)	0.9 (0.6--1.2)	2.1 (1.2--3.1)
L. punctatus	0.8 (0.4--1.2)	1.2 (0.8--1.4)	2.1 (1.4--2.9)
L. marginatus	0.9 (0.7--1.3)	0.9 (0.6--1.2)	1.7 (0.9--3.3)
L. macrochirus	0.9 (0.6--1.2)	0.8 (0.5--1.1)	1.7 (1.4--1.9)
L. symmetricus	0.9 (0.6--1.2)	0.9 (0.7--1.1)	1.1 (0.7--1.7)

M. chaetodon, 48/28; *E. gloriosus*, 74/38; *E. obesus*, 60/41. Cupulae were indicated only by slight traces.

There is very little distinction among the three species of enneacanthine fishes and between them and other sunfishes as far as the details of supporting cells are concerned (Table VII). However, one aspect of the supporting elements, which apparently escaped notice until observed by

Moore (1956), was found in E. obesus. Sections cut across the face of the neuromast very clearly demonstrate that these peripheral sustentacular cells are bound together by some protoplasmic bridges (Pl. X, Fig. 104 B). Further observations of these structures will be indicated below.

There are no very apparent differences in the sensory cells of this taxon to set them aside from other centrarchids. However, it will be noted from Tables VIII, IX and X that all of the cells are similar from one side of the organ to the other, e. g., no heteromorphic cells were seen. E. Gloriosus (Pl. X, Fig. 109) has sense cells and nuclei which are slightly larger than those of the other two members of its tribe and those of M. chaetodon are larger than those of E. obesus. In length, however, the sensory elements of the two Enneacanthus are nearly equal, whereas those of M. chaetodon average one to nearly three microns shorter (Table XI. Actually, except in Elassoma, few sunfishes have shorter sense cells than Mesogonistius. The sense cells of this group are suggestive of those in the Ambloplitini in being flattened at the apex (Pl. X, Fig. 109). The sensory hairs are like those already discussed, although in M. chaetodon they seem shorter than in the other two species of the tribe. Subnuclear granules were not observed in Enneacanthus.

Lepominae--Micropterini

The comparatively small size of the canals in this taxon has already been alluded to (see Table V). The cephalic canals are especially small in Micropterus salmoides and M. treculi, but, except in very large specimens, these tubes are not conspicuous in any of the species. M. notius and M. coosae have the largest canals of any of the basses. The bony passageways are comparable to those of Chaenobryttus, and larger than those of L. symmetricus. The bony passage of the other basses (Table V) are the smallest in the family (omitting Elassoma).

Although the absolute depth of the micropterine canal neuromast does not markedly differ from most other sunfishes (Table VI) the apparent depth does. This characteristic is shared in part with the Lepomini. Micropterus salmoides (Graph I) has the most narrow organ in the family except for L. humilis. It is followed closely by L. cyanellus, Chaenobryttus and a few others. The sensory elements occupy about the central two-thirds of the organ diameter as seen in Figs. 117, 118, 121, 128 and 129 (Pl. XI). These cells occupy a large percentage of the surface area (Graph II) as they do in many of the Lepomini, and the relationship between total organ diameter and diameter of the sensory area is maintained by a balanced number of cells in each category. The following represents the average number of the two kinds of cells (supporting/sensory) in the Micropterini: M. salmoides, 57/23; M. punctulatus, 52/22; M. dolomieui, 64/29; M. coosae, 115/46; M. treculi, 69/30; and M. notius, 112/49.

The shallow depth of the neuromasts in M. treculi and M. notius is mostly a response to short supporting elements (Table VII), which also occurs in M. salmoides and M. punctulatus. The sustentacular cells of M. coosae and M. dolomieui are longer than they are in L. symmetricus, but in most other sustentacular measurements the basses are similar to other centrarchids (Table VII). The smallmouth bass has the second largest supporting-cell nuclear endosomes in the family (Table XII), some of them measuring 1.5 microns in diameter (Pl. IX. Fig. 94). This species is one of the few forms in which the nucleosomes of the sustentacular cells are larger than those of the sensory elements.

A facial section, taken near the distal ends of the central supporting cells and through about the middle of the portion of the supranuclear sensory cells of a canal organ in M. treculi (Pl. IX, Fig. 91), reveals additional information concerning the intercellular bridges referred to above. At this level the "bridges" surround the sense cells on all sides. Presumedly this has not heretofore been reported in any fish. This observation also leads to the conclusion that the intercellular bridges occur for at least a part of the total length of the supporting cells.

As in the Enneacanthini there is very little tendency for the micropterine fishes to exhibit heteromorphic sensory cells (Table VIII). Excluding Elassoma, Lepomis megalotis, Enneacanthus gloriosus and Mesogonistius chaetodon (Table VIII) these cells average smaller in basal diameters than in most of the other sunfishes. The apical and nuclear diameters are similar to other centrarchids (Tables IX and X), but their lengths in M. dolomieui (Pl. IX, Fig. 94) are equal to those in A. rupestris, L. punctatus and L. marginatus (Table XI). The general sensory cytoplasm is as has been described for others, but the subnuclear granules were extremely minute in M. dolomieui, completely lacking in M. salmoides and quite distinct in the others. The terminal bars are very well-developed in the micropterine fishes as demonstrated in the largemouth bass (Pl. IX, Fig. 90) and M. punctulatus (Pl. IX, Fig. 89). Micropterus treculi (Pl. IX, Fig. 93) has the largest sense hairs observed in this study. and the basses in general possess sensory hairs that are longer than other sunfishes, equaling or surpassing those of the rockbass, but shorter than those of L. humilis and L. gibbosus (Table XII). The terminal ends of the sense cells are convex as in L. symmetricus.

TABLE XIII

COMPARATIVE NUMBERS OF SENSORY AND SUPPORTING CELLS IN THE CENTRARCHIDAE PER CROSS SECTION. SUPPORTING CELLS?SENSORY CELLS

Species	Supporting Cells/Sensory Cells
Ambloplites	90/76
Acantharchus	59/14
P. nigromaculatus	62/39
P. annularis	123/62
Centrarchus	70/43
E. gloriosus	74/38
E. obesus	60/41
M. chaetodon	48/28
M. salmoides	57/23
M. punctulatus	52/22
M. dolomieui	64/29
M. coosae	105/46
M. treculi	69/30
M. notius	112/49
C. gulosus	133/37
L. gibbosus	65/29
L. cyanellus	127/29
L. humilis	157/26
L. microlophus	82/29
L. megalotis	44/23
L. auritus	65/28
L. marginatus	66/29
L. punctatus	83/38
L. macrochirus	63/24
L. symmetricus	76/32
E. zonatum	38/13
E. evergladei	36/10
E. okefenokee	33/14

Lepominae--Lepomini

All of the Lepomini possess a rather thin basement membrane, as seen in L. symmetricus, that of L. macrochirus (Table V) averaging considerably less than any other species. The lateral-line tube formed by the tissue of the basement membrane is of relatively larger diameter than that of

Micropterus and equal to those of the members of the Amblopliitini, but slightly smaller than in the Centrarchinae. However, L. cyanellus, L. humilis, L. macrochirus and Chaenobryttus have the largest canals in the family. As noted previously the canals of L. humilis are very greatly expanded. This expansion involves both the connective tissue canal and its bony passage (Table V). The osseous components of the canals in L. cyanellus and L. humilis are over twice the size of many other species and, with the exception of Chaenobryttus, are at least one-third larger than those of any of the other forms.

The canal neuromasts of the Centrarchidae, with the exception of Elassoma, Enneacanthus and Mesogonistius (Tables V and VI), are of greater diameter than the connective tissue canals which contain them. This, at first sight, may seem incongruous, but this difficulty is resolved when it is realized that these organs are not simple planoconvex structures, since their edges roll upward around the walls of the canals and are elongated along the long axis of the canals. This is illustrated in L. marginatus (Pl. VIII, Fig. 86). The canal organs, if Ambloplites, Archoplites and the Centrarchinae are omitted, are the largest in the family. There are some exceptions to this statement. The organs of L. megalotis and L. macrochirus are surpassed by all of the other Lepomini in size, possibly because of the relatively narrow cephalic canals in these two species. In this study the canal organs of Chaenobryttus, L. cyanellus and L. humilis were found to be of much greater size than those of any of the other sunfishes (Table VI). In the orangespotted sunfish, except for Chaenobryttus, L. cyanellus, M. notius, M. coosae, Ambloplites, Archoplites and Pomoxis, these organs are twice the size of the remaining forms (Pl. XI, Fig. 132). The organ illustrated by Moore

(1956) was only 382 microns in diameter which is very small for this species (Table VI). In Figure 111 (Pl. X), representing a facial section of the lachrymal in which only the top of the canal has been removed (L. auritus), it will be noted that the neuromast is attached to the lateral-line canal basally and on two sides. This is the characteristic mode of attachment in all centrarchids.

The sensory elements are completely surrounded by sustentacular cells in all species of the tribe, but the relative areas occupied by the two classes of cells (supporting/sensory) varies from species to species (Pl. XI, Figs. 116, 124, 125, 126, 131, 132 and 133). The fact that the sensory cells are restricted to the center of the neuromast is contrary to Moore's (1956) findings in L. cyanellus, where it was stated that the sensory elements occupied the entire cross-sectional length of the organ. In 39 organs observed during this study, all of them were found to have central sensory cells. This author's findings, in regard to position of receptive cells, are in agreement with the last cited work as far as the orangespotted sunfish is concerned, Cupulae were observed in all species of the tribe, which, with the exception of Curd's (1959) record for L. humilis, is the first report for these structures in any lepomine fish.

The depth/diameter and diameter of the sensory area/total diameter of the organ relationships of the tribe Lepomini bring out some interesting facts that are not obvious in cursory observations. The data used for the following discussion and indices are found in Table VI. There is obvious similarity between the canal organs of lepomine species with those of M. notius, M. coosae and M. treculi (Graph I). This is accounted for by an increase in length of the organ without an increase in depth. Graph II illustrates another very interesting point in the Lepomini. The sensory areas of *Chaenobryttus*, *L. cyanellus* and *L. humilis* represent much less of the total organ diameter than is found in any other species except *Elassoma okefenokee* and *Enneacanthus obesus*. In *Elassoma* and *Enneacanthus* this relative decrease is accounted for by assuming a decrease in the number of sense cells while retaining a fairly large number of supporting elements. In *Chaenobryttus* and the two species of *Lepomis* named above, the number of supporting elements, when compared within the matrix of other lepomines, has become greatly increased whereas the sense cells have remained about the same as they are in the other related forms (Table XIII). *Lepomis humilis* has from one-third to more than three times as many supporting cells than any other species in the Centrarchidae.

The supporting cells of the Lepomini are quite like those of other centrarchids in shape and staining reactions. The measurements recorded in Table VII are not unlike those of other sunfishes, but the supporting elements of *L. megalotis* (Pl. IX, Fig. 102), excluding *Elassoma*, are the shortest in the family and those of *L. cyanellus* the longest. The measurements of length given by Moore (1956) for *L. humilis* are in general agreement with those herein reported, but his measurements of diameter are comparable to the apical diameters given for this species in Table VII. It has already been pointed out that the supporting cell nuclear endosomes of *L. punctatus* (Pl. X, Fig. 106) are much larger than those of its sense cells. The endosomes of *L. gibbosus* (Pl. X. Fig. 108) and *L. cyanellus* are also rather large. The nuclei of these cells, as seen in *Chaenobryttus*, *L. auritus* and *L. cyanellus* (Pl. IX, Figs. 96 and 103), are more distant from the basement membrane in the Lepomini than in any of the other centrarchids, an observation which agrees with the figures of Moore (1956). The supporting cell nuclei of *L. gibbosus* (Pl. X, Fig. 108) are considerably thicker than those of any fish thus far observed by this writer. Facial sections of neuromasts in *Chaenobryttus* and *L. auritus* made possible some further observations concerning the intercellular bridges. Fortunately, a few sections passed through the area of contact between the supporting cells and sense cells in the yellowbellied sunfish (Pl. X, Fig. 111). Here it appeared that the intercellular bridges involved not only the supporting cells, but the sensory cells as well. The sense cells are connected to each other and, at the periphery of the sensory area, to the sustentacular elements. A facial view of a section through some peripheral supporting cells in *Chaenobryttus* (Pl. VIII, Fig. 81) shows these cells to resemble those from other species.

There were no heteromorphic sensory cells observed in *Lepomis*, other than those already described in *L. symmetricus*. In *Chaenobryttus* there are some cells which equal those of *Pomoxis annularis* in size (Table VIII). Two such cells are shown in Fig. 81 (Pl. VIII) in which no other peculiarities were noted. Above the nucleus, as in *Acantharchus*, are some dark-staining, granular bodies which average 2.8 (1.5 - 3.8) microns in diameter. The receptive cells of *L. megalotis* resemble *Ambloplites* in being flattened distally (Pl. IX, Fig. 102), but subnuclear granules are lacking in the longear sunfish, a character which is shared with *L. punctatus* (Pl. X, Fig. 106). Moore's (1956) measurement of sense cell diameters in *L. cyanellus* are identical to those in Table VIII, but those for *L. humilis* are from 1.1 to 1.3 less than the ones herein recorded. Table IX shows that the apical diameters of the sense cells of *Lepomis* are like those in species of other genera. Since the apical diameters of the heteromorphic cells, restricted to the lateral region of the neuromast, are large, the great size of their basal diameters is correlative.

Measurements of the sensory cell nuclei (Table X) do not distinguish the Lepomini from other tribes, although the sense cells of L. punctatus and L. marginatus (Pl. X, Fig. 112) are equaled only by Ambloplites and Micropterus dolomieui (Table VIII). The lengths of these cells are likewise nondistinctive. The sensory cells of Elassoma are very short but are equal to those of the bluegill (Pl. IX, Fig. 99). The measurements for these species are similar to the ones reported by Moore (1956) in L humilis and L. cyanellus, but, as seen in Table XI, the measurements herein recorded for the last two forms considerably exceed 12 microns. Both L. cyanellus (Pl. IX, Fig. 103) and L. microlophus (Pl. IX, Fig. 100) approach L. marginatus and L. punctatus in sensory cell length.

Lepomis gibbosus and L. humilis (Pl. IX, Fig. 97) are surpassed only by Micropterus treculi in sense hair length (Table XII). However, other members of the Lepomini, such as L. auritus (Pl. IX, Fig. 95), are mostly similar to other sunfishes for this character. Moore (1956) found the sense hairs of the green sunfish to measure 2.8 microns, which is only slightly above the upper limits of variation indicated in Table XII. In certain aspects, the observations of Moore and those made during this study diverge sharply. In the above cited paper it was noted that the orangespotted sunfish lacked sensory hairs and cupulae. Nonetheless, as seen in Fig. 97 (Pl. IX), the first of these structures is actually present and Curd (1959) has already recorded the presence of cupulae. The vesicles which supertend each sense cell in Moore's specimens are believed to be artifacts, as suggested by the author of that paper. Additional evidence supporting this supposition is derived from the fact that many of the nuclei in the L. humilis studied by Moore were pycnotic. The triangular structures at the apex of the sensory elements represent the dark-staining region of the highly polarized cells and/or terminal bars.

Another point of disagreement is found in the basal part of the sense cells. The relatively long, hair-like basal extensions were not observed in any of the material prepared for this study, and, as has already been indicated, all of the supporting cells extend upward between the sensory elements, rather than ending below them. It is, therefore, suggested that the basal extensions represent artifacts resulting from some sort of disruptive forces which destroyed parts of the supporting cells. The extensions, then, could be the remnants of the cell membranes of the supporting elements.

Elassominae

As in many other characters, the elassomids diverge sharply from the other sunfishes in the soft anatomy of the lateral-line system. In Tables (XII through XV some measurements are lacking for _E_. _zonatum_, but probably the figures would be very similar to those given for _E_. _okefenokee_. In these tables it will be noted that the bony tubes and lateral-line canals of these small fishes are much smaller than all other sunfishes, except the largemouth bass. The reduction in size is doubtless correlated with an overall decrease in body size. The connective tissue canal (basement membrane) is considerably thicker than in many other species, especially in _E_. _zonatum_ and _E_. _okefenokee_.

Even the most cursory of observations will demonstrate that the canal organs of _Elassoma_ are much smaller than those of any of the typical centrarchids (Table 6). However, the depth of the pygmy sunfish neuromast is comparable to those of several other species. Consequently, the depth, when viewed as a function of total organ diameter (Graph I), is seen to represent a much greater percentage than found elsewhere in the family. The number of cells per section (Table XIII) shows us the real reason for the skewed depth/total diameter relationship; the number of cells per section is much less than in any other centrarchid, the only species approaching Elassoma in this regard being Lepomis megalotis. The sensory elements have also undergone a corresponding reduction in number so that the sensory area continues to represent a percentage of the entire diameter that is very similar to many other sunfishes (Graph II). Cupulae were found in the three species of Elassoma and, as with other species, the sensory elements are restricted to the central region of the neuromasts (Pl. XI, Fig. 123).

The supporting cells in pygmy sunfishes (Table VII) possess average measurements which are very similar to those of the more common forms, but are shorter than in any of the species thus far discussed, except Lepomis megalotis.

The supporting cells of Elassoma (Pl. X, Figs. 107 and 110) offer further proof that the intercellular bridges are probably universal in the family Centrarchidae.

The sensory elements (Pl. X, Figs. 107 and 110) are considerably smaller (Tables VIII and IX) than any of the other species, and heteromorphic cells are lacking. The lengths of these cells, however, are not conspicuously shorter than those in most centrarchids (Table XI). The sensory hairs, although equal to those of many other sunfishes in length, are very inconspicuous and in many cells it was not possible to determine whether the hairs were multiple or not. It is possible that in Elassoma, the hairs are single. The measurements given in Table XII indicate that the nuclear endosomes of Elassoma average smaller than in most other centrarchids, but the staining reactions are identical to those described above for other forms.

CHAPTER XII

COMPARISON OF CENTRARCHID HISTOLOGY WITH THAT OF OTHER TAXA

The characters of the general lining of lateral-line canals in most groups of fishes agree with those set forth in this treatise. The basement membrane of the lateral-line canal cells is similar, in all respects, to that observed in Cichlasoma cyanoguttatum (Branson, in press) but very little has been written about this tissue elsewhere, although it is usually illustrated along with the organ. We have described the cells lining the canals of sunfishes as being of a very low cuboidal nature but becoming pseudostratified near the organ. Mori (1931) stated simply that the canal was lined with "epithelium" in the goldfish and Hillier (1931) observed that the canals are paved by some very flat cells. However, very few authors have actually classified the type of cells belonging to this tissue. Moore (1950), although not primarily concerned with the lateral-line system, correctly illustrated the epithelium in Hybopsis aestivalis as becoming stratified near a canal neuromast and Brockelbank (1925) explained that there was a differentiation of the lining epithelium in the proximity of the organ.

Tretyakov (1950) denies that the lateral-line epithelium contains mucous glands, but these have been observed and described in many species (Martiis, 1924; Branson, in press). These elements, which look like goblet cells, are usually much more numerous in the cells contiguous to the neuromast than in the common lining and are probably of universal occurrence in fishes. Some peculiar velum-like thickenings described for the pirate perch by Moore and Burris (1956) and, though not so well-developed, by Moore (1956) in two species of Lepomis, have apparently not been discovered in any other bony fishes. According to Knox (1825), Treviranus observed some septa in sharks and rays which effected compartmentalization of their lateral lines. Published measurements of canals and of their osseous passageways are scarce, but this is not a particular shortcoming unless one is concerned with all of the species in a given category. As described herein, and as illustrated by Moody (1922) and mentioned by Branson (in press), this cellular lateral-line canal is surrounded and supported by areolar connective tissue in most species, and never comes into direct contact with enclosing bones.

It has been known for many years that the canal organs of both ostariophysine and non-ostariophysine fishes are distributed in a manner similar to that described above, i. e., usually localized between two side branches (Pollard, 1892). However, these organs become very numerous in such fishes as suckers and some minnows (Allis, 1904) and in Amia calva (Allis, 1889) so that the "usual" arrangement is secondarily masked. One neuromast per lateral-line scale, embedded in the proximal wall (Mori, 1931) as in all of the centrarchids, is apparently the common situation in most fishes (Hillier, 1931). The shape of the neuromasts is impressed upon these organs by the configuration of the canal in which they are found. Since in most fishes the canals are round or oval, there is a great deal of similarity between diverse groups of fishes as regards their neuromasts (Bonin, 1940; Dercum, 1879; Miyadi, 1929; Bamford, 1941; Moore, 1956; Branson, in press; and many others). The conformation of these organs is usually described as being lozenge-shaped, spindle-like, cushion-shaped, or simply as discoidal. As with many other lateral-line components it is difficult to find measurements of neuromasts in the literature.

Moore and Burris (1956) found the organs of Aphredoderus to be 791 microns in long diameter, a figure that is very similar to the large organs of L. humilis and Chichlasoma (Branson, in press). By visual inspection of several specimens of Roccus chrysops, it appears that the organs of this species are about the size of those seen in Ambloplites, but no measurements have been taken.

All workers who have described lateral-line organs have remarked upon its double cell-layer nature (Beard, 1884), but only a few have measured the cellular elements of the neuromasts. Comparison of the measurements herein presented for sunfishes with those given by the author in Cichlasoma cyanoguttatum shows some differences between the two taxa. The sensory cells of the Rio Grande perch, which are couched in the center of the supporting elements as they are in most species (Moore, 1950 and others), occupy about 50 per cent of the total organ diameter, or an area that is approximately that seen in the black basses. These cells are considerably larger than the "normal" cells of the Centrarchidae, i. e., excluding the heteromorphic elements, of which none were observed in Cichlasoma, averaging 8.4 (6.7 - 9.9) microns in basal diameter and 5.4 (4.2 - 6.2) microns at the apex. The sensory nuclei of Cichlasoma, although staining similarly and possessing endosomes like those of sunfishes, are also more capacious (average 5.1 microns). The sensory hairs observed by numerous workers (Moore, 1950; Moore and Burris, 1956) Dijkgraaf, 1952; Denny, 1937; Brockelbank, 1925; Bunker, 1897; Dercum, 1879; Hillier, 1931; and many others) have always been reported as single structures. As has been pointed out previously those of sunfishes and Cichlasoma seem to be multiple. The sensory hairs of the Rio Grande perch are similar in size to those of the Centrarchidae.

The sensory cells have been more completely described. Denny (1937), Bonin (1940), Bunker (1897) and Branson (in press) have remarked upon the decided polarization of the sensory elements in diverse groups of Osteichthyes, but few authors have given detailed descriptions of the receptive ends of the cells. Bonin (1940) described the sensory cells of *Amia* as having a brush border, Branson (in press) remarked upon the blepharoplast-like bodies associated with the sensory hairs of *Cichlasoma* and Denny (1937) described a short rod below the sense hairs in *Fundulus heteroclitus* which is similar to those illustrated in a catfish by Martiis (1924). All of these structures may be homologous.

As far as the general cytoplasm of the sense cells is concerned there is general agreement between this and other discourses. The epitheliofibrillae seen in the cells of *Fundulus* by Denny (1937) are similar to those seen in sunfishes, but the coarse axial filament described by her was not observed in the latter forms. Granules of various sizes have been illustrated or mentioned by several authors some preferring to call them mitochondria, but apparently only Martiis (1924) has mentioned a granular round body above the nucleus as described herein for *Chaenobryttus* and *Acantharchus*. Martiis (op. cit.), in *Ictalurus catus*, shows these bodies in variable positions, sometimes above, sometimes below and at times almost occluding the nucleus. Furthermore, some cells appear not to have a single large body but several lesser ones above the nucleus. In this respect they are similar to the sensory cells of *Fundulus* (Denny, 1937). These few records of such bodies are all that have come to our attention. Little can be said concerning the sensory cell nuclei as most workers have found that they all appear like those described for *Lepomis symmetricus* and other sunfishes.

As stated earlier, some physiologists have been able to indicate the possible presence of more than one kind of sensory cell in neuromasts of some fishes and that these cells may be unequally distributed in different sense organs. It was also stated that many observers have failed to demonstrate histologically or cytologically these different kinds of cells. This is not universally true for Cordier (1938) observed more than one kind of sense cell in some peculiar freshwater fishes (Mormyridae) from Africa. However, he described a definite cyclic metamorphosis of ordinary-appearing sense cells into some heteromorphic elements. Briefly stated, the findings of Cordier are as follows: three to five large pale cells, often with hypertrophied nuclei, were found per section. These cells were either flanked by slender cells or normal sensory ones which were connected together by intercellular tonofibrils for support. During regular intervals of time these cells are transformed into a type of holocrine secretion which is poured onto the skin surface. They are then replaced by typical sensory cells and others become metamorphosed into the holocrine type. Thus a few of these heteromorphic elements are always present in the "mormyromasts." According to Cordier such cells have also been found in Polypterus and in the organ of Fahrenholz in the Dipneusti. Cordier's tonofibriles may be the same structures which herein are termed "intercellular bridges" (Moore, 1956). Although Martiis (op. cit.) did not specifically say so, his figures indicate that there may be a few rather large cells in the neuromast of Ictalurus catus.

Cupulae have been described by several authors in many fishes. The ones figured by Dijkgraaf (1952) in a cyprinid are much taller than wide, wholly unlike those described or possible in the sunfishes. Many writers (Brockelbank, 1925; Dercum, 1879; Hillier, 1931) have simply mentioned their presence or described them as being mucilaginous or gelatinous caps over the sensory cells, probably because the bodies were disfigured by fixing fluids. In Gnathonemus, according to Cordier (1938), the cupula apparently extends along the entire wall of the lateral-line canal opposite the neuromast, reminding that author of the macula in mammals. Denny (1937) observed the structure in living Fundulus and described it in detail, with notes from fixed and stained specimens. As noted in sunfishes, the cupula of the last-mentioned fishes approximately covers the sensory surface of the organ. Denny also mentioned the shrinkage space between the cupula and sense hairs observed by this writer in the Centrarchidae.

Terminal bars proliferated by sensory cells have seldom been reported. Branson (in press) observed them in Cichlasoma and Cordier (1938) suggested that some dark-staining structures at the edges of cells in Gnathonemus might be of this nature.

Few nonmensurable differences can be demonstrated in the supporting cells from one fish taxon to another. The striated distal borders, discussed for sunfishes, were noted in addition to epitheliofibrillae by Denny (1937) in Fundulus. The latter structures were not seen in the Centrarchidae. Furthermore, Denny (1937) and Branson (in press) are apparently the only workers who have recorded terminal bars like those illustrated in most sunfishes. Many writers have shown the central supporting cells as ending just below the proximal ends of the hair-bearing cells or have seen only a few of them penetrating upward between the sensory elements. Very thin sections clearly demonstrate, in Cichlasoma and the fishes here investigated, that most or all of the supporting cells below the setiferous ones penetrate between the sensory cells and that the two kinds of cells are probably connected by some sort of protoplasmic extensions. Martiis (1924) has verified these observations in the catfish *Ictalurus catus*.

It appears that no one has successfully shown the manner in which the neuromast sensory cells are associated with their nerve supply. Several authors (Branson, in press; Denny, 1937; Bunker, 1897; and others) have described the nerve as effecting passage through the basement membrane, losing its medullation and then branching repeatedly below the sensory cells, but this is as far as most observations go. A technique is being developed by Mr. T. J. Walker (personal communication) for fixing and staining nerve endings which, if successful, should clear up some of the blank areas in our knowledge.

CHAPTER XIII

INNERVATION OF NEUROMASTS

Innervation of the centrarchid lateral-line organs is accomplished as described earlier in this paper. The only variation noted was in the lengths and number of nerve twigs going to neuromasts. The number of branches is, of course, correlated with the number of neuromasts possessed by a given species. Furthermore, in species with a strongly curved lateralis series the V. lateralis branches are considerably longer than in those with a lateralis nearly overlying the horizontal skeletogenous septum, through which the main lateral-line nerve progresses.

CHAPTER XIV

DISCUSSION

General Morphology

The most obvious gross characteristic of the centrarchid lateral-line system is its simplicity. Side branches, i. e., external canaliculi, are few and uncomplicated by secondary bifurcation. Although the six primary canals of lower fishes are represented, several of these are seen in a much reduced state, the greatest reduction being in Elassoma. The supratemporal canal, although complete in many perciform groups, is greatly abbreviated in sunfishes; and the infraorbital canal varies from complete to entirely lacking. Primitive fishes, and large numbers of recent ones, possess a kind of commissure between the supraorbital canals as seen in all of the centrarchids except Elassoma. With the exception of breaks at certain points the other canals are all present and relativ-ely well-developed, again except Elassoma in which all of the canals are much reduced. Percomorph fishes, rated more primitive than the perciformes, have rather narrow canals, whereas centrarchids, serranids, cichlids and related fishes have capacious canals. This tendency seems to be toward reduction in parts and increase in size.

The lateralis canal system in sunfishes is also of an uncomplicated design, but is present as a more or less continuous series in all of the species except Elassoma. External canaliculi are present in many fishes, but have never been discussed in North American fishes. Unlike the lower perciforms, the centrarchid canaliculi are simple diverticula from the mother canals without the slightest indication of further branching.

The lines of external neuromasts found in the Centrarchidae also represent an advanced stage of reduction. They are few in number and, except in the aberrant Elassoma, very difficult to homologize with the lines of lower forms such as Amia. Even in Elassoma, where most of the primitive lines are present, these organs are never as numerous as they are in the lower taxa (Allis, 1889).

Because of the ease with which lateral-line bones can be homologized in the perciform fishes, their apparent similarity is lessened when their skeletons are compared. In general, all of the centrarchids, except Elassoma, more closely resemble certain members of the Serranidae than they do other Perciformes. This is especially true in the Ambloplitini, except in Acantharchus, a highly specialized form, in which it would be very difficult, if only skull bones are considered, to differentiate between Archoplites and the Serranidae. Since the lateral-line bones have been discussed in detail above there is no reason for redescription here; however, the question of whether or not the lateral-line organs act as evocators for the formation of these bones deserves some consideration.

It is well-known that during embryological development most species do not exactly retrace their evolutionary history; nor do they closely repeat each step taken by their progenitors during the formation of the species' characters. Instead, many of the stages may be left out (lipogenesis) or much shortened (tachygenesis). Ideas and observations such as those above have been instrumental in causing the decline of Haeckel's Law (Aulie, 1955) and its replacement by the modernized versions of palingenesis.

During the early developmental history of all osteichthine fishes the lateral-line bones were probably caused to develop under the influence of neuromasts when these became entrenched in connective tissue canals. Later, as degeneration began to occur in certain groups, specialization may have taken several courses. There may have been a loss of lateral-line tubes without a corresponding loss of the lateral-line bones; in other words, during phylogeny, once the bones had received the impetus to form, they continued to do so after the directive force of the evocating neuromasts had been obliterated. In this instance there would be rows of lateral-line neuromasts on the skin over the old lateral-line bones embedded in the tissues below.

A second condition might arise if the lateral-line tubes degenerated and their ossicles failed to develop. It is postulated that the bones fail to form because the directive influence of invaginated lateral-line organs was absent. In such a condition there would be lines of neuromasts on the skin without ossicles underlying them. In fishes exhibiting such lipogenesis, embryonic studies would not prove anything one way or another.

As far as anasmestic elements are concerned, it is not surprising that other kinds of dermal elements developed in the skull during evolution and that lateral-line elements fused to them. In such compound bones degenerative changes might take place either by freeing of the lateral-line element from its anasmestic counterpart, followed by progressive reduction of the former; or, the lateral-line element could remain attached to the non-lateral-line part after the canal disappeared with the neuromasts being removed to an external position.

The adult morphology of centrarchids, supported by a few observations on young individuals, indicates that the neuromasts of these fishes do cause the formation of lateral-line ossicles. Some supporting evidence for such a supposition is as follows:

1. Given lateral-line tubes are always associated with the same bones and are always directed through approximately the center of the ossicles.
2. When neuromasts fail to sink into the skin the bones fail to form or, if they do form they are always of a very degenerate condition as in the jugal of several of the sunfishes. When the infraorbital first begins to disappear it always does so at the anterior end of the series between the lachrymal and the jugal. Behind this there is a graded series, i. e., an open, v-shaped ossicle followed by progressively more complete bones. Since the suborbitals are among the last of the lateral-line bones to be completed it may be that, by the time ossification has been finished elsewhere, the tissues surrounding the developing suborbital series have lost their competence for transforming into bone. The infraorbital canals seem to be in a process of being lost in the centrarchids. Degeneration is nearing completion in *Elassoma*, in which lateral-line bones are lacking or greatly reduced.
3. When extra organs are formed in some series (infraorbital) an extra bone appears.

It may be assumed that complete lateral-line canals, passing through well-formed bones, and an infraorbital series, consisting of seven suborbitals, are primitive characters in centrarchids. Furthermore, since it is agreed that the centrarchids have probably evolved from serranid ancestors (Bailey, unpublished), those centrarchids which possess characters of the skeleton most similar to those of serranids are considered primitive. It will be recalled that the sunfishes which are nearest the sea basses are Archoplites and Ambloplites.

Morphologically there is a very great similarity between the neuromasts of the lateral-line system and the maculae and cristae of the inner ear. This has been alluded to by several workers, but since there has been little actual comparison a few notes will be included on the auditory organs before discussing the centrarchid neuromasts. The reaction of maculae, cristae and of Corti's organs to Mallory's stain is nearly identical to that of lateral-line organs (Shambaugh, 1932). The organ of Corti, as well as the others mentioned above, are, like neuromasts, composed of two cell layers, those of support (phalangeal cells) and those of reception. The sense cells are much shorter than the supporting cells and possess round nuclei which have dark-staining granules. At the apex, where the sense hairs are inserted, the cell stains darkly. A rather important observation to be made here is that the sensory hairs are definitely multiple in Corti's organ and are often observed to form triangular associations (Shambaugh, 1932) similar to those described in the sense cells of sunfishes. The phalangeal cells are attenuate-rhopaloid in shape, possess basal, oval nuclei and extend upward between the sensory elements. A blue-staining cupula (tectorial membrane in the cochlea) caps the sensory organs of the ear and, by a shearing action, moves the hairs which in turn stimulate the sensory cells. Shambaugh (1932) was able to demonstrate that the red-staining hairs penetrate small canals in the cupula. The latter have not been seen in the cupula of lateral-line organs.

It is thus seen that lateral-line organs and those of the inner ear are structurally very much alike, as could be expected since both sets of organs are phylogenetically and functionally a part of the same sensory system. It does not seem surprising that the receptive cells of lateral-line neuromasts should possess more than one sensory hair. The blepharoplast-like bodies described in the discussion above are not novel since Speidel (1947) noted them at the base of sensory hairs in amphibians, and Denny (1937) found similar ones in Fundulus. Since the sense hairs appear to be attached to these bodies it is possible that the granules function somehow in transmitting sensory impulses through the sensory cell body. How this is accomplished is a matter of conjecture, but some weighted guesses may be in order at this point. Nerve cells commonly possess neurofibrilles and since the sensory elements of neuromasts are sensory receptors, or a type of neuron, the fibrous structures observed by Denny (1937) and reported herein may actually be cellular modifications for transmitting the impulses from the blepharoplast-like structures toward the proximal portion of the cell. It has already been pointed out that no actual connections between the sensory cells and their nerve fibers has thus far been demonstrated. Furthermore, it is known that in sensory receptors there are no synaptic junctions. In such cells transmission is initiated and accomplished by intracellular processes. These processes are concerned with the intracellular activation of bound and inactivated acetylcholine and its later deactivation and rebinding by acetylcholinesterase. It is possible that, when the cupula (discussed below) stimulates the hairs, acetylcholine is released in the apex of the sensory cells which causes a wave of depolarization to pass over the intracellular fibriles to a point on the proximal cell membrane where the nerve arborization would be stimulated (Elliott, Page and Quastel, 1955). Since the acetylcholine must be inactivated, and since the lateral-line organs are constantly being stimulated, the subnuclear granules may represent a stored form (proenzyme) of acetylcholinesterase which is released upon demand.

Since Sand (1937) and Dijkgraaf (1952) have indicated the physiological possibility that more than one kind of sensory element may be found in fish neuromasts, any observation of heteromorphic cells is an important one. Although the large pale cells found in some of the centrarchids may be such cells, the work of Cordier (1938) indicates a second possibility. The heteromorphic elements of sunfishes could be manifestations of holocrine function. The number of these elements per section is very similar to those found by Cordier, as is their position. It is known that the several kinds of cells located in secretory organs store substances, in the form of zymogens, which are expelled in the active form (Maximow and Bloom, 1944). The granular bodies above the nucleus in Chaenobryttus and Acantharchus and the various granules located in more basal parts of the cells might represent stored substances such as those of chief cells in the digestive system. All of the cells could be involved in a cyclical transformation from normal sense cells to the larger, secretory type.

Both of the above hypotheses are, of course, problematic and one or both of them may be erroneous. They are, nonetheless, possibilities and should be verified or disproved by special techniques. Another possibility is that some or all of the sensory cells are active in neurosecretory activity such as the cells in the posterior neuropophysis of mammals. Denny (1937) also suggested that the sense cells may possess some secretory abilities.

Cupulae have been discussed in considerable detail by Denny (1937), who gave an historical review of knowledge concerning the structures and several possibilities as regards the origin of the body. She concluded that the cupula is not a product derived from the numerous mucous cells in the vicinity of neuromasts nor is it derived from the sense hairs themselves. That the sense cells and/or supporting elements are responsible for the formation of the body, because of their apparent secretory nature, is a possibility. Denny, however, thought that the most likely source of the cupular material was the terminal bars or intercellular cement as they apparently are in the ear (van der Stricht, 1921). Whatever its source, it is felt that these bodies are real and not artifacts of fixation. The latter is especially improbable since they have often been observed in living fishes (Denny, 1937; Dijkgraaf, 1952). Being situated as they are the sense cells of neuromasts are exposed to the direct action of the viscous fluid in the lateral-line canals. A cupula would greatly increase the ease with which the sense hairs might be moved, since it functions, as that of the ear, in a shearing fashion. The septa described by Moore (1956) and Moore and Burris (1956) are not unlike the same thickenings of the epithelial lining of the ducts of the ear. These occur near the neuromasts and apparently cause an increase in the hydrostatic force applied on the cupula. It is doubtful that a very large exchange of fluid occurs between the lateral-line tubes and the external medium. As seen in the description of the external morphology, at points where side branches are emitted, vacuities are formed which are covered only by skin and connective tissue. These may be likened to the auditory oval window (Tretyakov, 1950). The tightly drawn skin covering these "oval windows" would, in life, function as drumheads upon which pressure changes in the water would impinge. The pressure changes would be transferred to the fluid in the lateral-line canals and finally cause the cupula to stimulate the sensory hairs.

It appears that the lateral-line neuromasts are admirably adapted to withstand deforming pressures. It is not surprising that the supporting and sensory cells of neuromasts should proliferate terminal bars and intercellular bridges since these structures are of common occurrence in vertebrates wherever a good deal of mechanical stress occurs (Greep, 1954; Maximow and Bloom, 1944). The intercellular bridges are especially well-developed in the skin. Since neuromasts are derivatives of the ectoderm it is logical that such structures would be present in their cells. Actually, it appears that these cells form nearly or truly a syncytium. Greep (1944) has pointed out that physiological syncytia are known in many mammalian tissues. In mammals, at the point where intercellular bridges from two cells meet, a small granule (desmosome) is formed, thought to be composed of phospholipids, which stains rather darkly with hematoxylins. This body was not noted in the fish tissues herein discussed. However, since no attempt was made to preserve fatty substances, the fixing and dehydrating fluids would dissolve the desmosomes, if they are actually present. In some tissues of various animals, histologists have demonstrated that minute fibers pass from one cell to the next via the intercellular bridges (Maximow and Bloom, 1944; Greep, 1954). These fibers, called tonofibrils, were also not observed in the Centrarchidae. Terminal bars, on the other hand, occur wherever epithelial cells of a columnar type are found. These are supposedly secreted (Maximow and Bloom, op. cit.) to fill in the intercellular spaces at the free ends of the cells. If the tissues are ciliated, the bars are nearly always below these. Although the sense cells of neuromasts cannot be termed "ciliated" they do bear analogous hairs. The distal ends of simple columnar epithelial cells in the intestines of all vertebrates exhibit a thin layer of modified protoplasm which seems to be striated. These striae are presumedly small tubes which aid in absorption. Whether the striated borders of the supporting cells in lateral-line organs are of a similar nature is, at present, impossible to say.

Correlation of Lateral-Line Morphology With Species Ecology

That there is some sort of correlation between the extent of development of the lateral-line system and habits and/or ecology is not doubted by anyone (Lowenstein, 1957). Consequently, before entering into a discussion of the Centrarchidae, some of the ideas on this subject will be reviewed. The generalization is that fishes which are continuously exposed to "relative" water currents, such as those which exist near wave-washed beaches or in torrential streams, or fishes which are continuous swimmers, possess well-developed canal systems, ostensibly for protection of the neuromasts, whereas bottom dwellers (except those which dwell in swift waters) and sluggish forms usually have secondarily reduced canal systems (Lowenstein, 1957). Some examples, taken from the literature, are included below for substantiating evidence. Nearly 75 years ago Garman (1888) observed that sharks of lethargic habits were less abundantly supplied with lateral-line tubules than the more active swimmers. Similar conclusions were reached by Hoagland (1933c) while working with Ictalurus nebulosus and a trout. In this sluggish bottom-dwelling catfish the sensory receptors are mainly concentrated near the anterior part of the body, but in the vigorous-swimming trout the receptors are just as well-developed caudally. Lowenstein (1957) remarked upon the contrasting characteristics of Misgurnus fossilis (a bottom dwelling, intermittent swimmer) and Esox lucius (an "inert" fish) with Hemacheilus barbatula (an inhabitant of swift waters). The first two forms have much abbreviated lateral-line canals, but the swift-water species possesses a strongly-developed one. The physiologist Dijkgraaf (1952) reached identical conclusions but went a step further. Experimentally-obtained data indicated to him in fishes possessing naked neuromasts, active swimming causes the receptive cells to be so strongly stimulated that they become fatigued and are no longer capable of stimulation. The same thing would doubtless obtain in rapidly-moving bodies of water. Fishes with only external neuromasts, or with poorly-developed canal systems, are not well-adapted for sustained rapid swimming or for living in turbulent waters.

Several other authors have attempted to correlate the structure of fishes with their habits and habitat. Moore, Pollack and Lima (1950) showed that the lower retina of Ericymba, a bottom dweller, is thicker than the upper portion, an obvious adaptation for concentrating light derived from an upward source. Other morphological observations, besides those derived from sensory systems, have been made which tend to show the relation between fish habits, ecological station and the form and structure of these animals. Nichols (1920) demonstrated in carangid fishes that some changes are associated with a loss of activity, such as deeper, more compressed bodies, a smaller mouth and often a reduction of scutellation. In fast swimming fishes a narrow caudal peduncle and a deeply forked tail are usual.

One area that has not been investigated thoroughly, but which should offer reqarding results, would be an attempt to correlate the degree of complexity of the lateral-line system with the extent of development in other sense organs, i. e., the eyes, taste buds and tactile receptors. A given lateral-line system might be poorly-developed and other sensory elements exhibit a much increased degree of complexity, or vice versa.

Linder (1958), working with two species of Etheostoma, found that eggs fertilized in the laboratory developed into individuals in which the lateral-line system (canals?) was mostly absent. However, such findings should not be construed to mean that the lateral-line system will be greatly modified in nature since the phenotype of a species represents the effect of the total number of genes in rapport with the environment. Many phenotypes are possible under the artificial conditions of the laboratory and one should be constantly on guard against the production of and failure to recognize phenocopies (Goldschmidt, 1955) and other anomalies of stringent environmental selection.

In an attempt to correlate a species' morphology with its habitat, that habitat must be defined. It is also highly desirable that the species habits be known. The members of the Centrarchidae are found in three major habitat types: lacustrine, fluviatile and paludal. However, some of them may also be found in subtypes, i. e., back waters, overhanging banks, etc. Since it has already been stated that reduction of lateral-line systems seems to be correlated with sedentary habits or with benthophilic affinities the problem here resolves itself into one of comparing the development of the canals in each centrarchid species with its observed habits and habitat. This poses no particular problem since at least some of these statistics are available for all of the sunfish species. According to Murphy's (1948) notes, the Sacramento perch is very similar to the rockbass in its habitat and habits. Acantharchus, the remaining member of the Ambloplitini, is a very secretive fish which lives in the sluggish lowland waters of the Atlantic coastal plain (Mansueti and Elser, 1953). Of the three species in the Centrarchini, *Centrarchus macropterus* is the only one which is continuously found in sluggish waters such as roadside pools and swamps. Although the flier does occupy such situations, the species is a very active one as are both forms of *Pomoxis* (Morgan, 1954; Huish, 1954). The three species of enneacanthine fishes are restricted to the slow streams and pools of the Atlantic Coast from Florida to New Hampshire (Bailey, 1938; 1941). All of the black basses are known to be vigorous swimmers and all live in streams, lakes and ponds (Webster, 1954; Dendy, 1954; Hubbs and Bailey, 1940; 1942; Bailey and Hubbs, 1949). The warmouth sunfish occupies a wide range of ecological conditions (Larimore, 1957), but wherever found it is an active fish. The ten species of *Lepomis* are also active species although some of them, *L. humilis*, *L. marginatus*, *L. punctatus* and *L. symmetricus*, are often found in quite sluggish waters (Moore, 1956; Reeves and Moore, 1950; Morgan, 1951a, b; Witt and Marzolf, 1954). Only two of the latter species, *L. humilis* and *L. symmetricus*, however, are very frequently found in turbid and non-flowing bodies of water. The pygmy sunfishes (three species) all live in sluggish streams and pools, as in the Okefenokee Swamp (Böhlke, 1956; Shortt, 1956), or Louisiana (Barney and Anson, 1920; Magnin, 1938). Personal observations of *Elassoma zonatum* in nature and in aquaria indicate that this fish is much like some darters (Percidae, Etheostomatinae) in behavior. Most of the time these small fishes remain motionless on the bottom under bits of wood, fallen leaves and other debris or in the leaf axillae of aquatic plants. During feeding, or when startled, the fishes seldom move more than a few inches. These observations are similar to the ones made by Shortt (1956) in *E. okefenokee* and in *E. evergladei* by Magnin (1938).

From the above discussion it is obvious that nine species of sunfishes fall into the category of living in very sluggish habitats, but only four of these species, *Acantharchus* and the three pygmy sunfishes, seem to possess phlegmatic habits. The Enneacanthini are not extremely active fishes, but are not as secretive as the last four mentioned species. *Lepomis humilis* is a voracious and pugnacious species, whereas *L. symmetricus* is a more retiring paludal species.

Although *Acantharchus* appears to be a lethargic fish, it is, from the appearance of its eyes, a fish of nocturnal habits and from its large terminal mouth, probably is predaceous. This species, like its nearest relative *Ambloplites*, is probably an active nocturnal swimmer and feeder, remaining hidden during the day in decaying logs or under overhanging banks. This would at least partially explain why the canal system of this species is as well-developed as in other Ambloplitini.

Enneacanthus and *Mesogonistius*, living in sluggish bodies of water, hang motionless in the water for long periods of time. In their hunting attitude these forms call to mind the same attitude in *Pterophyllum*, the common anglefish of aquarists. It will be recalled that the infraorbital canal in the three enneacanthine species is greatly reduced.

The species of *Elassoma* are the most seclusive species of the forms now included in the family Centrarchidae and their habitat waters are extremely sluggish. The canal system in this subfamily is reduced more than in most other percomorphs.

Lepomis symmetricus and its associates all have relatively well-developed cephalic canals, but the lateralis seems to reflect the semi-paludal existence of the last-named fish, as it is always reduced in its posterior parts. *Lepomis humilis*, on the other hand, is found in the muddy, sluggish Great Plains streams and other bodies of water, often to the exclusion of other sunfishes. Moore (1956) has hypothesized that the greatly inflated canals of the orangespotted sunfish are a functional modification for existing under the extremely turbid conditions of its habitat waters. The pores are often found to be clogged with mud in fresh specimens and even occasional ones which have been preserved for as long as ten years. The inflated canals might function as drumheads to transfer pressure to the neuromasts, via the fluid contained in the canals, instead of the changes being mediated through pores.

How such reduction came about during phylogeny is, of course, an academic question. Nonetheless, one can make some guesses in the light of the functional studies of Dijkgraaf (1934; 1952) and Hoagland (1933b, 1936). These workers have shown (see above) that constant stimulation of the neuromasts causes them to become adapted and after a brief period to cease functioning completely. Dijkgraaf (1952) demonstrated that the external neuromasts become adapted much more rapidly than the canal organs. Thus a fish with a reduced lateral-line system would not be adapted to live in a rigorous habitat or as a fast-swimming form since its lateral-line organs would quickly become overstimulated and cease to function. Such species as Elassoma, are then, obligatory recluses in nature.

CHAPTER XV

PHYLOGENY OF THE CENTRARCHIDAE

The fossil record, however incomplete, indicates that the Centrarchidae originated sometime during the Cenozoic (Berg, 1946), probably with a form similar to the now extinct Centrarchites of the Eocene (Romer, 1945). By the beginning of the Pleistocene many of the extant genera were in existence as well as some forms which were to disappear before the end of that period. From the distribution of present species and of species and genera known only as fossils it would appear that the center of origin for the sunfish family was located in the Mississippi Valley. In attempting to determine which of the living forms is the most primitive centrarchid, several points must be considered. Matthew (1915) suggested that at any one time the most primitive (conservative) stage in a group should not be sought near the center of dispersal, but at some region remote from it. The conservative form, then, would mark the periphery of the range. However, as pointed out by Darlington (1957) this type of evidence must be used judiciously and in conjunction with other knowledge. A form, in this instance Archoplites, which is widely separated from the main range of its family is quite often a relict (Darlington, op. cit.). In the Centrarchidae it is obvious that in past times the family occupied a much greater range than it does at the present. There is a relative abundance of extinct centrarchid fossils in the Miocene and Pliocene rocks of Oregon, Nevada and Utah and, to a lesser degree, of fossil representatives of the extant genus Lepomis from the Pleistocene of Oregon (Miller, 1959). These latter remains probably represent an invasion from the east which was halted by the uplift of the Rocky Mountains (Cope, 1883). The centrarchid fish fauna of this region according to Miller (1959), may have been extirpated by chilling of the waters during the Pleistocene glaciation, which would kill the eggs of fishes adapted to the warmer conditions of lowland streams, such as those occupied by most of the recent forms. In some manner the Archoplites assumed to be a holdover from the pre-Rocky Mountain era (Miller, 1946, 1959), escaped extinction and persisted, whereas the other sunfishes perished or withdrew eastward and southward.

Most recent workers (Bailey, 1938; Miller, 1959) are agreed that the Centrarchidae probably arose from some specialized serranid progenitor which invaded fresh water during or before the Eocene. The earliest sunfishes must have resembled closely their serranid ancestors. Consequently, when the migration westward began, the fishes extending the range would be more like the sea basses than would the species arising later. Since Archoplites seem to have been isolated on the west coast for a long period of time it would represent the edge of the family's range in what is now the United States if our hypothesis is correct that the Mississippi Valley actually was the center of origin of the family. Bailey (1937) remarked upon the similarity between Ambloplites and Miocentrarchus (Miocene age) and herein we noted its likeness to serranids. Thus, it is assumed, although the species has doubtless become somewhat modified, that the Sacramento perch is the most primitive member of the Centrarchidae. The sunfish species which occupy any of the waters of the glaciated region in the north are doubtless forms which reinvaded the area during and after retreat of the ice cap. The species found in the lowlands of the Atlantic Drainage and in Florida also represent specialized forms, some of them greatly modified, since much of this latter area was uplifted during more recent times. With the retreat of the Pleistocene ice, correlated with the opening of new habitats in the south, speciation in the Centrarchidae probably went forward at a rapid pace to fill the newly available niches.

The placement of Archoplites near or at the bottom of centrarchid phylogeny may be criticized because the fish, and its congeners, have five anal spines as well as other morphological innovations. However, since so many of the other characters agree with those of serranids, this one character is considered to be of a divergent nature, indicating further specialization from the serranids. Forthermore, it is obvious that the primitive member of any group may, in its adult morphology, possess some characteristics which tend to obscure the true relationships of that animal because of a loss of some primitive characteristics or of some of the latter being cryptic (Orton, 1957). This is considered to be the condition in the Sacramento perch. Since many sea basses have three anal spines, this would seem to be a primitive character, but one cannot use one character to the exclusion of all others. The presence of the well-developed supramaxilla in Archoplites and in some other sunfishes is a primitive character. Numerous toothed bones and spiny lateral-line bones in the Centrarchinae place this group, especially Archoplites, nearer to the Serranidae than any other sunfish. Juvenile characteristics are very often indicative of relationship (Orton, 1957) not seen in the adult. Most of the centrarchids are marked by bands or bars in immature stages and, although probably not applicable to the family as a whole, these may be used as corroborative evidence for primitiveness within genera.

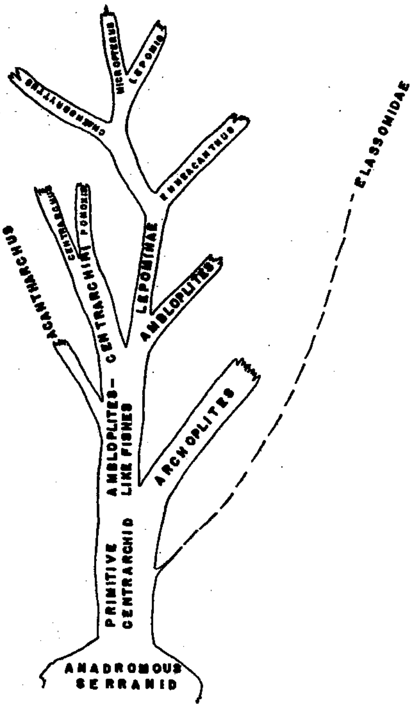
Complete lateral-line canals are primitive and specialization is indicated by reduction of canals and/or of sense organs contained in them. The amount of specialization is determined by the relative degree of incompleteness or interruption of the canals. Hypertrophy, as that seen in *Lepomis humilis*, is also usable as an index of deviation from the norm. Some of Myers' (1958) criteria for specialization have been discussed previously but can be used here. These are: 1, reduction in the number of fin rays; 2, reduction or supression of the lateral line; and 3, reduction or simplification of cranial sculpture, which is actually a function of the second as far as centrarchids are concerned. All of these characteristics are expressed in *Elassoma*. One set of characteristics, although not of a morphological nature, which may be utilized are those of distribution and habitat. If it can be shown that there is correlation between ecological characteristics and those of a morphological nature, several questions concerning phylogeny within a taxon may be answerable (Ross, 1957). Consequently, those species which exhibit habitat preferences, such as *L. humilis* with a tolerance to turbid waters and *Enneacanthus* restricted to the sluggish waters of the Atlantic Drainage, and *Elassoma* and *Acantharchus* to swamps, are considered to be specialized fishes. The correlation between these habitats and the lateral-line system have been discussed above.

The phylogeny of the Centrarchidae may now be considered. The hypothetical primitive-centrarchid probably was a free-swimming inhabitant of lowland waters and with a shape and size comparable to that of *Ambloplites*. It probably had a complete, rather capacious lateral-line system, with only a few side branches; a very few external neuromasts sunken into the dermis; an incomplete supratemporal canal; a complete preoperculomandibular canal with a pore at the junction with the supratemporal canal; lateral-line canals passing through complete tubes, except at points where branches arose; a complete suborbital series consisting of six or seven ossicles; a peltate, spiny lachrymal with four openings; a spiny posttemporal having four openings and a spiny supracleithrum with two openings; a spiny preopercle with the lower arm forming an angle with the upper of 100° or more and possessing six or seven openings; a dentary bone with five lateral-line openings and of the long-jawed type; a rather large supramaxilla; a notched preopercle; a well-developed, deeply sculptured frontal bone, with four lateral-line openings; a complete lateralis progressing through ctenoid scales; relatively large canal neuromasts, with the sense cells occupying about one-half of the total diameter; five to seven anal spines; and an emarginate caudal fin. The genus which most closely approaches such a form is, of course, _Archoplites_. This conclussion is more closely aligned with the findings of Schlaikjer (1937) than it is with those of Bailey (1937), who concluded that the warmough (a three spined form) was primitive. Schlaikjer considered _Centrarchus macropterus_, because of its deep body and high number of anal spines, to be the most unspecialized of all living centrarchid fishes. But the small size of this fish (although some Florida populations sometimes attain the size of a rockbass) and its obvious restriction in range, as well as some structural modifications precludes the species from being primitive. The supratemporal lateral-line canal is covered by scales as it is in _Acantharchus_. This is a specialization and is seen only in highly modified forms such as _L. punctatus_. Though possessing several characteristics in common with _Archoplites_, _Chaenobryttus_ is distinctly lepomine in its affinities and all species of _Lepomis_ are considered to be derived types.

The spiny condition of lateral-line bones, as indicated above, is a primitive condition. These bones are most heavily serrate in Archoplites, which is the only species in the family possessing a spinose supracleithrum. Furthermore, the serrate condition of the posttemporal is lacking in all sunfishes except the Centrarchini, which clearly aligns this group with Archoplites. The lack of serrae on any of these bones in Acantharchus, its highly modified lachrymal and preopercle, the large cycloid scales, the single posterior lateral-line opening on the posttemporal, reduction in suborbitals, and rounded caudal fin demonstrate that this species is a modified one. Its adult shape, eye size, five anal spines, distribution and habits seem to place Acantharchus nearer to the rockbass than any of the other sunfishes, but the relationship is an obscure one. As seen in the description of the external and internal morphology of the lateral-line system, Chaenobryttus is near the bottom of lepomine evolution and stands closer to the rockbass than to Archoplites. Ambloplites is thus considered to be in the main line of centrarchid evolution whereas the Sacramento perch, rather early isolated from the rest of the family, though being primitive, is nonetheless a divergent form which has become evolutionarily stagnated and is not even capable of competing with more modern sunfishes. The rockbass, or a related form gave off a shoot which has ended in Acantharchus, a specialized carnivore.

Sometime during the Pliocene--Pleistocene times divergence seemingly occurred in the ranks of the rockbass-like fishes in which one branch led to the recent forms with strongly serrate lateral-line bones (Centrarchini) and another to the Lepominae and the modern rockbass. Since in skeletal characteristics and other anatomical features, Chaenobryttus resembles Ambloplites, the former species is regarded as the primitive member of the tribe Lepomini. The Chaenobryttus (three anal spines) and Ambloplites (five anal spines) lines diverged to give origin to the recent rockbass on the one hand and the members of the highly evolved members of the Lepominae on the other. Another divergence occurred when one group of fishes with only four dentary pores, a single posterior opening in the posttemporal, a much reduced infraorbital canal and a single anterior arm on the lachrymal bone, a decrease in serration of the lateral-line bones, as witnessed by the very smooth condition of the lachrymal and preopercle, ended in Mesogonistius and the two species of Enneacanthus. The other branch, Chaenobryttus and the members of the genus Lepomis, are more generalized than are the basses and it is thought that some large-mouthed fish, corresponding closely to the warmouth, diverged to give rise to the lepomine forms and basses. That Chaenobryttus is more closely related to Lepomis than to other groups is clearly demonstrated by its ability to hybridize with various lepomine forms (Hubbs, 1955). The large-mouth Lepomis, very probably a form close to the green sunfish, L. cyanellus, which diverged from Chaenobryttus, may also have been the progenitor of the black basses, which are morphologically more closely related to Lepomis than to the other sunfishes. The reasoning behind this last point is that the rather robust form, large supramaxilla, proportionally small lateral-line canals, and neuromast morphology of L. cyanellus are more similar to those characters in Micropterus than are any of the other members of Lepomis or Chaenobryttus. The smooth lateral-line bones of Micropterus are considered to be specialized.

The genus Elassoma poses a very difficult and special problem. Its affinities seem to lie with the Centrarchidae (Eaton, 1953), but there has been so much modification and specialization that it is very difficult to decide from whence these fishes may have been derived. They are obviously not closely related to any existing sunfish. The following are characteristics in which Elassoma differs from all of the other Centrarchidae: 1, no suborbitals; 2, no lateral extrascapular; 3, lateral-line segment of posttemporal separate from the pectoral girdle; 4, no mandibular canal; 5, no articular canal; 6, all lateral-line bones open grooves, which are not even similar to very young sunfishes; 7, no lateralis canals; 8, very few and small canal organs; 9, numerous external neuromasts which differ markedly from those of most centrarchids; 10, only one sense hair per neuromast sensory cell (?); 11, supraorbital commissure not connected across the head; 12, posterior nasal pore opening into the posterior nostril; 13, rudimentary olfactory organ; 14, no ocular sulcus; 15, gill membranes broadly joined across the isthmus; 16, rounded caudal fin (in part); 17, very few fin rays; 18, cycloid scales (with one exception); 19, a sub cylindrical body shape; 20, very reclusive, sedentary habits; 21, different breeding habits. Eaton (1953, 1956), who noted several of the above differences, prefers to call these forms "neotenic" sunfishes because of the larva-like nature of some of them. If Elassoma is truly a neotenic fish, this is only another characteristic in which they differ from the other centrarchids. It appears to this writer that Elassoma is very distantly related to any centrarchid. Either the elassomids diverged from the centrarchid stock early in the history of the group or they have entirely different affinities. They are considered to be highly specialized fishes which are related to the centrarchidae, but which have diverged sufficiently to be considered as a distinct family. These hypothetical relationships are shown in Text Figure 9.

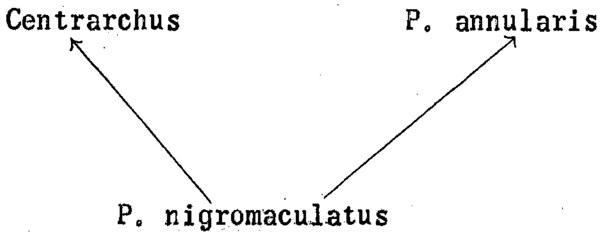


Text Figure 9. Hypothetical Phylogeny
of the Centrarchidae.

Specific Divergence Within Genera

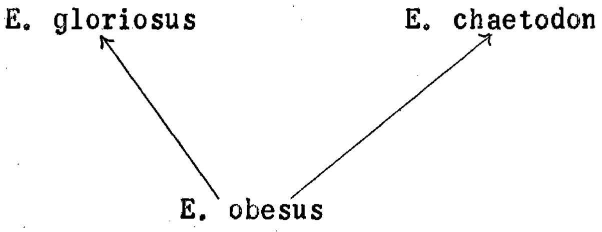
Hybrids between *Pomoxis* and *Centrarchus* do not appear to occur in nature (Hubbs, 1955). Furthermore, the restricted range of the flyer and its habitat suggest that the two genera are not really closely related, and that *Centrarchus* is a specialized, derived form (Text Fig. 10). *Pomoxis*, then, would be the more primitive genus and *P. nigromaculatus*, with its complete preoperculomandibular canal and more numerous pterygiophores, probably gave rise to *P. annularis*.

The banded sunfish, *M. chaetodon*, having a strongly compressed body is herein considered to be a specialization from *Enneacanthus obesus*.



Text Figure 10. Hypothetical Phylogeny in the Centrarchini.

Both of the last-named forms have relatively complete lateral-line systems and both are banded whereas E. gloriosus has a much reduced suborbital series and is spotted. Consequently, it is postulated that the evolutionary sequence must have progressed as seen in Text Fig. 11.



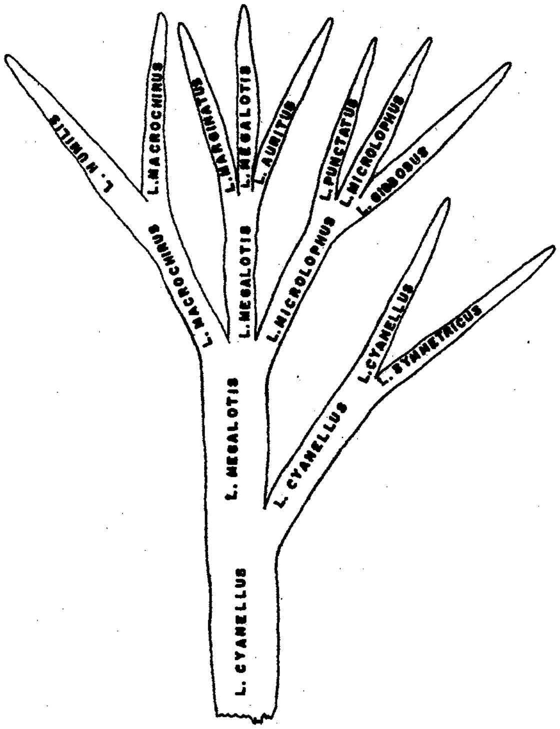
Text Figure 11. Hypothetical Phylogeny in the Enneacanthini.

It is a different situation in Micropterus and Lepomis as far as developing a tenable phylogeny is concerned. Some evidence has already been given that the green sunfish, L. cyanellus, is the most primitive member of its genus. Its least specialized characteristics are: four lateral-line pores in the frontal, 12 preoperculomandibular pores (seven in the preopercle), seven suborbitals, complete infraorbital canal, one canaliculus in the postocular commissural canal, lachrymal about as long as wide and with its lateral-line canal as in Chaenobryttus, a large canal neuromast (average 532.5 microns in total diameter) with numerous supporting cells in relation to sensory cells (127/29), a comparatively large sensory area (average 192.3 microns in diameter) and a large supramaxilla.

Lepomis symmetricus is a specialized species, but is most closely related to the green sunfish. The configuration of its frontal, preoperculomandibular and postocular commissural canals agree with those of L. cyanellus, but the species has some other characteristics which are of a divergent nature. Some of these are as follows: only ten suborbital pores, the canal in this position being interrupted; only one posteriorly-directed tube on the posttemporal; lachrymal like that of a young green sunfish, but differing in the adult state; and a reduced canal organ. The green sunfish is thought to be in the main line of lepomine evolution and L. symmetricus a specialized congener of that species (Text. Fig. 12).

The L. cyanellus branch probably gave rise to the other species of Lepomis. Some of the changes which could account for this are: a reduction in mouth size and in the size of the supramaxilla; a reduction in number of preopercular pores; compression and deeping of the body; reduction in neuromast size and in the number of supporting elements; a tendency toward the loss of spines on the lateral-line bones; the lachrymal, although retaining some similarity to that of the green sunfish, tending to become prolonged at the anteroventral margin, with a corresponding depression of the ventral, anterior lateral-line arm.

The longear sunfish, L. megalotis, is the most logical and morphologically reasonable candidate for the position nearest the branch originating from the green sunfish line. The species is very widely distributed and has many races (subspecies), several of which are yet to be described. Some of its characteristics definitely show such a proposed alignment, whereas others reflect the changes concommitant with evolutionary advance. The lachrymal is essentially like that of L. cyanellus, but



Text Figure 12. Hypothetical Phylogemy of Lepomis.

spination has become much reduced. The other ossicles of the infraorbital canal are very much like those of the green sunfish, both in configuration and in number (7) of pores; and the canal is complete. Another similarity is that there are 12 pores in the preoperculomandibular canal. Several divergent characters occur in the longear, some of which were noted in L. symmetricus; others reflect tendencies which are seen in most of the more advanced species of Lepomis. In the last category are found: five frontal pores, two postocular commissural canaliculi and decreased spination and organ size. However, organ diminution apparently has not always occurred at the same rate in all species. In some species, L. humilis for example, there appears to have been a secondary increase in size of the organ.

The two species most closely related to the longear sunfish (Text Fig. 12) are obvious deviates as far as the characters discussed above are concerned. Lepomis marginatus and L. auritus both have more restricted ranges than their prototype. Morphologically, L. marginatus is more closely related to L. megalotis than it is to L. auritus. Like the longear, L. marginatus has seven suborbital ossicles, a complete infraorbital canal and five frontal pores, but is divergent in possessing only one postocular commissural canaliculus and 11 preoperculomandibular pores. The lachrymal of this species resembles that of L. megalotis, but is practically devoid of serrae. In body configuration L. marginatus is very like the longear, of which it has been considered a subspecies (Reeves and Moore, 1949). This and the next species have either retained a larger organ than L. megalotis or the neuromasts have become secondarily enlarged. Since a similar tendency is seen in other Lepomis, the second possibility seems more plausible.

The lachrymal of L. auritus has become considerably modified over that of L. megalotis, mainly in the lack of spines and in the development of the rather long ventral spur. Although the infraorbital canal is complete there are only six suborbital bones. Points of morphological similarity are found in the presence of 12 preoperculomandibular and five frontal pores and the two postocular commissural tubes. The general external morphology of this species is similar to that of L. megalotis but the extremely long opercular membrane and the presence of palatine teeth are considered as modifications.

Many of the remaining species of Lepomis have restricted ranges and definite habitat requirements which tend to augment the morphological data utilized here in assuming that the L. megalotis line gave rise to these fishes. The presence of five frontal pores, seven suborbitals and two postocular commissural canaliculi indicate the relationships of the higher Lepomis, but the latter group bristles with divergent characteristics. A reduction of the preoperculomandibular pore number to 11, advanced smoothing of the lachrymal and elongation of its anteroventral margin, a secondary increase in neuromast size, and disjunction of the infraorbital canal between the lachrymal and the suborbitals behind it, all are indicative of specialization. The generalization at this point is that divergence, as seen in the above characteristics, gave rise to one branch which leads to L. microlophus and its two close relatives and another one which ends in the bluegill and the orangespotted sunfish (Text Fig. 12). The L. microlophus branch is probably more closely related to the longear stock than is the bluegill--orangespotted sunfish branch. In L. microlophus the lachrymal is very similar to that of the longear, whereas in L. macrochirus, and especially in L. humilis, the lachrymal has a tendency to be taller than wide. The three species of the redear group all have five frontal openings; L. macrochirus only has four and in L. gibbosus there are 12 preoperculomandibular pores and seven suborbital ossicles; there are also seven of the last-named bones in L. punctatus and in L. macrochirus of the other branch. In body shape the redear sunfish is most nearly like the bluegill or orangespotted sunfish.

The Lepomis microlophus group differs from L. megalotis in having two postocular commissural canaliculi, except L. gibbosus which has one, and in having an incomplete infraorbital canal, except L. punctatus, where it is complete. It is thought, because the greater part of the range of L. gibbosus lies in the glaciated region that the species is a derived one. The neuromasts found in the pumpkinseed are secondarily smaller than those of L. microlophus, mainly because of a decrease in the number of supporting cells. In having 12 instead of 11 preoperculomandibular pores, one postocular commissural canaliculus and seven suborbitals, L. gibbosus shows further divergence from L. microlophus.

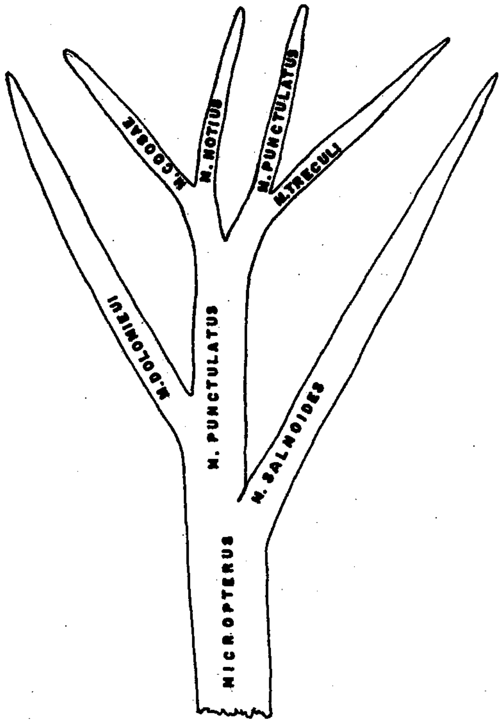
Lepomis punctatus is also considered to be a specialized offshoot from the L. microlophus branch (Text Fig. 12). Some relationship is indicated by the 11 preoperculomandibular pores, five frontal pores and body configuration, but there are many divergent characteristics. The lachrymal is taller than wide and nearly completely smooth, and its neuromasts are usually slightly larger than those of the redear sunfish. There are seven instead of six suborbitals and a complete rather than an incomplete infraorbital canal. One character which is definitely of a divergent nature is that of the supratemporal canal being covered by scales; no other Lepomis possesses such scales. The fact that hybridization between L. punctatus and Chaenobryttus or L. cyanellus has never been reported has some bearing on this question. Such combinations have been recorded (Hubbs, 1955) in both L. gibbosus and L. microlophus, indicating specialization in L. punctatus, possibly in selection of habitat station.

In the other branch, L. macrochirus and L. humilis possess several characters which show divergence from the main line of lepomine evolution. Some of these have already been mentioned (see above) but others are seen in Lepomis macrochirus, which, because of its great geographical range and tendency to form races, is considered to be the more genaralized member of the two fishes in its branch. The bluegill canal neuromast is of moderate size, as in the longear, but the first-named fish has two postocular commissural canaliculi and only four frontal pores. Lepomis humilis is an obvious deviate on several counts. Its range indicates a preference for turbid waters; it has only six suborbitals, a huge canal organ, one postocular commissural canaliculus, greatly inflated lateral-line tubes, five frontal pores and is the only species in Lepomis which possesses an interrupted preoperculomandibular canal.

Phylogeny of the Micropterini

The species of Micropterus form a very natural unit and exhibit little variation as far as the lateral-line system is concerned. It is very difficult to propose a workable phylogeny for such a closely related group. Knowledge of geographical distribution within the tribe allows some insight into this problem. The original range of Micropterus salmoides, the large mouth bass, was the most extensive of any of the species in the tribe. This species has a rather deeply emarginate dorsal fin, rather large scales, and a very large mouth. The lateral-line canals of the largemouth are relatively the smallest in the tribe. There are 11 infraorbital canaliculi, 12 preoperculomandibular pores and the lachrymal neuromasts are of moderate size, but shallower than in any other bass. The number of supporting cells in relation to sensory elements is 57/23. Some of these characteristics are shared with the other species of Micropterus, but some of the other Micropterus have undergone modification. Micropterus salmoides is here considered as the most generalized member of the bass tribe.

The only species which approached the wide range of the largemouth is the spotted bass, M. punctulatus, which was originally distributed in the Ohio River System of Illinois and Indiana, south to Alabama and Georgia and west to Oklahoma and Texas (Moore, 1957). Both of the species are capable of existing in a fairly wide range of habitat conditions, but it appears that the largemouth prefers quiet waters, whereas the spotted



Text Figure 13. Hypothetical Phylogeny of the Micropterini.

bass is often seen in rapidly-flowing streams in such situations as at the foot of riffles. The small mouth bass, M. dolomieui, is a species of clear running streams from Minnesota south to Alabama and west to eastern Oklahoma (Moore, 1957). Both its range and habitat are thus seen to be somewhat more restricted than that of the largemouth and the spotted basses. M. dolomieui is, however, often taken from the same habitat as the spotted bass. The remaining three species of micropterine fishes are severely restricted in both geographical range and habitat. Micropterus treculi is found only in the Edwards Plateau region of southcentral Texas (Hubbs and Bailey, 1942) which is near the western limits of the range of M. punctulatus. M. coosae is restricted to the upland waters of Alabama and Georgia, but comes into contact with the spotted bass in that region (Hubbs and Bailey, 1940). M. notius was originally found only in a spring-fed tributary of the Sante Fe River in Florida (Bailey and Hubbs, 1949). The disjunctive ranges of the last three species indicate that these fishes are specialized forms. What little is known concerning hybridization in the Micropterini seems to confirm the latter proposal. There are no hybrids involving the largemouth bass (subgenus Huro) (Hubbs, 1955). In the remaining species (subgenus Micropterus) hybrids observed to date are between M. coosae and M. punctulatus and between M. dolomieui and M. punctulatus (Hubs and Bailey, 1940), species which overlap or come into contact in their ranges. The probable reason that Huro does not hybridize is that there is stringent ecological disassociation during the breeding season, which in itself is indicative of specialization in the other basses.

Two main lines of descent are indicated in the bass tribe. One of these, embracing those fishes with a deep cleft in the dorsal fin, a relatively large mouth, 11 infraorbital and 12 preoperculomandibular pores and a relationship between the sensory and supporting cells in which the former occupying about 50 per cent of the neuromast diameter, eventually gave rise to M. salmoides. The other branch, including forms mostly with 11 preoperculomandibular pores, a rather shallow cleft in the dorsal fin, a smaller mouth, a tendency toward larger lateral-line canals and canal neuromasts, and smaller scales which encroach upon the dorsal-fin membranes, led to all of the other Micropterus (Text Fig. 13).

Micropterus punctulatus, being much more widely distributed, possessing several subspecies and enjoying a relatively wide range of environmental freedom in habitat selection, is probably very near the base of speciation in the subgenus *Micropterus*. However, Bailey and Hubbs (1949) suggested that *M. notius* was a relict species and near the prototype of the subgenus, but there are several reasons why this species is probably not a generalized one but a highly specialized form. Florida is located in a region that is geologically rather young as compared to parts of the Mississippi Valley. Some morphologically divergent characteristics are as follows: *M. notius* and *M. coosae* have the most capacious canals in the subgenus, nine infraorbital pores, 12 preoperculomandibular pores and a neuromast which (with *M. coosae*) is nearly twice the size of the other basses, including *Huro*. *Micropterus punctulatus* has a neuromast which is approximately comparable to that of the largemouth bass (supporting cells/sense cells, 52/22), small canals and 11 pores in the preoperculomandibular and infraorbital canals.

The smallmouth bass, *M. dolomieui*, although being fairly widely distributed, has more definite habitat requirements and many characteristics, such as a smaller mouth, small scales and nine infraorbital pores, which are of a divergent nature. The neuromasts of this species (64/29) and the 11 preoperculomandibular pores show some relationship with the spotted bass, but these two species probably diverged very early in the phylogenic history of the subgenus (Text Fig. 13).

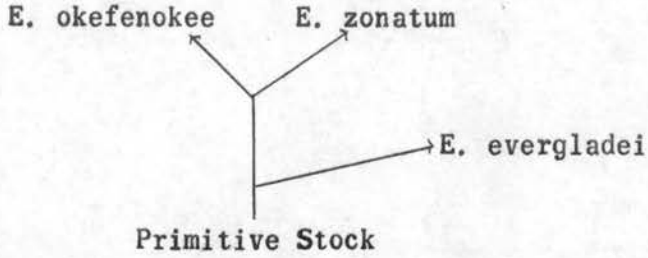
On comparing the ranges of *M. treculi* and *M. punctulatus*, it becomes apparent that the former is probably a geminate species of the latter. There is a great deal of morphological similarity between the two, but *M. treculi* is a considerably smaller species. Its lateral-line canals agree with those of the spotted bass in size and in number of infraorbital pores (11), but there are 12 instead of 11 preoperculomandibular pores.

The sensory area occupies a greater percentage of the total diameter of canal neuromasts (69/30) than in any other bass and the sensory hairs are much longer than in related forms. All of these characters show divergence from the main line. During a collecting trip to the Edwards Plateau in 1958 it was noted that M. treculi seemed to be found only in the fastest waters of riffles and that the species color, when alive, was of a light golden hue. Micropterus treculi is considered to be more nearly related to M. punctulatus than to any other form.

Both Micropterus notius and M. coosae possess characteristics which refer them to a relationship with the spotted bass branch, but they doubtless arose from an offshoot distinct from the M. treculi division. Of the two species M. coosae most closely resembles M. punctulatus, whereas the spring-dwelling M. notius recalls M. dolomieui in coloration and in having only nine infraorbital pores. M. coosae has 11 infraorbital pores. Divergence is indicated in the M. coosae--M. notius line by the 12 preoperculomandibular pores and the very long neuromasts. The canal organs of M. notius were found to possess 112 supporting cells to 49 sensory elements and in M. coosae the average ratio was 115/46. It has already been shown that the lateral-line canals of the last two species are the largest in the Micropterini. All of these characteristics demonstrate relationship between M. notius and M. coosae and divergence from the main stock of the spotted-bass line. Since the redeye bass is morphologically similar to M. punctulatus (Hubbs and Bailey, 1940), with which it has been confused, it is herein assumed that this species lies nearer the point of divergence than does M. notius (Text Fig. 13).

Phylogeny of Elassoma

The pygmy sunfishes are difficult to arrange in satisfactory phylogenic relationship since there is practically no morphological distinction between the three species, the lateral-line system is of very little help. However, for the sake of completeness, an attempt has been made to develop a tentative phylogeny (Text Fig. 14).



Text Figure 14. Hypothetical Phylogeny of *Elassoma*.

Elassoma zonatum has by far the widest range of any *Elassoma*, extending from the lowlands of Illinois south to east Texas and east in the Gulf States to Florida and North Carolina. *Elassoma evergladei* ranges from Florida to South Carolina (Moore, 1957) and *E. okefenokee* known only from the Okefenokee Swamp of Georgia) probably occupies a range of similar size (Böhlke, 1956). *E. zonatum* has 38 to 45 scales in the lateral series whereas *E. okefenokee* has 31 to 34 and *E. evergladei* 27 to 30 in the same region. Since reduction of parts is considered to be indicative of evolutionary advancement, the more numerous scales of *E. zonatum* would indicate the primitive condition. However, this is not always true. It has been shown that scales sometimes secondarily occur where they are most often absent. The acquisition of a scaly-head dorsum in *E. evergladei* is considered as a characteristic deviating from the naked condition in the other two species. As pointed out in the discussion of *Lepomis*, banding is thought to be a primitive characteristic. *E. zonatum* is strongly banded and *E. okefenokee* less so, and *E. evergladei* is not bended at all, but appears to be lightly streaked longitudinally because each of its scales has a light center (Jordan, 1884). It is evident that the first two species are much more similar to each other than is either to the last-named one. As shown in the description of external neuromast lines, *E. zonatum* and *E. okefenokee* also show greater relationship to each other than to *E. evergladei*. One lateral-line characteristic, which may or may not be valid (because of the small sample size), that can be used to demonstrate divergence is the number of mandibular neuromasts: *E. zonatum* possesses more than two times as many of these as the other two species.

From the meager data above it is suggested that *E. zonatum* is the most unspecialized member of the genus and that *E. okefenokee* is its nearest relative. The supposed phylogeny of the group is seen in Text Figure 14.

CHAPTER XVI

TAXONOMIC IMPLICATIONS

Characters of the lateral-line system have often been utilized in taxonomic works to distinguish species. The characters chosen have usually been ones concerning the degree of completeness of certain canals (or canal series), such as the infraorbital or lateralis. However, the morphology of the canals and their associated bones have been put to little use in classifying members of the Centrarchidae. This study has shown that these characteristics are useful in distinguishing genera but in some groups, Micropterini, Enneacanthini and Elassomidae, their usefulness in characterizing species is very slight. Hubbs (1943) demonstrated on several occasions that in fishes the genus is an arbitrary taxonomic entity without apparent objective criteria. The characters which hold such a taxon together are those which can withstand the test of unvarying consistency.

In describing the genus *Elassoma*, Jordan (1877) found it impossible to refer the fish, *E. zonatum*, to a family, but thought the new form to be a member of the primarily South American family Cichlidae. Berg (1946) considered these small fishes to be centrarchids but, from the evidence herein presented, it seems best to place the pygmy sunfishes in a separate family, the Elassomidae Jordan.

Topotypes of the fossils *Pomoxis lanei* Hibbard and *Chaenobryttus kansasensis* Hibbard from the Middle Pliocene in Logan County, Kansas

(Hibbard, 1936) are here regarded as conspecific with Pomoxis nigromaculatus LeSueur and Chaenobryttus gulosus (Valenciennes) respectively. The bones of P. lanei fall well within the limits of variation for P. nigromaculatus and C. kansasensis is indistinguishable from the recent warmouth. The mere occurrence of a form in a certain stratum of rocks does not, in itself, imply that the form should be given specific recognition nor is there any reason why subspecies should not be extended into time as well as in space. If these forms are races they will have to be distinguished with statistically obtained data.

We have shown that there is a great deal of similarity between the nominal genera Enneacanthus and Mesogonistius. The characteristics reflecting this relationship are very constant and are of such a magnitude that closer affinity than tribal relationship is indicated. Mesogonistius is considered as congeneric with Enneacanthus. Although Eddy (1957) effected such a union he gave no reasons for so doing. Nomenclaturally speaking, there does not seem to be a question of priority involved, since, according to Jordan, Evermann and Clark (1930), Gill described both in 1864 on the same page. The rule of the first reviser thus applies. Although Eddy's (op. cit.) keys to North American freshwater fishes are not to be considered as a revision, he did include the three species as members of the genus Enneacanthus. In the interest of avoiding confusion it seems most logical to follow this worker in name choice.

The key to the members of the family Centrarchidae presented below is intended to be a natural one based largely upon the data secured during this study.

Key to the Genera and Species of the Centrarchidae and Elassomidae

1. Dentary and articular penetrated by the lateral-line; lateral

extrascapular and at least two suborbital ossicles present; supraorbital commissure complete; lateralis never completely absent ____________________ Centrarchidae ________________ 2

Dentary and articular not penetrated by the lateral-line; lateral extrascapular and lateralis lacking; supraorbital commissure incomplete __________ Elassomidae _____________ 28

2. With five anal spines ___________________________________ 3

With three anal spines __________________________________ 9

3. Upper, posterior edge of supracleithrum bearing serrae _____ ______________________________ *Archoplites interruptus*

Supracleithrum smooth ___________________________________ 4

4. Posterior edge of posttemporal smooth; infraorbital canal complete ____ 5

Posterior edge of posttemporal serrate (sometimes obsolete in *Pomoxis*); infraorbital incomplete ________________________ 7

5. Posterior edge of lower preopercle serrate, its lower arm forming an angle of about 90° with the upper; two posteriorly-directed pores on the posttemporal; supratemporal canal not covered by scales; anteroventral margin of lachrymal serrate; scales ctenoid___________________ *Ambloplites* ___________ 6

Posterior edge of preopercle smooth, its lower arm forming an angle of about 110° with the upper; one posteriorly-directed pore on the posttemporal; supratemporal canal covered by scales (except its branches); anteroventral margin of lachrymal smooth; scales cycloid ____________ *Acantharchus pomotis*

6. Rows of scales above the lateralis seven to nine; cheeks fully scaled ______________________ *Ambloplites rupestris*

Rows of scales above the lateralis ten to 12; cheeks only partially scaled ________________ *Ambloplites cavifrons*

7. Dorsal spines five to eight __________________________ 8

Dorsal spines 11 to 13 _________ *Centrarchus macropterus*

8. Dorsal spines 7 (rarely six or eight); preoperculomandibular canal complete _________________ *Pomoxis nigromaculatus*

Dorsal spines 6 (rarely five or seven); preoperculomandibular canal interrupted _______________ *Pomoxis annularis*

9. Lachrymal with two anteriorly-directed branches; two posterior openings on the posttemporal canal; infraorbital canal not greatly interrupted, reaching to or beyond middle of eye; five mandibular openings ______________________________ 10

Lachrymal with a single anteriorly-directed branch; only one posterior opening on the posttemporal canal; infraorbital canal greatly interrupted, usually not reaching middle of eye; four mandibular openings ________ *Enneacanthus* __________ 26

10. Preopercle not boomerang-shaped, usually serrate posteriorly, its upper arm forming an angle of less than 100° with the lower (except in *L. symmetricus*, in which the angle is 110 to 115°); lachrymal usually serrate at the anteroventral margin, its enire posterior edge involved in forming the anterior orbit; lateralis curving upward from its origin; cephalic external canaliculi usually not longer than the width of the canal bearing them ___11

Preopercle boomerang shaped, never serrate posteriorly, its upper arm forming an angle of 100° to 105° with the lower; lachrymal smooth, only its upper one-half involved in forming the orbit; lateralis curving downward for two or three scales from origin then curving upward; cephalic external canaliculi usually longer than the width of canal which bears them ________________________________ *Micropterus*

11. Teeth on tongue and pterygoids; lachrymal bearing a posteroventral notch; supramaxilla longer than width of maxilla ________________________________ *Chaenobryttus gulosus*

    No teeth on tongue or pterygoids; lachrymal lacking a posteroventral notch; supramaxilla shorter than width of maxilla ___ 12

12. Width of supracleithrum contained 3.5 or more times in its length ________________________________ 13

    Width of supracleithrum contained 3.0 or fewer times in its length ________________________________ 14

13. Lateralis extending to a point behind the end of soft dorsal, usually complete; two posterior pores on posttemporal; preopercle angle 90° to 95°; lachrymal about as wide as tall ________________________________ *Lepomis cyanellus*

    Lateralis ending under soft dorsal; only one posterior pore on posttemporal; preopercle angle 110° to 115°; lachrymal nearly twice as tall as wide _____ *Lepomis symmetricus*

14. Posterior edge of opercle fimbriate; supraorbital pore formula 2(1 + 3) ________________________________ 15

    Posterior edge of opercle not fimbriate, or if it is, then supraorbital pore formula 2(0 + 3) ________________________ 17

15. No canaliculi in the cephalic lateralis except the two posterior openings of the posttemporal, its formula 2(0 + 2 + 0) ________ ______________________________ <u>Lepomis</u> <u>megalotis</u>

A third canaliculus present in cephalic lateralis, its formula 2(0 + 2 + 1) ____________________________________ 16

16. Postocular commissure with one canaliculus; preoperculomandibular canal with 11 pores; external canaliculi of lateralis short and directed caudad along the main axis; no long posteroventral spur on lachrymal _______________ ______________________________ <u>Lepomis</u> <u>marginatus</u>

Postocular commissure with two canaliculi; preoperculomandibular canal with 12 pores; external canaliculi of lateralis relatively long and deflected away from main axis; lachrymal with a long posteroventral spur ___ <u>Lepomis</u> <u>auritus</u>

17. Posterior edge of opercle fimbriate; supraorbital pore formula 2(0 + 3) ____ 18

Posterior edge of opercle not fimbriate; supraorbital pore formula 2(1 + 3) ________________________________ 19

18. Preoperculomandibular canal joined dorsally to cephalic lateralis; four frontal openings; width of supraorbital canals not greater than the space between them __ <u>Lepomis</u> <u>macrochirus</u>

Preoperculomandibular canal disjunct dorsally from cephalic lateralis; five frontal openings; width of supraorbital canals greater than the space between them ____________________ ______________________________ <u>Lepomis</u> <u>humilis</u>

19. Preoperculomandibular canal formula 2(JP1 + 12) or 2(JP1 + 10); supratemporal canal not covered by scales; width of lachrymal into its length less than 1.5; lower pharyngeal width into its length 3.0 or less ______ 20

Preoperculomandibular canal formula 2(JP1 + 12); supratemporal canal covered by scales; width of lachrymal into its length 1.5 or more; lower pharyngeal width into its length 4.0 or more ______ Lepomis punctatus

20. Preoperculomandibular formula 2(JP1 + 10); postocular commissure with two canaliculi ______ Lepomis microlophus

Preoperculomandibular formula 2(JP1 + 11); postocular commissure with one canaliculus ______ Lepomis gibbosus

21. Dorsal fin deeply emarginate, the shortest spine only about one-half the length of the longest; pyloric caeca most often bifurcate ______ Micropterus salmoides

Dorsal fin shallowly emarginate, the shortest spine more than one-half the length of the longest; pyloric caeca usually simple ______ 22

22. Preoperculomandibular pore formula 2(JP1 + 11) or 2(JP1 + 10); scales above the lateral line seven to 10, those below 14 to 19______ 23

Preoperculomandibular pore formula 2(JP1 + 10); scales above the lateral line 12 or 13, those below 20 to 23 ______ Micropterus dolomieui

23. Preoperculomandibular pore formula 2(JP1 + 10) ______

Micropterus punctulatus

Preoperculomandibular pore formula 2(JPl + 11) ____ 24

24\. Postocular commissural canal with two external canaliculi ____ 25

Postocular commissural canal with one canaliculus ____ *Micropterus notius*

25\. Sides with vertical bars; restricted to Edwards Plateau of southcentral Texas ____ *Micropterus treculi*

Sides with a broken lateral band; restricted to upland streams in the Alabama and Savannah river basins of Alabama and Georgia ____ *Micropterus coosae*

26\. Palatine teeth usually present; dorsal fin not emarginate ____ 27

Palatine teeth absent; dorsal fin emarginate ____ *Enneacanthus chaetodon*

27\. With at least four suborbitals including the lachrymal and dermosphenotic ; sides with dark bands ____ *Enneacanthus obesus*

With three or fewer suborbitals; sides marked by longitudinal rows of spots ____ *Enneacanthus gloriosus*

28\. Top of head naked; sides of body marked by bars ____ 29

Top of head scaly; scales on sides of body with light centers giving the appearance of longitudinal streaking ____ *Elassoma evergladei*

29. A dark blotch (double in Oklahoma specimens) just below the origin of the dorsal fin ______________ *Elassoma zonatum*

Dark blotch lacking ____________________ *Elassoma okefenokee*

CHAPTER XVII

SUMMARY AND CONCLUSIONS

The lateral-line system of centrarchid fishes is characterized by simplicity and the lack of numerous branches. Those branches (external canaliculi) which are present are simple and uncomplicated by secondary bifurcation, ending in simple pores. All of the major canals of the higher bony fishes are represented. For the sake of convenience some of the lateral-line nomenclature has been revised, the revision being mainly concerned with the cephalic canals behind the eye. The point of junction between the supraorbital, infraorbital and the canal which connects the cephalic canals with the lateralis, has been termed the "postocular sinus;" the connecting piece is called the "postocular commissure." The external lateral-line morphology of all species has been illustrated and a system proposed for denoting pore distribution.

Another characteristic of the sunfish lateral-line system is the paucity of external neuromasts. These structures are not remarkably different from those of many other fishes, and occupy body regions as usual for percids. In Lepomis punctatus, L. megalotis, L. gibbosus and L. cyanellus and in the three species of Elassoma, opercular organs were noted. This is a rather peculiar distribution and has been seen in only a few other fishes, such as Esox. In the pygmy sunfishes there has been extensive reduction of the lateral-line canals and concomitant replacement by external neuromasts. The infraorbital canal, has, with the exception of a much reduced lachrymal, disappeared completely; The supraorbital canal is interrupted; the preoperculomandibular canal is interrupted above and incomplete ventrally; and the lateralis canals are lacking.

The osseous portion of the system has been discussed in detail and many parts of it illustrated. The skeletal elements associated with the lateral line where found to be very similar to those of many other fishes as far as penetration route is concerned but in shape and in spination they are more like those of serranids than other fish taxa. This is especially obvious in the subfamily Centrarchinae, which are considered to be the primitive members of the family. The Enneacanthini have undergone considerable reduction and modification in their lateral-line bones but not so much as in the pygmy sunfishes. Of all the centrarchids, the Lepomini are most similar to the Centrarchini and especially to the rockbass.

Comparative histological observations revealed that the canal organs are not notably different from those of other fishes except that the sensory cells possess multiple sense hairs. This has heretofore been observed only in <u>Cichlasoma</u> <u>cyanoguttatum</u>. The presence of cupulae and intercellular bridges was observed. One of the more important observations was that more than one kind of sensory cell is present in the canal neuromasts of several species. Physiological evidence for the existence of heterogeny in the sensory elements of fishes has been noted before, but to our knowledge this is the first report of morphological differentiation. Several differences between species were discovered but few inter-tribal or inter-generic differences in soft anatomy were noted. Suggestions concerning the functional aspects of observed histology and cytology were made.

The external neuromasts were found to differ from the canal organs mainly in size. However, it was also found that the sensory elements of these smaller organs possessed only single sensory hairs. The neuromasts of Elassoma differ markedly from those of the true sunfishes in morphology (except Enneacanthus), distribution and in number.

Utilizing the rather large amount of evidence compiled during this study the following conclusions were reached:

1. The Centrarchidae are most nearly related to the family Serranidae.
2. Archoplites interruptus is the primitive member of the family. However, it has become highly specialized through long-continued isolation and is probably not in the direct line of Centrarchid evolution.
3. Ambloplites is the most generalized member of the Centrarchidae and is in the direct descendency of the family.
4. Acantharchus is a derived form.
5. The tribe Centrarchini is related to the Ambloplitini, but is more specialized. Pomoxis nigromaculatus is considered to be the generalized member and a form like it probably gave rise to P. annularis and Centrarchus macropterus.
6. Chaenobryttus gulosus is the progenitor type of the lepomine tribe and is intermediate between Ambloplites and Lepomis cyanellus, the primitive member of its genus. L. symmetricus is a congener of the last-named species.
7. Lepomis megalotis is a divergent form, but a form similar to it probably gave rise to the remainder of the family.

8. Two branches from the main lepomine line gave rise to L. macrochirus and L. humilis on the one hand and to L. microlophus, L. punctatus and L. gibbosus on the other.
9. The main L. magalotis sequence ended in the production of L. marginatus, L. auritus and L. megalotis.
10. Divergence from the lepomine stock gave rise to Enneacanthus and Micropterus and the recent Chaenobryttus.
11. Micropterus is a natural unit with very little morphological distinction between species as concerns the lateral line.
12. M. salmoides is the primitive member of its genus.
13. M. dolomieui diverged early from the main evolutionary sequence.
14. M. punctulatus is clearly most nearly related to M. salmoides and it is thought that a form like it was probably the progenitor of the more highly specialized forms.
15. M. treculi and M. punctulatus are geminate species.
16. M. coosae and M. notius are divergent forms, the former being more closely related to M. punctulatus than the latter.
17. Enneacanthus is another natural unit derived from the ancestral Lepomini.
18. E. obesus is considered as the most generalized species of its tribe and that a form like it probably gave rise to E. gloriosus and E. (Mesogonistius) chaetodon.
19. The genus Elassoma differs from the Centrarchidae in 20 or more major characteristics and is considered to have diverged from the sunfishes very early in the evolutionary history of the group. There is sufficient evidence for the recognition of the monotypic family Elassomidae Jordan.

20. E. zonatum is the generalized form, E. evergladei and E. okefenokee being the result of specialization.
21. E. okefenokee is most nearly related to E. zonatum.
22. Mesogonistius is merged with Enneacanthus and the latter epithet preserved.
23. The fossil species Pomoxis lanei is conspecific with P. nigromaculatus and Chaenobryttus kansasensis is indistinguishable from C. gulosus.
24. It is possible to correlate lateral-line morphology with the habitat in which some species are found.

A key is offered for the diagnosis of genera and species, based in a large degree upon the characteristics herein discussed.

CHAPTER XVIII

SUGGESTIONS FOR FURTHER STUDY

1. An attempt to correlate the relative development of other sensory organs with the habitat of the various centrarchids and with the development of the lateral-line system would probably yield important results. A comparative morphology of centrarchid eyes would be particularly interesting.
2. An attempt to correlate the diameter of the lateral-line nerves with the observed external anatomy of the system should be made.
3. In the area of histology and cytology it would be most interesting to perform microchemical analysis of the cellular constituents of the neuromasts. The use of selective stains for mitochondria, Golgi bodies, various proenzymes and hormones would be most helpful in this study.
4. Special physiological experiments directed toward discovering the function of the heterogeneous sense cells should be attempted.
5. The embryological development of all members of the family should be studied in detail and the following aspects decided: a, whether or not the lateral-line organ and primitive ear form from a common anlage; b, the time of separation of the above two structures; c, the method and route of migration of the neuromasts from their point of origin, d, the time and method of

of canal formation; e, the degree of correlation between neuromast position and the formation of lateral-line bones; and f, particular attention should be given to the development of the canal neuromasts to determine how the heterogeneous cells come into being and if they are involved in some sort of holocrine function.

6. Serological tests should be accomplished on all of the centrarchids and an attempt be made to test the degree of relationship between species. This would serve as a check on the findings herein presented.

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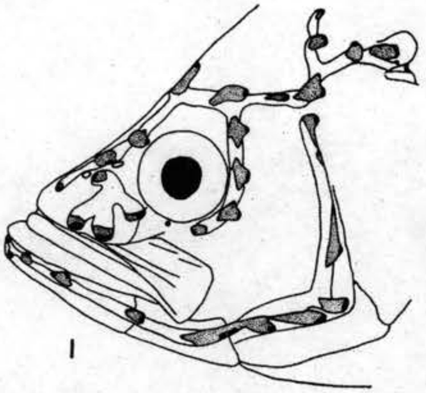
APPENDIX

Plate I. External Morphology of the Centrarchidae. Proportional drawings of India-ink injected specimens; stippling represents areas covered by tissue only.

Figure:

1. *Pomoxis annularis* X 0.5
2. *Centrarchus macropterus* X 1.4
3. *Pomoxis nigromaculatus* X 0.5
4. *Archoplites interruptus* X 1.4
5. *Acantharchus pomotis* X 1.4
6. *Ambloplites rupestris* X 0.5
7. *Lepomis cyanellus* X 0.5
8. *Lepomis symmetricus* X 1.4



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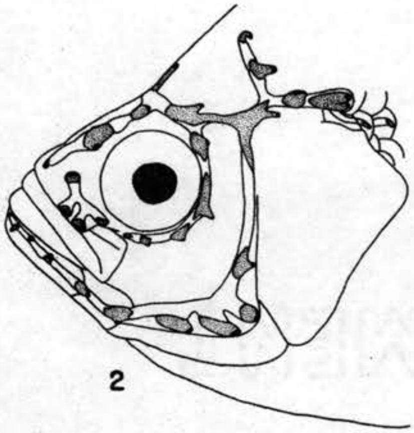

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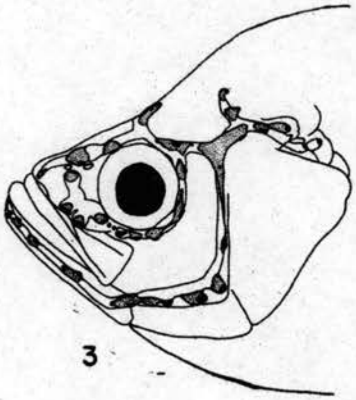

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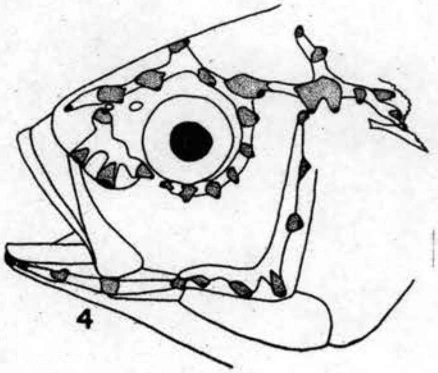

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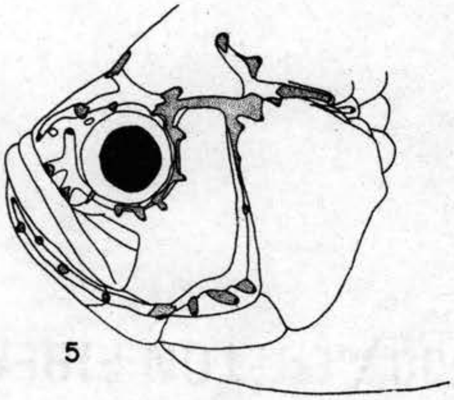

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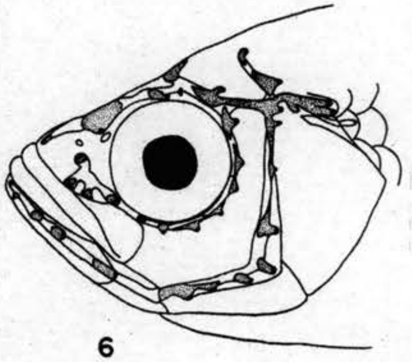

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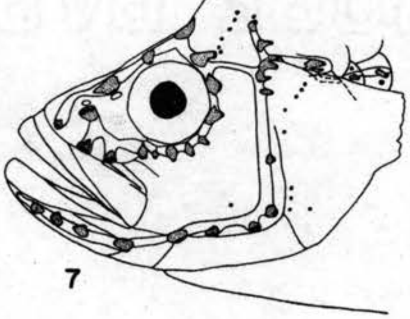

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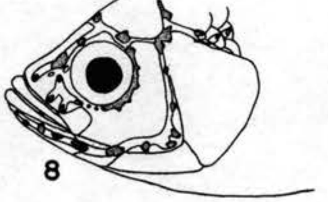

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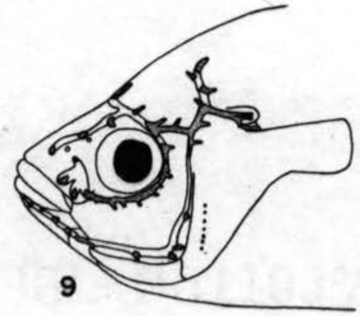
Plate II. External Morphology of the Centrarchidae (continued).

Figure:

9. *Lepomis megalotis breviceps* X 0.5
10. *Lepomis punctatus* X 0.5
11. *Lepomis auritus* X 0.5
12. *Lepomis marginatus* X 1.4
13. *Lepomis microlophus* X 0.5
14. *Lepomis macrochirus* X 0.5
15. *Lepomis gibbosus* X 0.5
16. *Lepomis humilis* X 1.5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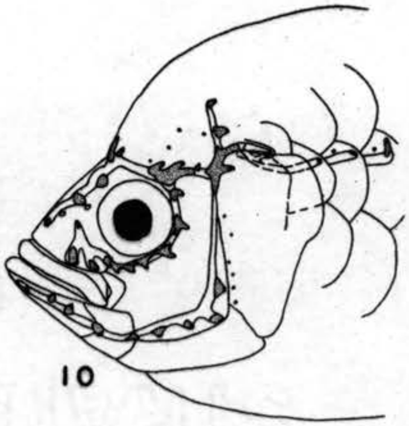
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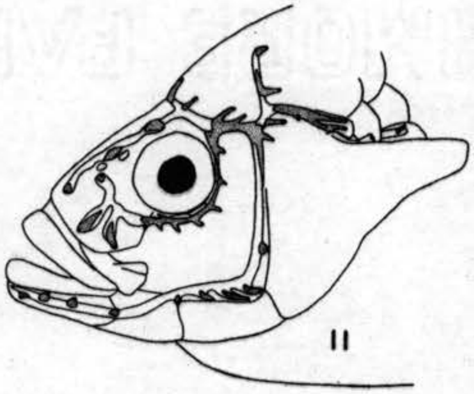
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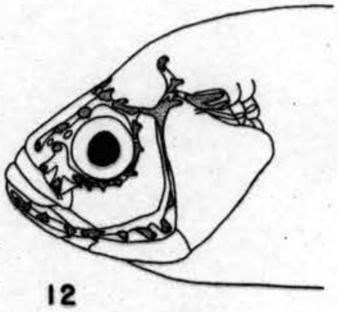
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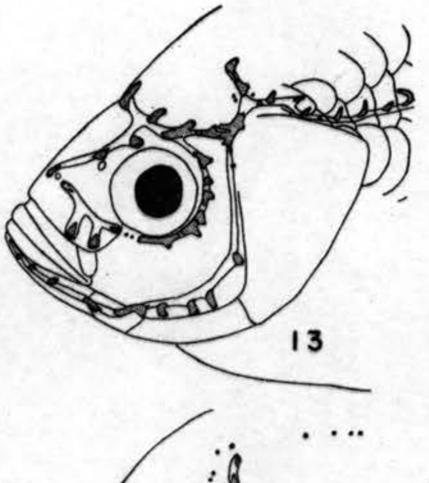
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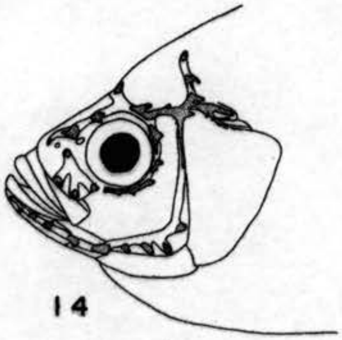
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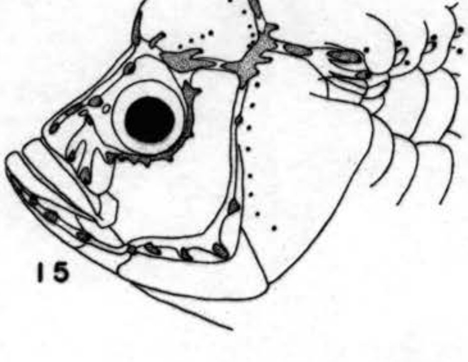
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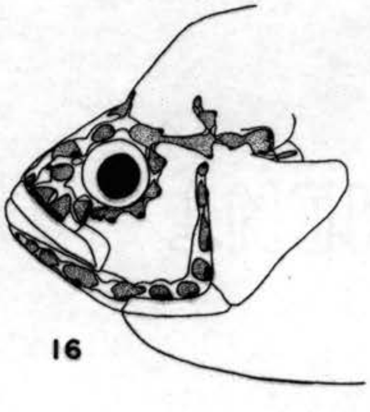
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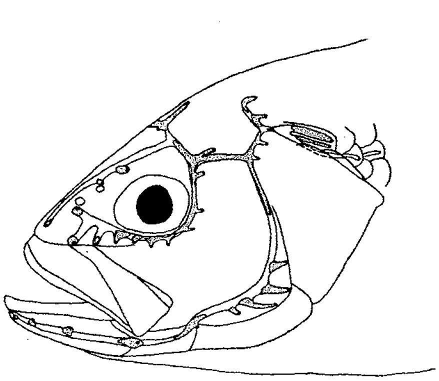
Plate III. External Morphology of the Centrarchidae (continued).

Figure:

17. *Micropterus salmoides* X 0.5
18. *Micropterus punctulatus* X 0.5
19. *Micropterus treculi* X 0.5
20. *Micropterus notius* X 1.5
21. *Micropterus coosae* X 1.5
22. *Micropterus dolomieui velox* X 1.1
23. *Enneacanthus obesus* X 1.4
24. *Enneacanthus gloriosus* X 2.8



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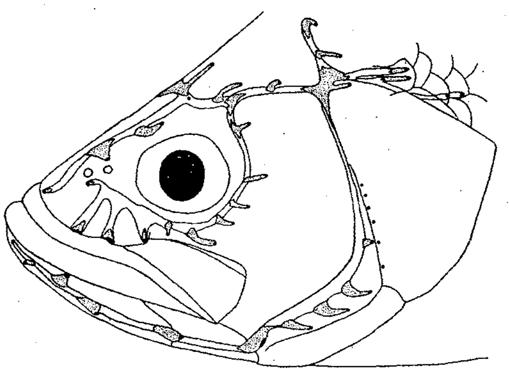

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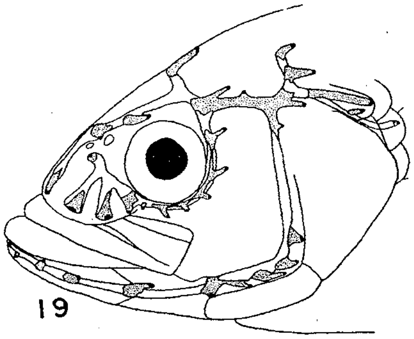

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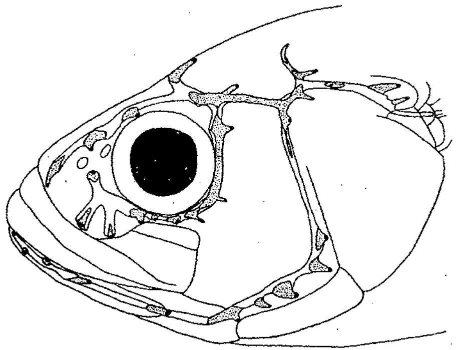

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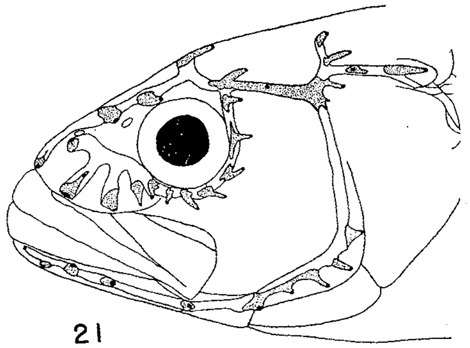

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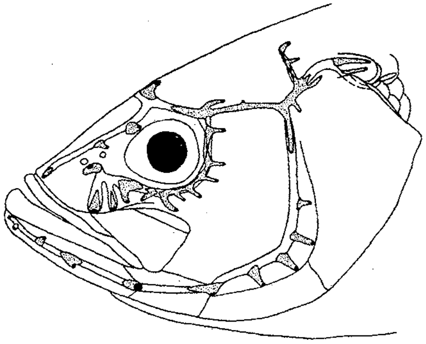

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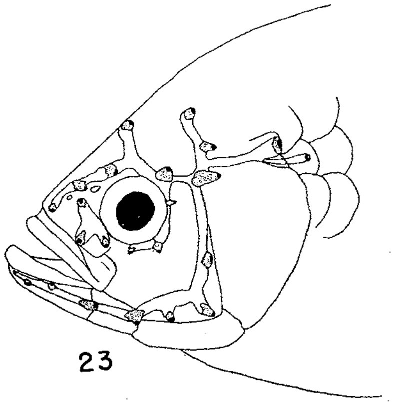

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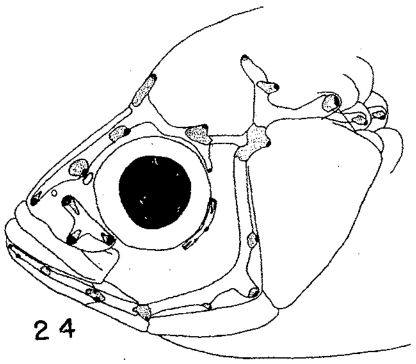

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Plate IV. External Moropology of the Centrarchidae (continued). A, anterior; E, external canaliculus; N, lateralis-canal neuromast.

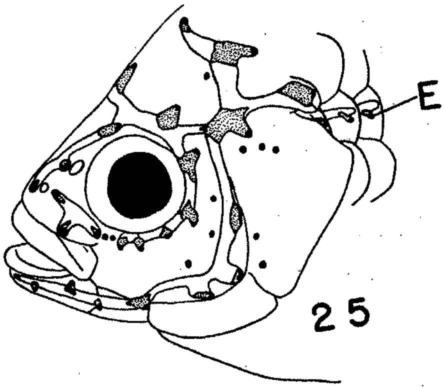
Figure:

25. _Enneacanthus_ (_Mesogonistius_) _chaetodon_ X 2.6

26. Scale of _Chaenobryttus_ _gulosus_ as seen from the edge, showing peg-like articulating structures at anterior end. Free hand, not to scale.

27. Lateral-line scale of _Chaenobryttus_ _gulosus_. Not to scale.

28. A series of lateral-line scales from _Lepomis_ _gibbosus_ showing external canaliculi and method of connection. X 8.2



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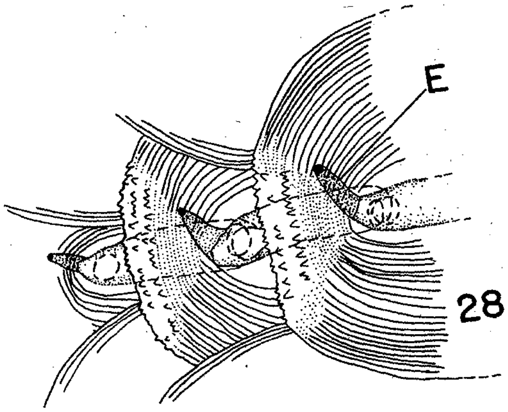

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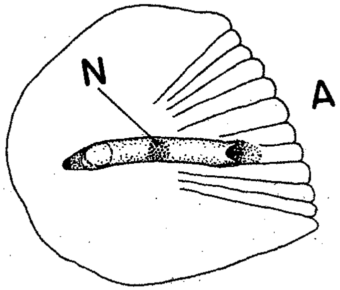

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Plate V. Osseous Components of the Lateral-Line system in the Centrarchidae.

Figure:

29. Posttemporal and upper end of supracleithrum of Archoplites. X 11.1

30. Posttemporal of Centrarchus macripterus. X 38.9

31. Supracleithrum of Lepomis cyanellus. X 18.8

32. Posttemporal and upper end of supracleithrum of Pomoxis nigromaculatus. X 1.4

33. Posttemporal and upper end of supracleithrum of Enneacanthus (Mesogonistius) chaetodon. X 20.0

34. Posttemporal of Lepomis microlophus. X 6.3

35. Supratemporal-intertemporal, posttemporal and upper end of supracleithrum of Enneacanthus gloriosus. X 17.5

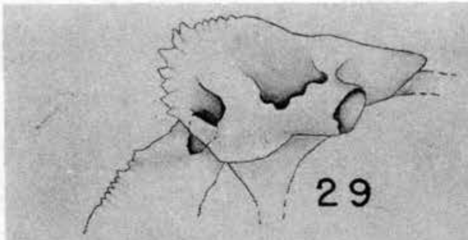
36. Dermopterotic of Pomoxis nigromaculatus. X 6.5

37. Posttemporal of Lepomis auritus. X 5.2

38. Dermopterotic of Lepomis cyanellus. X 3.9

39. Posttemporal of Elassoma okefenokee. X 18.7

40. Dermopterotic of Archoplites interruptus. X 13.5



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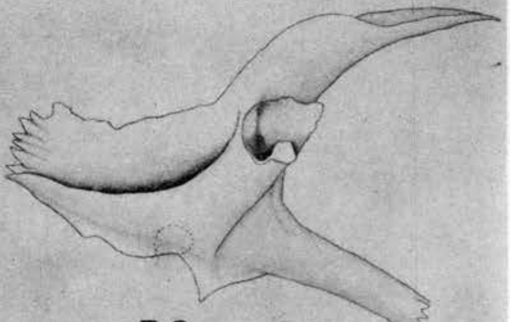

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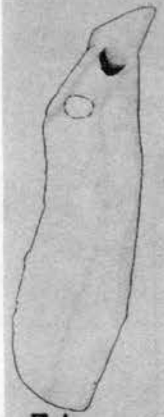

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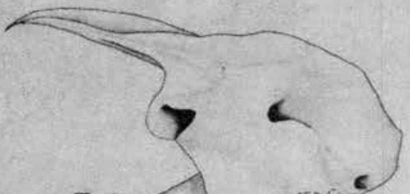

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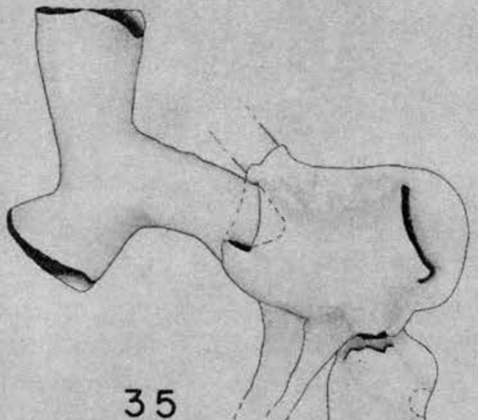

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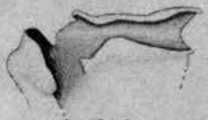

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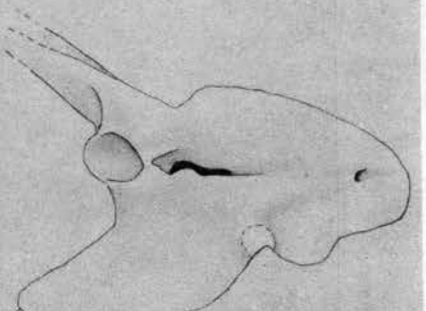

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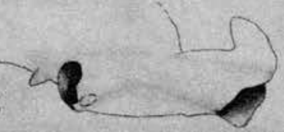

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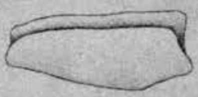

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Plate VI. Osseous Components of the Lateral-Line System in Centrarchidae (continued).

Figure:

41. Frontal of _Centrarchus_ _macropterus_. X 8.6

42. Posttemporal and upper end of supracleithrum in _Lepomis_ _humilis_. X 7.4

43. Dentary of _Lepomis_ _macrochirus_. X 3.6

44. Dentary of _Lepomis_ _cyanellus_. X 2.4

45. Frontal of _Lepomis_ _auritus_. X 3.3

46. Frontals of _Micropterus_ _punctulatus_. X 3.6

47. Frontals of _Elassoma_ _okefenokee_. X 11.7

48. Nasal of _Micropterus_ _punctulatus_. X 2.6

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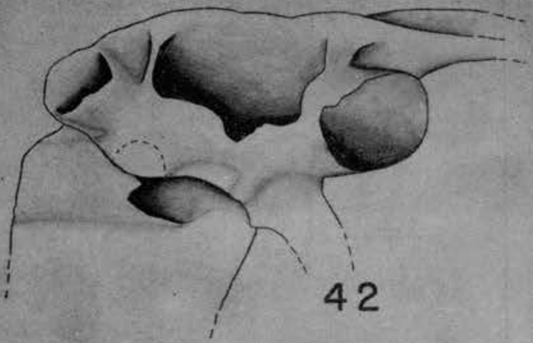

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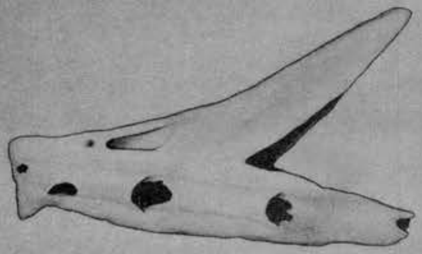

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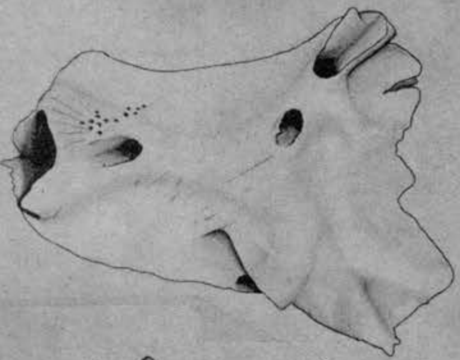

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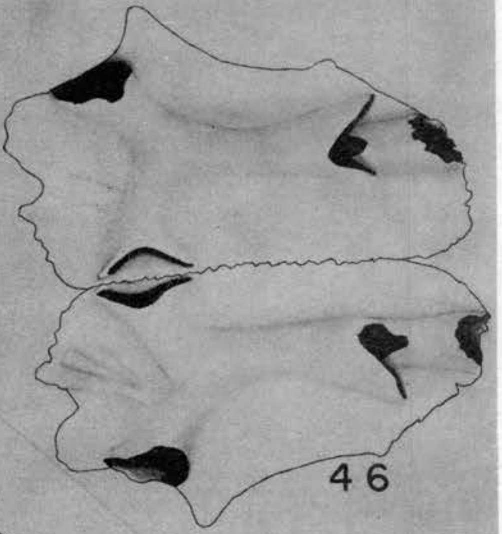

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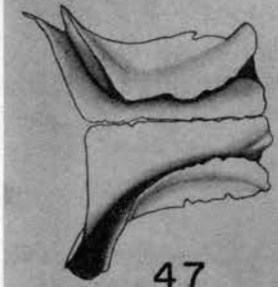

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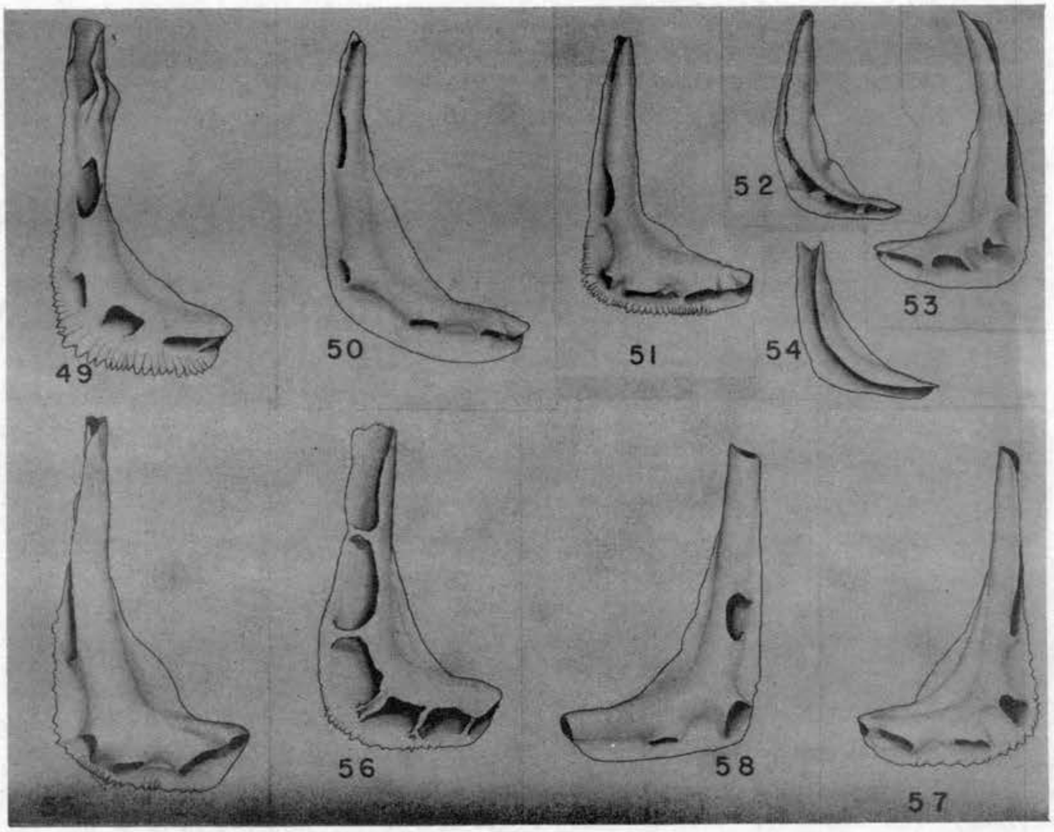
Plate VII. Osseous Components of the Lateral-Line System in Centrarchidae (continued).

Figure:

49. Preopercle of *Archoplites interruptus*. X 4.3
50. Preopercle of *Acantharchus pomotis*. X 2.1
51. Preopercle of *Centrarchus macropterus*. X 2.5
52. Preopercle of *Micropterus treculi*. X 2.0
53. Preopercle of *Lepomis auritus*. X 1.6
54. Preopercle of *Elassoma okefenokee*. X 7.0
55. Preopercle of *Lepomis macrochirus*. X 2.0
56. Preopercle of *Lepomis humilis*. X 6.1
57. Preopercle of *Lepomis megalotis*. X 2.0
58. Preopercle of *Enneacanthus gloriosus*. X 6.5
59. Jugal of *Lepomis gibbosus*. X 6.5
60. Preopercle of *Lepomis cyanellus*. X 1.5
61. Preopercle of *Lepomis symmetricus*. X 4.0
62. Lachrymal of *Pomoxis nigromaculatus*. X 0.9
63. Lachrymal of *Chaenobryttus gulosus*. X 2.9
64. Lachrymal of *Lepomis cyanellus*. S. L. 187 mm., X 2.9
65. Jugal of *Micropterus salmoides*. X 15.6
66. Lachrymal of *Lepomis marginatus*. X 4.1
67. Lachrymal of *Lepomis cyanellus*. S. L. 11.0 mm., X 13.2
68. Lachrymal of *Lepomis symmetricus*. X 5.7
69. Lachrymal of *Lepomis microlophus*. X 4.1
70. Lachrymal of *Lepomis macrochirus*. X 4.0
71. Lachrymal of *Enneacanthus gloriosus*. X 3.7
72. Lachrymal of *Lepomis auritus*. X 4.0
73. Lachrymal of *Lepomis megalotis breviceps*. X 3.5
74. Lachrymal of *Elassoma okefenokee*. X 11.4
75. Lachrymal of *Lepomis humilis*. X 6.5
76. Lachrymal of *Lepomis punctatus*. X 5.2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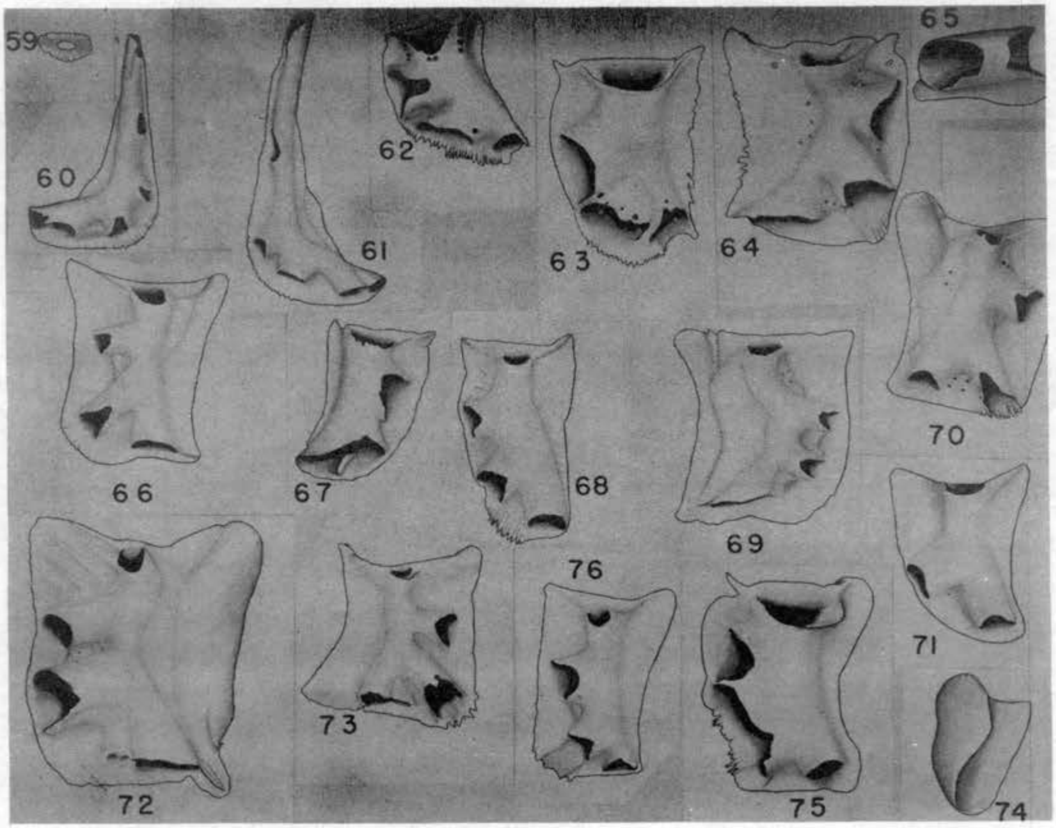
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Plate VIII. Osseous Components of the Lateral-Line System in Centrarchidae. a, Heteromorphic sensory cells; b, normal sense cells; c, cross-section of supporting cells below the level of sense cells; d, supranuclear body.

Figure:

77. Lachrymal of Acantharchus pomotis. X 8.6

78. Lachrymal of Micropterus treculi. X 2.0

79. Compound jugal and suborbital three of Micropterus coosae. X 13.0

80. Suborbital four of Archoplites interruptus. X 11.0

81. Neuromast cells of Chaenobryttus gulosus.

82. Canal neuromast of Centrarchus macropterus.

83. Central cellular elements of Ambloplites rupestris.

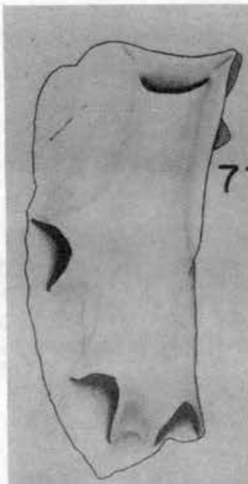
84. Marginal cellular elements of Acantharchus pomotis.

85. Cellular elements of Pomoxis annularis.

86. Canal neuromast of Lepomis marginatus.

87. Cellular elements of Centrarchus macropterus.

88. Cellular elements of Pomoxis nigromaculatus.



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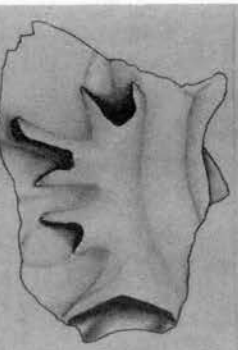

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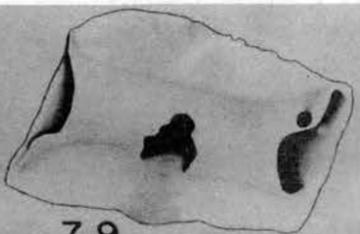

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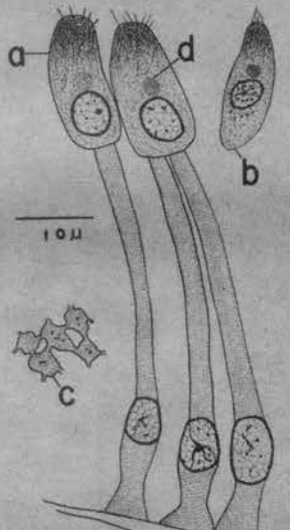

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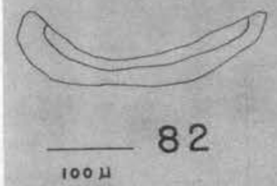

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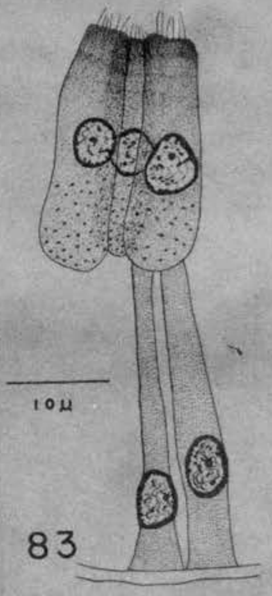

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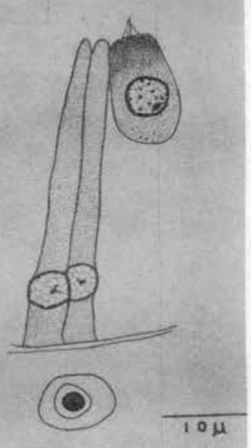

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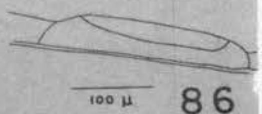

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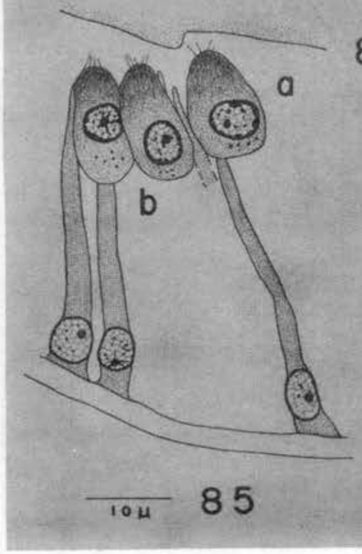

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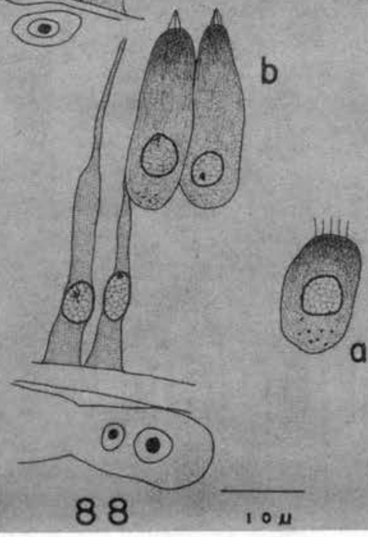

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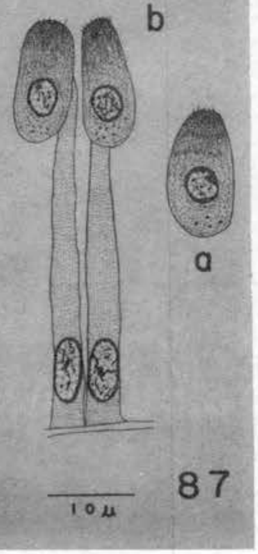

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Plate IX. Cellular Components of the Lateral-Line (continued). s, Sense cell; i, intercellular bridges of sustentacular cells; j, intercellular bridges of some sense cells.

Figure:

89. Supporting and sense cells of *Micropterus punctulatus*.

90. Supporting and sense cells of *Micropterus salmoides*.

91. Facial section of supporting and sensory cells of *Micropterus treculi*.

92. Supporting and sensory cells of *Micropterus treculi*.

93. Outline of external neuromast of *Micropterus treculi*.

94. Supporting and sensory cells of *Micropterus dolomieui*.

95. Supporting and sensory cells of *Lepomis auritus*.

96. Facial section of supporting and sense cells of *Lepomis auritus*.

97. Supporting and sensory cells of *Lepomis humilis*.

98. Supporting and sensory cells of *Enneacanthus (Mesogonistius) chaetodon*.

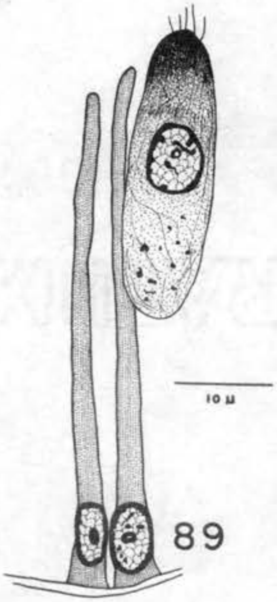
99. Supporting and sensory cells of *Lepomis macrochirus*.

100. Sensory cells of *Lepomis microlophus*.

101. Cross section of some supporting cells of *Elassoma zonatum*.

102. Supporting and sensory cells of *Lepomis megalotis breviceps*.

103. Supporting and sensory cells of *Lepomis cyanellus*.



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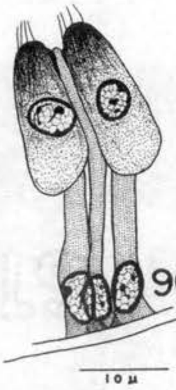

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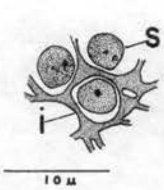

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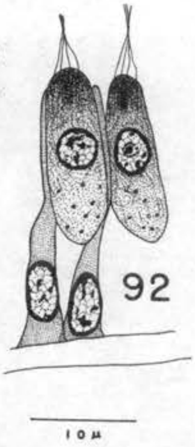

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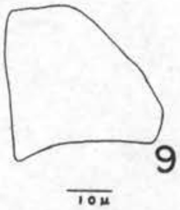

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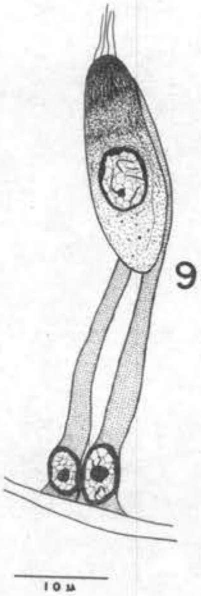

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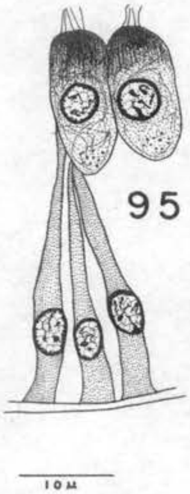

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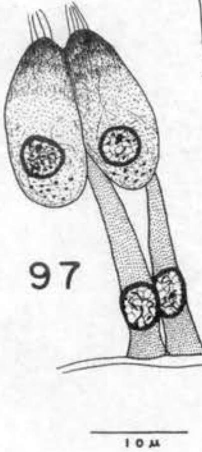

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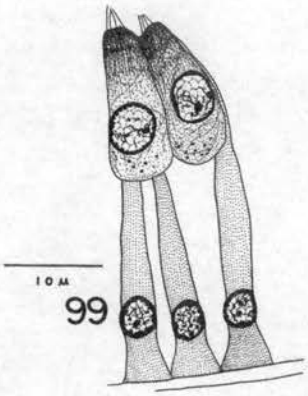

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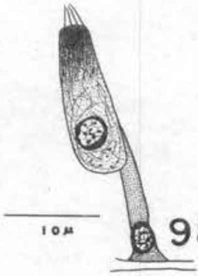

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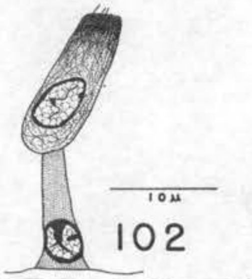

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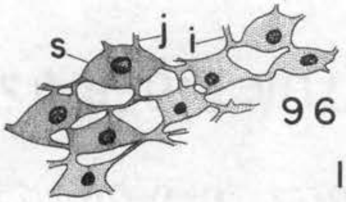

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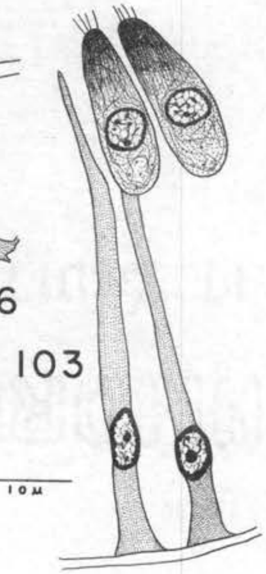

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Plate X. Cellular Components of the Lateral-Line (continued). c, cupula; co, basement membrane; cr, red blood cell; cw, canal wall; e, supporting-cell nuclear endosome; ec, epidermis; l, lumen; o, lachrymal bone; r, sensory cells; s, supporting cells; t, terminal bar.

Figure:

104. A, canal neuromast of Enneacanthus gloriosus; B, facial section of supporting cells in E. obesus.

105. External neuromast of Micropterus notius.

106. Supporting and sense cells of Lepomis punctatus.

107. Canal neuromast of Elassoma zonatum.

108. Supporting and sense cells of Lepomis gibbosus.

109. Supporting and sensory cells of Enneacanthus gloriosus.

110. Supporting and sense cells of Elassoma evergladei.

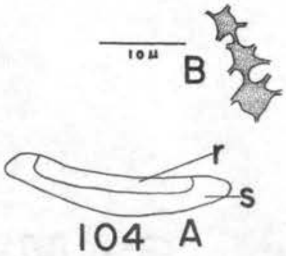
111. Canal neuromast, facial view, of Lepomis auritus.

112. Supporting and sense cells of Lepomis marginatus.

113. Cross section of lachrymal canal and organ of Acantharchus pomotis.

114. External neuromast outline of Enneacanthus gloriosus.

115. Longitudinal section of upper, anterior lachrymal lateral-line branch of Pomoxis nigromaculatus.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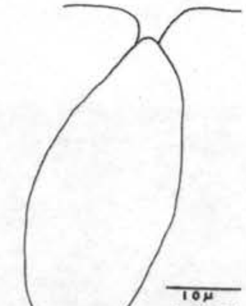
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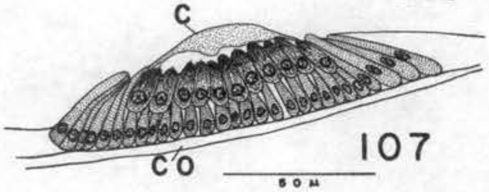
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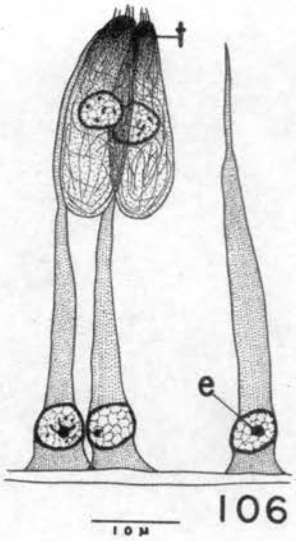
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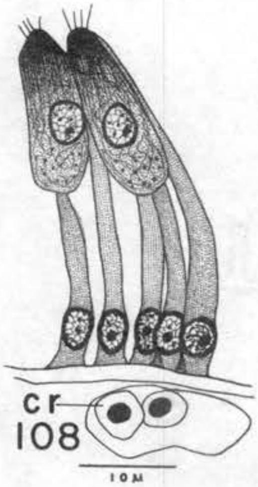
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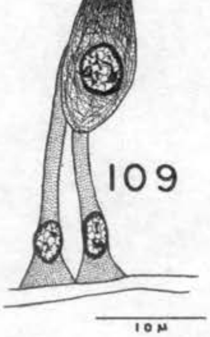
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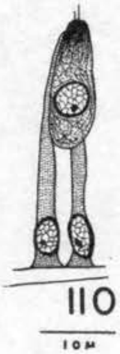
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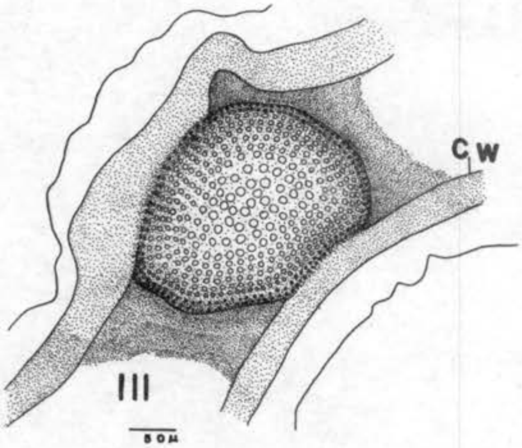
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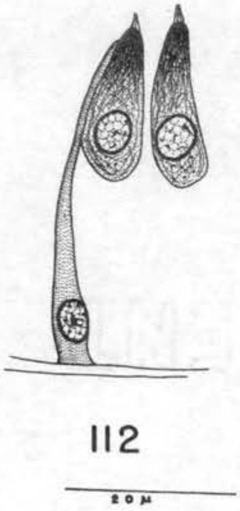
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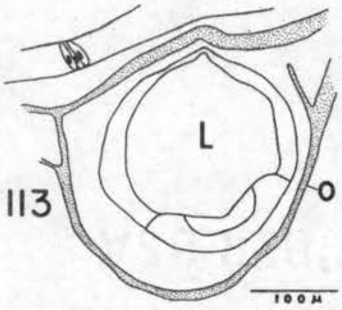
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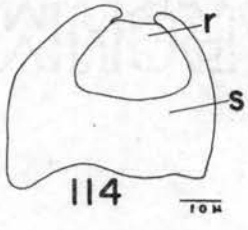
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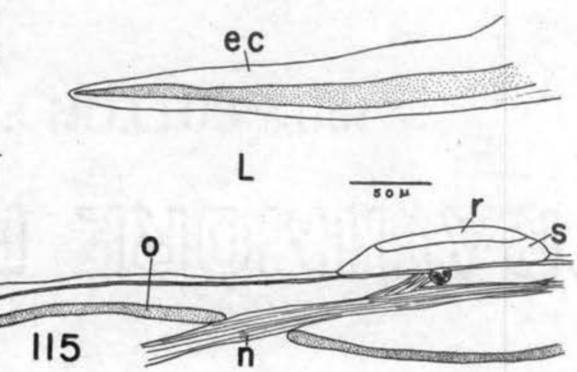
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Plate XI. Outlines of Lachrymal Neuromasts in the Centrarchidae. c, cupula; r, sensory-cell area; s, supporting cells.

Figure:

116. *Lepomis cyanellus*.

117. *Micropterus salmoides*.

118. *Micropterus coosae*.

119. *Enneacanthus (Mesogonistius) chaetodon*.

120. *Chaenobryttus gulosus*.

121. *Micropterus treculi*.

122. *Ambloplites rupestris*.

123. *Elassoma evergladei*.

124. *Lepomis microlophus*.

125. *Lepomis megalotis breviceps*.

126. *Micropterus notius*.

127. *Lepomis macrochirus*.

128. *Micropterus dolomieui*.

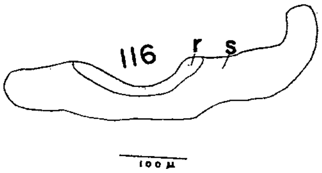
129. *Micropterus punctulatus*.

130. *Pomoxis annularis*.

131. *Lepomis auritus*.

132. *Lepomis humilis*.

133. *Lepomis punctatus*.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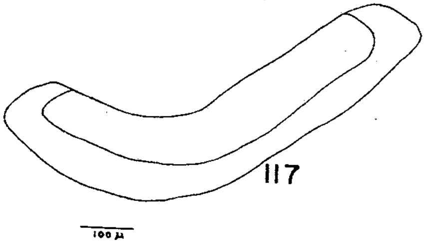
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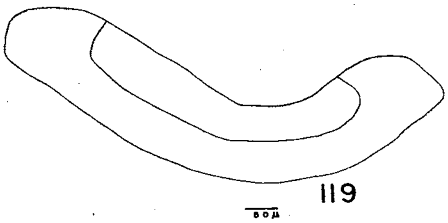
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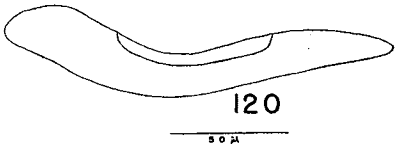
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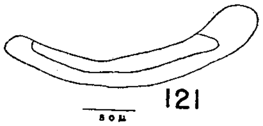
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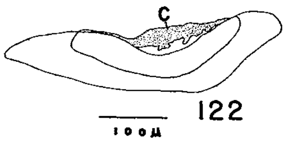
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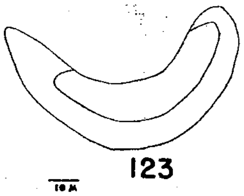
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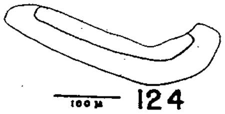
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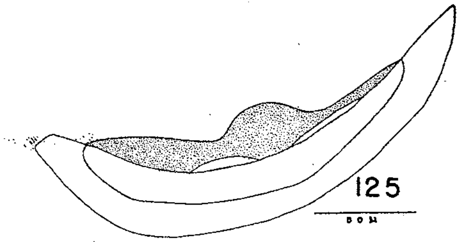
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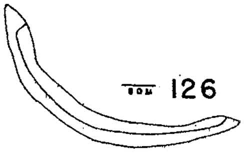
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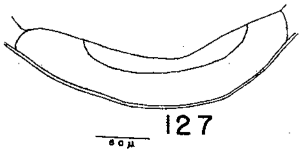
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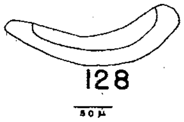
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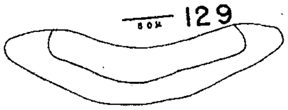
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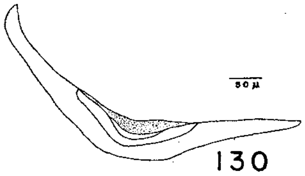
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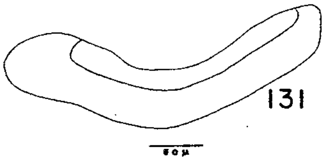
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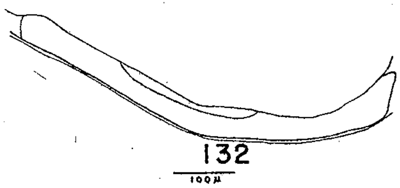
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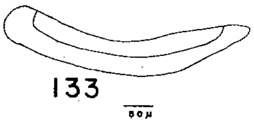
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VITA

Branley Allen Branson

Candidate for the Degree of

Doctor of Philosophy

Thesis: THE LATERALIS COMPONENTS OF THE ACOUSTICO-LATERALIS SYSTEM IN THE SUNFISH FAMILY CENTRARCHIDAE

Major Field: Zoology

Biographical:

Personal Data: Born at San Angelo, Tom Green County, Texas, 1929, the son of Branley A. and Era E. Branson.

Education: Attended grade school in Gladewater and Beaumont, Texas; Salem, Illinois; Lawton, Afton and Pryor, Oklahoma. Graduated from Afton Highschool in 1948; received the Bachelor of Science from Oklahoma State University, with a major in Zoology in May, 1956; received the Master of Science degree from Oklahoma State University, in August, 1957; and completed requirements for the Doctor of Philosophy degree in August, 1960.

Professional Experience: Electrocardiographic and field technician, U. S. Navy; served as laboratory assistant in general zoology and botany, 1952-1954, Northeastern Oklahoma A. and M. College; laboratory and research assistant in embryology, biological science and general zoology, 1954-1960, Oklahoma State University; served as lecturer in general zoology 1957-1960, Oklahoma State University, conducted taxonomic studies upon mollusks and morphological studies on fishes since 1957; took part in a collecting expedition to Sonora, Mexico, August, 1959; member of the Society for the Study of Evolution, American Society of Ichthyologists and Herpetologists, American Malacological Union; Southwestern Association of Naturalists, Oklahoma Academy of Science, Phi Kappa Phi, Sigma Xi, Phi Theta Kappa; Fellow of the Oklahoma Academy of Science (pending).