

THE INFRAORBITAL CANAL, ITS LATERAL-LINE OSSICLES AND NEUROMASTS,
IN NOTROPIS VOLUCELLUS (COPE) AND NOTROPIS BUCHANANI MEEK

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TABLE OF CONTENTS

Chapter	Page
I. INTRODUCTION.	1
II. METHODS AND MATERIALS	3
III. OBSERVATIONS.	5
A. Cephalic Lateral-line System.	5
B. Infraorbital Canal Osteology.	8
C. Sense Organs And Canal Histology.	11
IV. DISCUSSION AND CONCLUSIONS.	18
V. SUMMARY	22
VI. SUGGESTIONS FOR FURTHER STUDY	24
VII. LITERATURE CITED.	25
VIII. APPENDIX.	28

LIST OF ILLUSTRATIONS

Plates and Figures	Page
Plate I	30
Figure 1. Lateral view of the cephalic lateral-line system in <u>N. volucellus</u> .	
2. Lateral view of the cephalic lateral-line system in <u>N. volucellus</u> showing modifications in each canal.	
3. Lateral view of the cephalic lateral-line system in <u>N. buchanani</u> .	
4. Lateral view of the cephalic lateral-line system in <u>N. buchanani</u> showing typical reduction in the system.	
5. The infraorbital ossicles of <u>N. volucellus</u> .	
6. Modifications in the infraorbital ossicles of <u>N. volucellus</u> .	
7. The infraorbital ossicles of <u>N. buchanani</u> .	
8. Modifications in the infraorbital series of <u>N. buchanani</u> .	
Plate II	32
Figure 9. Transverse section through the lachrymal of <u>N. buchanani</u> .	
10. Transverse section through the lachrymal and canal of <u>N. buchanani</u> .	
11. Transverse section through the supposed jugal and superficial neuromast of <u>N. volucellus</u> .	
12. A superficial neuromast of <u>N. buchanani</u> .	
13. Sense and supporting cells in <u>N. volucellus</u> .	
14. Sense and supporting cells in <u>N. buchanani</u> .	

INTRODUCTION

In the past many investigators have speculated on whether neuromasts are the primary evocators for lateral-line bones or whether they are passively enclosed in bone. Allis (1936), Westoll (1937), Pehrson (1940 and 1944), Lekander (1949) and Branson and Moore (1962) considered the neuromasts to exert some evocating force which stimulates lateral-line bones to form. Contrary to this belief is that held by Moodie (1922), DeBeer (1937), Moy-Thomas (1941) and Parrington (1948). They argued that the neuromasts lack any tropic ability in stimulating bone formation. A third concept proposed by Stensiö (1947), according to Branson and Moore (1962), and supported by Kapoor (1962) considers the bone to be of composite origin, part stemming from anasmestic forces and part from tropic activities of the neuromasts. Whatever the case, it can be shown that when the lateral-line system degenerates or vanishes, there is a corresponding reduction or loss of associated bones (Branson and Moore, 1962).

This close association of the lateral-line system with its ossicles is well illustrated in Notropis volucellus (Cope) and Notropis buchanani Meek. It was found that N. volucellus, for the most part, has a complete infraorbital canal and a normal complement of associated ossicles. Contrary to Bailey's (1951) observation, N. buchanani very rarely has an infraorbital canal; consequently, the ossicles are degenerate and reduced in number.

Why the canal and bones develop normally in one species and not in the other is problematical. Stensiö's (1947) reasoning seems to be the

most logical explanation in elucidating the neuromast, canal, bone relationships in these fishes. The possibility that the neuromasts stimulate bone development and subsequently degenerate, leaving the bone to form without a canal (Branson and Moore, 1962), can not be completely disregarded. This contingency, however, does not thoroughly explain the problem because, frequently, portions of the canal in N. volucellus are independent of the bone, at which time they are suspended in the overlying dermis. When this condition occurs, the canal may or may not be encased by bone. The one time a tube was observed in N. buchanani indicates that it too may be fused with the ossicles or be wanting and sometimes ensheathed by bone.

To substantiate the above observations, the cephalic lateral-line system and the infraorbital canal osteology and histology are discussed here. In describing the various canal systems and the bones of the infraorbital canal, the nomenclature used follows that of Harrington (1955) with modifications from Branson and Moore (1962).

METHODS AND MATERIALS

For this study only spawning adults, 21 to 38 mm in length, were used.

To demonstrate the variability of the cephalic lateral-line system, the tubes were blown free of liquid with jets of air and, with the aid of a capillary pipette, injected with black India ink. With this method the relative completeness of the canal system and the number of pores in each could be easily ascertained. To analyze the infraorbital canal in relation to its bones, specimens were bleached in one per cent potassium hydroxide and the bones stained in situ with Alizarin Red-S. The bones were removed, mounted on 3 X 5 cards and illustrated with the aid of a camera lucida. Specimens from which the bones had not been removed were stored in glycerine for future reference.

Specimens studied histologically were fixed in either Kolmer's fluid, a histological fixative and decalcifying agent, or formalin. Formalin fixation required decalcification in two per cent hydrochloric acid.

The paraffin method was used to make serial sections of the infraorbital canal. The celloidin method was followed for studying the histological structure of the infraorbital canal and its neuromasts.

In the paraffin method, specimens were dehydrated and embedded as directed by McNamara (1931), Guyer (1953) and Weesner (1960). Of the three methods, McNamara's quick paraffin method produced the best results. Infiltration was done in vacuo as suggested by Lillie (1948) but with slight modifications. Serial sections were cut with a rotary microtome at ten

microns thickness, mounted on slides with Sass's section adhesive, stained with Mallory's triple connective tissue stain, cleared in xylene and mounted in Permount or Piccolyte.

Whole heads were embedded in celloidin according to Walls (1932), but only the lachrymal component of the infraorbital series was chosen to be studied histologically. Sections were cut with a rotary microtome at five and ten microns, stored in 80 per cent ethanol, stained with Mallory's triple connective tissue stain, cleared in beechwood creosote and mounted in Piccolyte.

All measurements of histological and bone preparations were made with an ocular micrometer mounted on a compound microscope.

The specimens for this study were obtained from collections at Oklahoma State University; Museum of Zoology, University of Oklahoma; and the University of Oklahoma Biological Station, with the data indicated below.

Notropis volucellus: Fall River, Greenwood County, Kansas; Mountain Fork River, McCurtain County, Oklahoma; Illinois River, Sequoyah County, Oklahoma; Bayou Manard, Muskogee County, Oklahoma; Blue River, Johnston County, Oklahoma; and Current River, Fulton County, Missouri.

Notropis buchanani: Verdigris River, Nowata County, Oklahoma; Muddy Boggy Creek, Caddo County, Oklahoma; Buncombe Creek, Marshall County, Oklahoma; Gaines Creek, Pittsburg County, Oklahoma; and Cache Creek, Cotton County, Oklahoma.

OBSERVATIONS

Cephalic Lateral-line System

N. volucellus, in most instances, has a complete infraorbital canal (Fig. 1) as observed by Bailey (1951). The canal begins slightly anteroventrad to the nostril, from whence it turns ventrad connecting the terminal and second pores with a short tubular segment. It then proceeds posteriad below the eye, later turning dorsad to outline the general contour of the eye. Posterodorsal to the eye, it once again bends sharply caudad, now termed the "postocular commissure" (Branson and Moore, 1962), and continues as a straight line making connection with the supratemporal canal and cephalic lateralis. The postocular commissure has been variously termed by other authors: the "lateral canal" by Hubbs and Cannon (1935), the "cephalic lateralis" by Branson (1961) and as part of the infraorbital canal by Illick (1956).

The cephalic lateralis is a short canal extending posteroventrad from the postocular commissure to the lateralis proper.

Branching off the postocular commissure-cephalic lateralis complex is the supratemporal canal. This canal begins where the postocular commissure intersects the cephalic lateralis, and terminates lateral to the parietal suture. There is no indication that this canal completely traverses the posterior portion of the skull to connect with its homologue on the other side.

The preoperculomandibular canal starts slightly posterolateral to the mandibular symphysis. Proceeding posteriad it traverses the

anteroventral portion of the preopercle. Here it turns dorsad terminating about midway up this bone.

The supraorbital canal, like the preoperculomandibular, is always incomplete, that is, it never intersects the postocular commissure. It begins slightly medial to the anterior border of the nostril. From here it proceeds posteriad, bending slightly laterad between the nostril and eye. At this point it turns mesad until past the midportion of the eye where it turns laterad, thus forming an arc over the eye. It again bends slightly mesad terminating near the suture between the frontal and parietal.

While the condition just described is the norm for N. volucellus, variations are common. For instance (Fig. 2), the infraorbital canal at times exists as a series of short tubes, some united by grooves, others independent of each other. The postocular commissure is frequently reduced to a single segment attached to the cephalic lateralis posteriad and connected anteriorly to the infraorbital by a groove. The supraorbital canal is often a series of single segments, or segments united by grooves. In this case, the grooves are open tubes through the bone proper. Occasionally this canal possesses lateral branches, or bifurcations, which are not to be confused with canaliculi. Variations in the supratemporal canal often occur, for it may be absent, composed of one or several segments, or even exist unilaterally or as a combination of any of the conditions mentioned above. The preoperculomandibular canal is more consistent in its variability, for a section of the mandibular portion large enough to contain from one to four pores is often lacking.

Excluding the rare occurrence of the infraorbital canal in N. buchanani,

departures from the norms of both species are almost negligible. Each component of the cephalic lateral-line system will, for the most part, begin, traverse and terminate in approximately the same areas as do their counterparts in N. volucellus (Fig. 3); consequently a descriptive discussion of each canal is unnecessary. Due to excessive canal degeneration, variability in N. buchanani attains greater extremes than it does in N. volucellus. In N. buchanani the entire cephalic system, with the exception of the preoperculomandibular canal, may almost totally disappear (Fig. 4). The supratemporal may vanish, as was noted in N. volucellus, the supraorbital become segmented, the cephalic lateralis disappear and the postocular commissure be represented by a short tubular segment. It is probable that the postocular commissure also completely vanishes, although this has not been observed. Variation within the preoperculomandibular canal is quite uniform, for when modifications do occur, they are similar in form and location to those noted in N. volucellus.

In both species the pore counts per canal varied within equal limits; therefore, the counts given for N. volucellus will also suffice for N. buchanani. Pores in the preoperculomandibular varied from six to 13; in the supratemporal from zero to five; in the cephalic lateralis from zero to two; and in the supraorbital from six (rarely five) to nine. Illick (1956) noted that in N. volucellus the infraorbital canal possessed 15 or 16 pores. This, however, is explained by her consideration of the postocular commissure as part of the infraorbital canal. My observations indicated that there are 11 or fewer pores in the infraorbital canal and one to five in the postocular commissure. The infraorbital canal in N. buchanani is so aberrant and inconspicuous that an accurate pore count was impossible.

Infraorbital Canal Osteology

Since the infraorbital canal is present in N. volucellus, its bones must be also (Fig. 5). The infraorbital series is composed of five ossicles. Anteriorly, the first element is the large rhomboidal lachrymal. Its canal begins on the anterodorsal corner, then, in sigmoid fashion, passes along the anteroventral border terminating on the posteroventral corner. Frequently, however, because of variability noted earlier, the canal is often incomplete, rudimentary, or, in some cases, a combination of both. When this latter condition occurs, the tubes may be connected by grooves.

Chabanaud (1945) indicated that before a bone can be designated as the jugal, a ligamentous attachment between it and the hyomandibular must be demonstrated. In N. volucellus the second element probably corresponds to the jugal as described by Harrington (1955) in Notropis bifrenatus, but as yet a ligamentous attachment to the hyomandibular has not been established. Until such a connection is verified, this element will be referred to as the supposed jugal or infraorbital 2 (postlachrymal of Chabanaud, 1945). This bone articulates anteriorly with the lachrymal and posteriorly with infraorbital 3. Since the bone is small and rectangular, being widest anteriorly, the canal traverses it in about a medial position. In most instances this bone exists as a single element, but occasionally is divided into two ossicles (Fig. 6). When this occurs, the canal's path is unaltered, that is, if the bone is of two units or a fusion of two earlier elements, the canal still traverses it medially. It should be noted that occasionally this bone may not articulate with either the lachrymal or the

third infraorbital, but rather exists as a small rudiment between them. Under this condition the entire infraorbital canal is greatly reduced.

The third infraorbital is the largest member of the series. Basically it is crescent shaped, being pointed anteriorly and becoming broader and more rounded posterodorsally. Articulated to the supposed jugal by ligaments, it gradually turns dorsally from below the eye to articulate with infraorbital 4 behind the eye. The canal enters the ossicle anteriorly from whence it turns dorsally outlining the bone's inner border.

The fourth infraorbital, situated dorsal to the third and articulated to it by ligaments, is thought to be a fusion bone composed of elements four and five (Harrington, 1955). This element is ovate to deltoid in shape with its canal as a straight tube oriented dorsoventrally along the inner margin. Frequently, however, the bone is modified for in some individuals it may be oblong, exist as two independent elements (increasing the number of ossicles to six), or even completely degenerate leaving only a tube or tubes to suggest its previous existence.

The last infraorbital ossicle is the rudimentary dermosphenotic, represented by a small bony tube. This bone, situated in the bend of the canal, is the point of demarcation between the infraorbital canal and the postocular commissure.

The number of infraorbital ossicles in N. buchanani is reduced from five as in N. volucellus to two or three (rarely 4). The two bones most consistently encountered in specimens examined were the lachrymal and infraorbital 3, both of which are smaller than those in N. volucellus (Figs. 7 and 8). Infraorbital 4 is the third ossicle that consistently appeared; however, it is seldom the same, being modified from specimen to

specimen or from side to side in an individual. In some specimens this ossicle attained two thirds the size of infraorbital 3, while in others it was represented by its two anlagen. As a result, the two primordia from which it is derived failed to develop normally, thus explaining the rare occurrence of four ossicles. One might misconstrue this extra element as being a rudimentary dermosphenotic, except that: (1) in N. volucellus infraorbital 4 manifested a similar condition; and (2) as noted by Harrington (1955) and seen in N. volucellus, the dermosphenotic is already a rudiment. Therefore, any further reduction in size would probably obliterate this tubular ossicle. Infraorbitals 2 and the dermosphenotic, (5) are apparently nonexistent, at least they were never observed. The appearance of the infraorbital canal is probably an exhibition of an ancestral character. Only one fish in all those examined possessed a portion of the canal, most of the others exhibited a condition similar to that seen in Figure 9. The infraorbital ossicles are normally deeply embedded in connective tissue without grooves or means of communication with the exterior. However, at times the lachrymal and infraorbital 3 developed grooves, parts of which were covered by bone. Whether these grooves are the result of an obliterated embryonic canal or parts of one persisting through adulthood is problematical. Nevertheless, this suggests the possibility that canals occur more frequently than previously anticipated. The one time a canal segment was observed indicated that the infraorbital canal attains fullest development around or adjacent to the sense organ. Here the neuromast was ensheathed by a series of bony fragments joined by ligamentous connective tissue (Fig. 10). Distal to the neuromast, the canal lost its connection with the lachrymal to become a connective tissue tube in the

overlying dermis. The number of bony fragments in the tube were reduced to a few scattered pieces. With this in mind, it is not too improbable that a bony fragment might be established close enough to an ossicle to become fused with it. This would result in partial roofing. Consequently, it could not be ascertained whether the roofing always occurred at the sense organ or somewhere between organs.

Although the infraorbital canal in N. volucellus is variable, it is primarily encased by bone and solidly fused to its ossicles. The only connective tissue portions along its entirety are those between ossicles. However, there were times when the bony canal did not wholly fuse with the ossicles, but rather portions between sense organs remained suspended in the above subcutaneous connective tissue. As a result, the canal manifested what Moodie (1922) has termed "drain-pipe bones." This occurrence is by no means unusual, since lateral-line canals, either connective tissue or bone, frequently traverse bones via slight grooves or depressions, as observed by Moodie (1922), Branson and Moore (1962) and Branson (1962) in other fishes. The canal is forced to return to close proximity of the ossicle in the region of the sense organ. Here the canal either fuses with the ossicle or is so situated in a groove that fusion ultimately occurs. It might be noted that at times the bony sheath surrounding the canal is partially absent, that remaining fuses with the ossicle to act as a support for the canal.

Sense Organs And Canal Histology

All of the superficial neuromasts in N. volucellus and N. buchanani are sunken into pits or crypts with their distal extremities either flush

with or slightly below the skin surface. In N. volucellus the organs are bell-shaped, ranging from 31.0 to 86.4 (average 40.2) microns in greatest diameter and from 30.0 to 47.6 (average 36.6) microns in greatest depth. Those in N. buchanani are onion-shaped, ranging from 29.5 to 71.4 (average 49.6) microns in greatest diameter and from 26.4 to 48.1 (average 34.9) microns in greatest depth. It appears that the thickness of the epidermal tissue greatly influences the shape and size of the neuromast, for in areas where the tissue is thick (33.0 or more microns), the organs are more slender than wide; but as the tissue decreases in thickness the organs become flatter and rounder. The slender organs are primarily restricted to the ventral surface of the head, while the others are characteristic of the lateral and dorsal surfaces.

The neuromasts consist of sensory cells couched among supporting or sustentacular elements. In an intact sense organ, the supporting cells do not terminate at the proximal ends of the sensory cells, but rather extend upward, as a slender process, to actually surround the latter (Figs. 13 and 14). Similar conditions were observed in centrarchids by Branson and Moore (1962). In N. volucellus the peripheral supporting elements extend above the organ forming what has been termed the "tremognostic chamber" (Branson and Moore, 1962). This condition obtains in those sense organs situated on the ventral surface of the head. Neuromasts found elsewhere are more flattened with the peripheral sustentacular cells only slightly elevated above the sense organ (Fig. 11). In N. buchanani the ventral neuromasts superficially resemble the corresponding organs in N. volucellus. However, critical analysis of the tissue surrounding the "tremognostic chamber" revealed it to be epidermal in nature

rather than consisting of peripheral supporting cells (Fig. 12). The other sense organs have their apices flush with the skin surface and the peripheral supporting elements slightly, if at all, extended above the organ proper.

Sustenacular Cells. In both species the sustentacular cells of the external neuromasts are attenuate and club-shaped (Figs. 13 and 14). For N. volucellus the cells measured 34.1 to 47.6 (average 36.5) microns in length and about 3.2 (2.1-3.7) microns in greatest diameter. In N. buchanani the cells measured 30.8 to 38.4 (average 32.6) microns in length and about 3.3 (2.1-3.9) microns in greatest diameter. The difference in average cell lengths between these fishes is due to the presence of the long peripheral supporting cells noted in N. volucellus. The nuclei, ellipsoidal in shape, are situated near the basal ends of the cells. When stained with Mallory's triple connective tissue stain, they appear light red and homogeneous throughout. The cytoplasm, too, is homogeneous (without inclusions), having a bluish hue when stained.

Sensory Cells. In both species the club-shaped sense cells are morphologically similar, being strongly polarized distally and bearing two, possibly more, "sense hairs" per cell (Figs. 13 and 14). In N. volucellus the cells averaged 15.3 (14.1-19.7) microns in length and 3.8 to 4.8 (average 4.2) microns in greatest diameter. Those in N. buchanani measured about 15.3 (13.2-14.8) microns in length and from 3.2 to 4.6 (average 3.9) microns in greatest diameter. The nuclei, situated near the base of the cells, are larger and more rounded than those in the supporting cells. When stained with Mallory's stain, there are many dark-staining bodies (chromatin or endosomes?) scattered throughout the nucleus.

The cytoplasm, containing numerous granules, gradually increases in density toward the apical end of the cell. At the tip, the granules are so concentrated and deeply stained that the cytoplasm appears solid. This, unfortunately, prevented critical examination of the sense hair bases. The "hairs" extend from the tips of the sense cells into the base of the encompassing cupula. In N. volucellus the hairs averaged 6.6 (3.1-10.9) microns in length and those in N. buchanani about 5.1 (3.1-7.2) microns in length. However, the length of the hairs is dependent upon two factors: (1) mechanical destruction of the cupula in life or during fixation, and (2) the angle at which the neuromast is cut. In the first instance, the hairs are partially or wholly obliterated with the destruction of the cupula, provided there is no tremognostic chamber or similar structure present. When the chamber is present, the hairs remain intact even though the cupula is destroyed. Vertical sections through the neuromast results in hairs of near normal size, but as the cut becomes more acute, error in hair length increases. Therefore, it is felt that the averages given above are misleading and should be considered conservative estimates of actual hair length.

Since the appearance of an infraorbital canal in N. buchanani is a rare occurrence, only the infraorbital canal of N. volucellus is here discussed. Before actively discussing the histology of the canal and its neuromasts, it is worth while to note the position and number of sense organs contained therein. One can usually estimate the number of sense organs in the canal by counting the number of ectopic pores, since, under normal circumstances, a single neuromast is located between two consecutive pores. However, this method is frequently in error, for the space between pores is sufficiently variable that two organs, rather than the normal one,

may appear. Disregarding canal variability, the infraorbital canal normally possesses 10 organs, one between each two pores, but as many as 14 were observed.

The neuromasts, contained within well-defined canals, are structurally similar to the superficial organs, but generally larger. The quarter-sphere bowl-shaped organs averaged 72.5 (62.0-82.8) microns in diameter and 25.9 (21.6-32.5) microns in depth. This odd shape is attributed to the organ having to conform to the curvature of the canal. As illustrated in Figure 11, the sense cells are not as localized as, and are more numerous than those of external organs. The number of sense cells per section is usually 14 while there are five to seven per section in the unprotected organs. However, the number of supporting cells in each is not sufficiently different, although the increase in receptor cells has resulted in the loss of the tremognostic chamber.

The cells of the canal neuromast are essentially like those in unprotected organs. The attenuate club-shaped sustentacular cells averaged 13.8 (12.4-15.6) microns in length and 4.2 (3.6-4.8) microns in greatest diameter. At first glance the cells appear cuboidal, but analysis of partially fragmented organs revealed slender processes extending upward to surround the distal elements. The cytoplasm is of the same relative consistency referred to earlier. The nuclei, situated basally, are ellipsoidal and homogeneous.

The sense cells, like those noted earlier, are club-shaped with two apical "sense hairs." The cells averaged 14.8 (13.9-16.0) microns in length and 4.7 (3.2-6.2) microns in greatest diameter. The cytoplasm contains numerous supranuclear granules which gradually become concentrated distally, hence the cells appear polarized. The major difference between

internal and external sense cells is the size of the "sense hairs." The "hairs" of canal sense cells are shorter and, when viewed with high power or oil immersion objectives, are aggregated into cones, the "triangular structures" of Branson and Moore (1962). The hairs measured 5.8 to 8.6 (average 7.0) microns in length. It has been noted that the hairs of external sense organs remain independent of each other when the cupula is destroyed, provided the tremognostic chamber is present. However, the cupula within the canal is not subject to mechanical destruction, but rather shrinkage during fixation. Hence, shrinkage is probably the cause of the sense hairs being pulled together in the form of a cone.

Moore (1956), Branson and Moore (1962), and to a lesser extent Maximow and Bloom (1944), and Greep (1954) illustrated intercellular bridges between sustentacular elements. Attempts to demonstrate similar structures in the superficial and canal neuromasts of N. volucellus and N. buchananii failed.

Generally the connective tissue portion of the canal is composed of two tissue layers, the inner being separated from the outer by the basement membrane. Throughout its entirety, the inner layer is largely simple cuboidal epithelium and scattered goblet cells, but as the neuromast is approached, the number of goblet cells increases and the tissue becomes pseudostratified (Fig. 11). At the ectopic pores, the cuboidal epithelium gradually merges with the stratified squamous epithelium of the skin. The outer layer appeared to be composed of loose areolar connective tissue. Directly beneath the sense organ is a foramen through which the lateral-line nerve and blood capillaries pass. According to Branson and Moore (1962), the nerve penetrates the basement membrane and loses its myelin

sheath before innervating the sense organ. This, however, is not always true, for occasionally suspended within the areolar connective tissue is an interceding structure (Fig. 11). This structure, with dimensions varying from organ to organ, is composed of many cell bodies. The lateral-line nerve enters it basally, splits into fibers and passes out distally to innervate the organ. Whether this structure is functional (ganglion?) or not is problematical, but heretofore no similar structure has been reported.

DISCUSSION AND CONCLUSIONS

The problem of lateral-line bone formation revolves around whether or not the neuromasts are the primary evocators for bone development. From taxon to taxon, the impetus for bone formation may be derived from varying sources, hence authors have contrasting ideas concerning bone origin. Briefly reviewing these ideas, some authors contend that the sense organs are the primary evocators for bone development; some assert that the organs are only passive in stimulating bone formation; and others believe that the ossicles are of composite origin, part stemming from anasmestic forces and part from tropic activities of the neuromasts.

Allis (1936), Westoll (1937), Pehrson (1940 and 1944), Lekander (1949), and Branson and Moore (1962) showed that during ontogeny skin neuromasts sink beneath the skin surface to become intrenched in connective tissue canals; osteoblasts then accumulate around their bases to become the bone primordia. However, if during phylogeny the primordia became established and the original evocating force destroyed, the bones would continue to develop, but without canals or neuromasts. Further modification ensues when the skin neuromasts fail to invaginate. Without this initial evocating force, bones fail to develop.

Moodie (1922) indicated that the deposition of calcium salts in the inactive connective tissue surrounding the canal resulted in a solid matrix. This bony case rather than a neuromast is the directive force for further ossicular development. Parrington (1949), with a slightly different approach, contended that precursors for dermal bone formation are in position before the lateral-line organs are established. The bone has already

begun its development before the sense organs are capable of initiating any evocating response. This lead him to conclude that dermal bones influenced the course of the lateral-line canals rather than the canals influencing the position of the dermal bones. To justify this statement, he hypothesized that "fields," whose centers are the centers of future dermal ossification, have the "property of deflecting branches of the lateral-line growing towards them." This assumption, he said, would explain why lateral-lines normally pass through centers of ossification as well as those that endow the lateral-line with the ability of affecting the position of dermal bones. DeBeer (1937) indicated that dermal bones are not dependent upon neuromasts for their origin, because homologous bones in higher vertebrates develop without lateral-lines and that the sense organs serve to determine the localization of bone primordia.

Stensiö (1947), according to Branson and Moore (1962), and Kapoor (1962) reasoned that neuromasts stimulate bone formation in limited areas around themselves and the canal; the bone proper originates from anasmestic sources. Kapoor, working on Ophicephalus punctatus, indicated that the membranous frontal develops before the supraorbital canal. Later, latero-sensory components arise from the underlying bony plate and fuse with each other to form the characteristic bony tube around the canal. He concluded that neither the membranous bones nor the latero-sensory components of dermal bone originate from morphogenetic activities of the canal neuromasts. The value of the sense organ in the development of these bones is limited to the extent that it exerts some kind of tropic influence for stimulating ossification in its immediate neighborhood.

All three hypotheses are, at one time or another, equally applicable

to some condition in N. volucellus or N. buchanani. It was noted in N. buchanani that the lachrymal and infraorbital 4 are reduced in size and that canals are rare. It was also pointed out that the supposed jugal was never observed. Both examples tend to imply that during phylogenetic development two things have occurred: (1) During the evolution of the species, the failure of skin neuromasts to invaginate has resulted in the loss of infraorbital 2, and (2) the primordia from which the remaining ossicles develop have persisted, but the canal and neuromasts have degenerated. However, this idea fails to explain the frequent occurrence and variability of infraorbital 4. Moy-Thomas (1941) showed that when the supraorbital canal is artificially interrupted, the frontal continues to develop although never reaching normal size. Applying these results, one might be tempted to assume that the sense organs are passive in stimulating, and active in insuring complete development of the ossicle. Hence, the presence of the canal in N. volucellus and its absence in N. buchanani could account for the difference in bone size between species.

In N. volucellus the only portions of the infraorbital canal consistently associated with the ossicles are the areas around sense organs; the other portions are free to "wander" through the overlying connective tissue. Obviously, the idea of the canal stimulating bone formation (Moodie, 1922) can not be applied here. Furthermore, it is felt that neuromasts lack any tropic ability in stimulating bone development. Occasionally, in N. volucellus a neuromast and its bony case are independent of, but allied to the ossicle. The space separating them is small enough that the slightest deposition of bone results in fusion. This suggests that

the evocating powers of the sense organs are restricted to the development of a bony canal rather than the ossicles. Such cases have lead me to conclude that Stensiö's (1922) scheme of composite origin is the most applicable in elucidating the relationships between the neuromasts and bones in these fishes.

In N. volucellus and N. buchanani lateral-line morphology can be correlated with habitats. N. volucellus, being predominantly a moving water species (Moore and Paden, 1950; Cross and Moore, 1952; Linder, 1955; and Trautman, 1957), conforms to the generality that fishes living in moving water or fishes that are continuous swimmers have well-developed lateral-line systems (Lowenstein, 1957). In N. buchanani the loss or near loss of the infraorbital canal and the reduction and disappearance of associated ossicles is attributed to its sluggish water environment. Lowenstein (1957) pointed out that secondary reduction in the lateral-line system is typical of quiet water species with sedentary or sluggish habits. Hence, it is felt that N. buchanani is a recent phylogenetic derivative of N. volucellus and that invasion of lotic environments is resulting in the loss of the lateral-line system.

SUMMARY

1. In Notropis volucellus and Notropis buchanani the lateral-line systems are basically alike. However, major differences do occur: (1) the lateral-line reaches greater degrees of degeneration in N. buchanani; and (2) the infraorbital canal is complete or incomplete in N. volucellus, but absent or rudimentary in N. buchanani.
2. In N. volucellus there are five infraorbital ossicles: the lachrymal, supposed jugal, infraorbitals 3 and 4, and the dermosphenotic. In N. buchanani the number is reduced to two or three (rarely 4). Those consistently present are the lachrymal and infraorbital 3. It is believed the jugal and dermosphenotic are non-existent. Infraorbital 4 is extremely variable, seldom remaining constant within or among individuals.
3. The infraorbital canal in N. volucellus is not confined to its ossicles, but rather free to "wander" through the overlying connective tissue. The only portion that is always associated with the ossicle is the area surrounding the neuromasts. Although the infraorbital canal was observed in N. buchanani only once, it indicated that the sense organs are confined to the ossicles, but the portions between organs are not.
4. The superficial sense organs in both species are essentially alike, except that the peripheral supporting cells in N. buchanani are not appreciably elevated above the sense cells to form a tremognostic chamber as seen in N. volucellus. The supporting cells have long

processes which extend upward to surround the sense cells. On each sense cell there are two "sense hairs."

5. In N. volucellus the canal neuromasts are structurally similar to the superficial organs. The number of sense cells has increased without apparent increase in supporting cells. There are two "sense hairs" per sense cell. The "hairs" are aggregated into "cones" instead of being independent like those in superficial organs. This is attributed to cupular shrinkage rather than mechanical destruction of the cupula.
6. A cellular enlargement in the innervating nerve of the canal sense organ was described. So far as known no similar structure has been described in the literature.
7. Of the three hypotheses concerning the evocating properties of neuromasts, the idea of composite origin (Stensiö, 1922) best explains the neuromast-bone relationships in these fishes.
8. N. buchanani is considered a recent phylogenetic derivative of N. volucellus. Invasion of sluggish or calm water has resulted in secondary degeneration of the canal system in N. buchanani.

SUGGESTIONS FOR FURTHER STUDY

1. The embryological development of N. vollucellus and N. buchanani should be studied to determine: (a) whether or not the primitive ear and lateral-line organs are derived from the same placode; (b) the method and direction of migration of the neuromasts from their point of origin; (c) if the infraorbital ossicles are dependent upon neuromast stimulation or if the former develops independently of the latter; and (d) if the swelling in the nerve of the canal sense organ is homologous to a ganglion.
2. It would be interesting to establish if there are heteromorphic "sense hairs" on each sense cell. To further expand this idea, it would also be advantageous to know if the sense cells are heteromorphic, that is, are there cytological differences between cells which could suggest delegation of function within a sense organ.

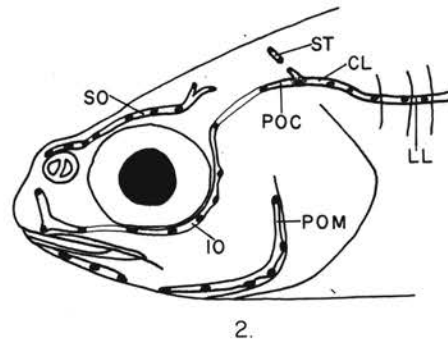
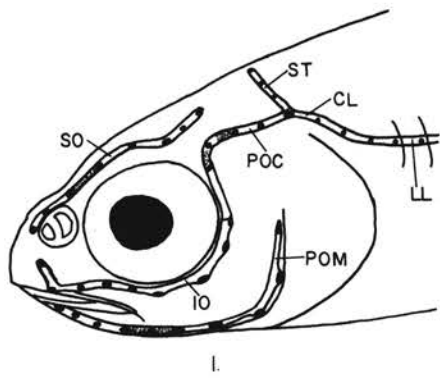
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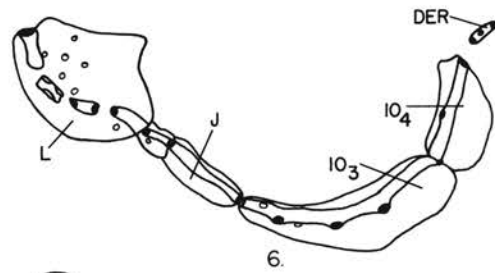
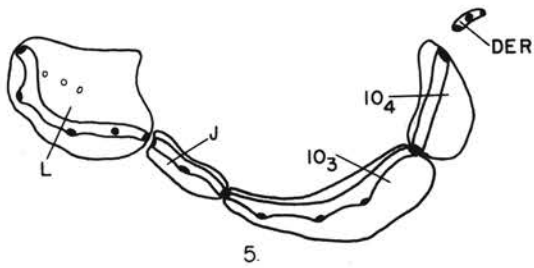
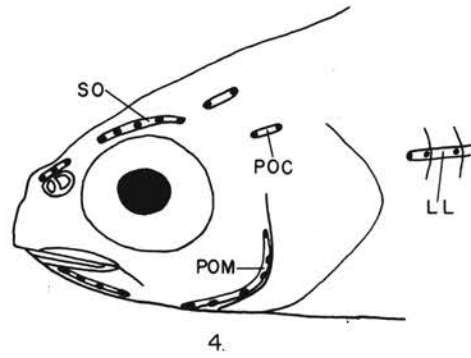
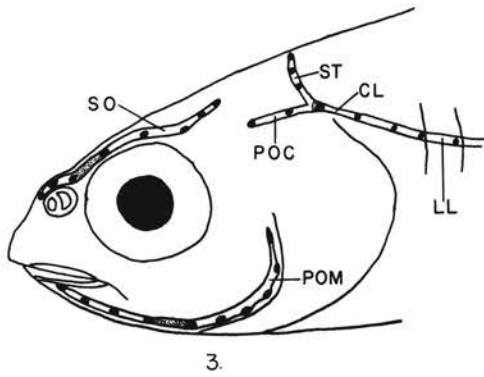
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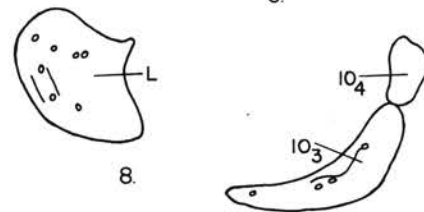
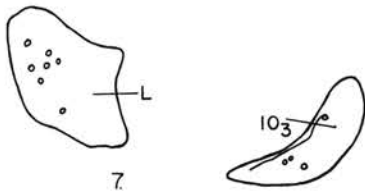
APPENDIX

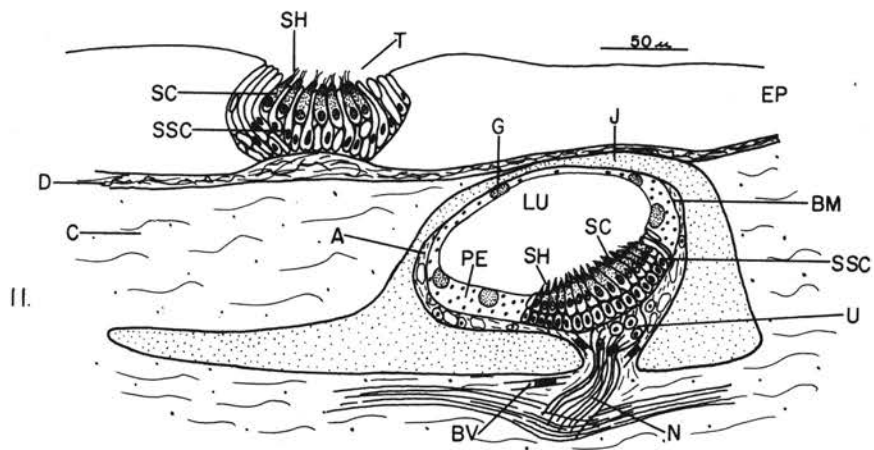
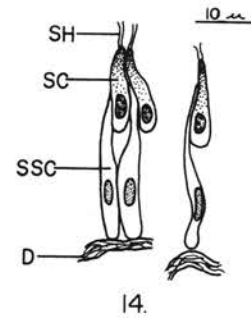
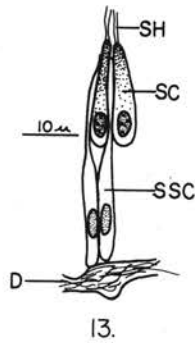
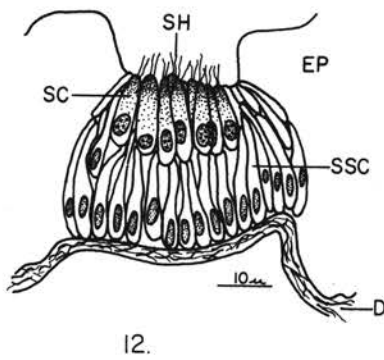
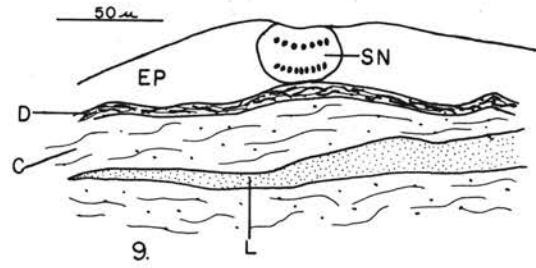
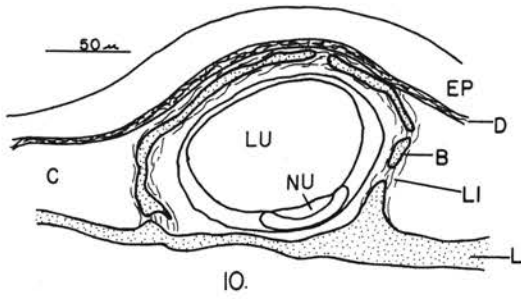


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VITA

Harley Wayne Reno

Candidate for the Degree of

Master of Science

Thesis: THE INFRAORBITAL CANAL, ITS LATERAL-LINE OSSICLES AND NEURO-
MASTS, IN NOTROPIS VOLUCELLUS (COPE) AND NOTROPIS BUCHANANI
MEEK

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