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The Lateral Line System in Siluroids

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THE LATERAL LINE SYSTEM IN SILUROIDS

BY

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A. B. Tufts College, 1914

THESIS

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I HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER MY SUPER-
VISION BY James Ernest Kindred

ENTITLED The Lateral line System in Siluroids.

BE ACCEPTED AS FULFILLING THIS PART OF THE REQUIREMENTS FOR THE
DEGREE OF Master of Arts.

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*Required for doctor's degree but not for master's.

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THE LATERAL LINE SYSTEM IN SILUROIDS

Introduction.

This paper describes the topography, histology, innervation and later development of the lateral line system of *Amiurus catus*. The lateral line system has long been a favourite problem of the morphologists and has been studied in all classes of fishes and in some of the Urodele Amphibia. Leydig (1868) gave an impetus to the study of this system, when he pointed out that the so-called mucous canals of the Ichthyopsida did not secrete mucus, but were sensory in character. Yet the majority of investigators have referred to the lateral line as a field in which, though much has been done, there is still a large opportunity for study. Few have dealt with all the morphological features of this system. R. Ramsay Wright (1884) gave a short description of the topography of the canals in *Amiurus catus*, but paid more attention to a detailed description of the histology of the skin and the sense organs of the lateral line canals. Herrick ('01) gives the topography and innervation of the lateral line system in *Amiurus melas*. Other descriptions of the lateral line in the Siluroids have been given by Pollard (1880), Bunker (1897), Collinge (1894), and Allis (1897). Aside from these I find no mention elsewhere of the system in the Siluroids. Historical accounts and summaries of the researchers in the field of the lateral line will be found in Collinge (1894), Cole (1896), and Clapp (1897).

I. Method of Study.

The specimens were studied both by dissection, surface views, and by section. The following method was used in the preparation of specimens for section: the larger fishes of thirty or more mm

in length were decalcified in Gage's decalcifying fluid for ten days and after being washed thoroughly in running water were placed in Delafield's haemotoxin in 70% alcohol for four days, until the parts were entirely stained. They were then washed in running water, dehydrated, cleared, imbedded and cut in sections in whatever plane desired, usually at a thickness of fifteen μ . The sections were differentially stained in a 1% solution of erythrosin in 95% alcohol. The smaller forms were treated in the same way, but without decalcification. From these sections the course of the canals, their innervation and the positions of the sense organs were reconstructed. Several small specimens were dissected under the binocular microscope to verify the reconstructions.

II. Adult Form. (a) General Description.

In an adult *Amiurus catus*, numerous pores are scattered over the surface of the head and body. Certain of these are arranged in regular rows: one row above the eye, another below it, and one on the ventral side of the lower lip, which extends up into the operculum, and the well-known lateral line along the side of the body. Other pores very much smaller and scattered irregularly over the head, operculum and barbels, are the openings of terminal buds, described for *Amiurus* by Wright. The lateral line pores are the external openings of tubules which lead into the canal system beneath the skin. These pores are never part of a dendritic system of tubules as are the surface pores of *Amia calva*, but open directly into the canal by a longer or shorter tubule.

In fresh or alcoholic specimens, the pores of the lateral line canals have a whitish border, due to the absence of pigment in that region, and, when fully formed are approximately circular

in outline. Although different in shape in different individuals or even on opposite sides of the head in the same individual, the pores are normally definite in number and position. In adults the greater part of each canal into which these pores lead is enveloped in the bones of the head and certain of these bones are developed only for the support of the canals. A tubule is always given off from the canal when it passes from one bone to another, but tubules may penetrate the bone itself. The canals appear long before there is any trace of bone, hence, as is well-known, the bone in which it is enclosed must grow around it.

(b) Course of the Canals.

On each side of the head are the three well-known canals: the infraorbital, supraorbital and operculo-mandibular, and, on each side of the body the main body canal. The relations of these canals to each other, their sense organs and innervation are shown in figure 1 (Plate I).

The infraorbital canal of the adult curves backward and downward from the first suborbital bone below the anterior naris, passing through the second, third, fourth and fifth suborbitals below the eye. At the junction of the fifth and sixth suborbitals it turns upward at right angles, and, passing through the sixth and seventh suborbitals, joins the supraorbital canal in the frontal bone, posterior to and above the eye. From this union the canal continues backward through the post-frontal to join the operculo-mandibular canal in the squamosal. From here it courses through the extrascapular and post-temporal bones and bending downward behind the opercular flap, lies below the epidermis the remaining length of the body.

The supraorbital canal starts in the nasal bone above the anterior naris, and, curving upward, enters the frontal in which it continues until its union with the infraorbital canal as described above. Above the middle line of the eye, a transverse canal, slightly enlarged in the middle, connects the supraorbitals of the two sides; this is the only connexion of the systems of the two sides of the body. In this respect *Amiurus* differs considerably from *Amia*, in which there are two commissures, one in the extrascapulars and one in the ethmoid. In *Amiurus* the commissure crosses in the region of the frontal bones and corresponds to the frontal cross commissure which Pollard figures for *Clarias* and *Chaetostomus*. Collinge mentions such a canal for *Amiurus*, but did not describe its position; neither Herrick or Wright found such a cross commissure. Figure 2 (Plate II) shows the relation of the frontal cross commissure in *Amiurus catus*.

Beginning on the ventral tip of the dentary bone a little to one side of the middle line, the operculo-mandibular canal follows the margin of the dentary and passing through the articulare, curves upward into the preopercular bone. Passing from the preopercular it enters the squamosal region and unites with the continuation of the supra and infraorbital canals, ventral to the upper end of the operculum.

The main body canal has been described in connexion with the infraorbital canal.

(c) Surface Pores of the Canals.

The peripheral canal system is represented on the surface of the head by distinct lines of pores, the number of which can be easily determined by the examination of the skin in adult forms. This arrangement in the adult is shown in figure 1 (Plate I).

The most anterior pore of the infraorbital canal is large; it lies behind the anterior naris and its tubule connects in the first suborbital bone with the canal. The second pore is posterior to the anterior naris and its tubule connects with the canal through the suture between the first and second suborbital bones. The third, fourth, fifth, sixth, and seventh pores all open into the canal through sutures between the corresponding suborbital bones. The third pore lies below and anterior to the eye; the fourth below the eye and above the angle of the mouth, the fifth a short distance behind this; the sixth posterior to the eye and slightly above the fifth; the seventh and last pore posterior to and above the line of the eye.

The supraorbital canal starts with a pore in the nasal region, anterior to and above the anterior naris; the tubule, after penetrating the dermis, enters the nasal bone. The second pore lies close behind the anterior naris and its tubule also connects with the canal in the nasal bone. The third pore, median to and above the posterior naris, leads into the canal between the nasal and frontal bones. The fourth pore is situated above the roof of the cranium in the transverse plane passing through the middle of the eyes and penetrates by its tubule the frontal bone, to enter the canal. Behind the fourth pore the canal bends downward, and, in the posterior part of the frontals gives off along horizontal ^{tubule} to pore five, which lies some distance posterior to and above the line of the eye.

The operculo-mandibular canal begins in front with a large rounded pore on the ventral side of the lower lip at the tip of the dentary bone. It is terminal in character and has no connexion with its fellow of the opposite side of the head. The

second and third pores lie above the origin of the barbels of the lower lip and open into the canal through the dentary bone. The fourth pore lies anterior to and below the angle of the mouth and its tubule also passes into the canal through the dentary bone. The fifth pore is immediately posterior to it and its tubule leads into the canal between the dentary and articulare bones. The tubule from pore six enters the canal as it passes from the articulare into the preopercular bone. Pores seven, eight, and nine lie in the operculum, one above the other, and open into the canal through the preopercular, with the exception of pore nine which connects with it at the junction of the squamosal and preopercular bones.

Herrick says that the first pore of the body canal has anastomosed with the ninth of the operculo-mandibular canal. If this is to be assumed, then the next surface pore above the operculum is the second pore of the body canal and leads into the canal by a tubule, between the squamosal and extrascapular bones. The third pore lies below this and connects with the canal at the anterior end of the post-temporal bone. Pore four is still further ventral and connects with the canal between the post-temporal and the first lateral line ossicle. The fifth pore lies above this and leads into the canal between the first and second lateral line ossicles. Behind the second lateral line ossicle the canal passes below the epidermis and thereafter a pore and sense organ occur in each segment of the body.

(d) Sense Organs of the Canals.

Between each two consecutive dermal tubules along the entire length of each canal, there is a single sensory spot or patch

containing a well-developed sense organ or neuromast. In most cases this sense organ is followed by a surface pore, but the fourth sense organ of the supraorbital canal and the first one of the body canal are followed by a union of the canals instead. As this condition is not found in the larval form that the pores following these two sense organs have anastomosed with the terminal pores of the adjacent canals as is true in *Amia*. Therefore the pore which originally followed sense organ four of the supraorbital canal with the terminal pore of the infraorbital canal and the double pore so formed has closed over and sunk below the surface. In the case of the first sense organ of the body canal, the pore following it is assumed to have united with the ninth pore of the operculo-mandibular canal and has remained on the surface.

In a transverse section through a sense organ in the head region (figure 1; Plate II) the upper half of the wall is formed by a continuation of the Malpighian layer of the epidermis. The specialized epithelium, neuro-epithelium, containing the sense organ projects inward so that the cavity of the canal is lessened at this place. Two kinds of cells, sensory and supporting occur in the neuro-epithelium. The sensory cells occupy the inner of the neuro-epithelial lining, the remainder being constituted by supporting or indifferent cells, some of which extend the whole height of the neuro-epithelium, though all have a nucleus in the basal end. The sensory are short and pear shaped with a large rounded nucleus in the basal part of the cell and all bear a sensory hair on the free surface. Here and there between the cells are rounded structures with a deeply staining centre.

Wright suggests that these may be nerve fibres in cross-section but in my preparations they are much too large to be regarded as such.

The distribution of the sense organs throughout the canals and bones is shown in figure 1, (Plate I). Their position is as follows:

The first sense organ of the infraorbital canal lies on the median side of the canal in the first suborbital bone. The remaining five sense organs of this canal lie in the corresponding suborbital pores and between each two consecutive pores.

The first and second sense organs of the supraorbital canal occur in the nasal bone between the first, second, and third pores respectively. The third sense organ lies in the frontal bone anterior to the frontal commissure and the tubule to pore four. The fourth sense organ is anterior to the union of the supraorbital and infraorbital canals, but unlike all the others of this canal is not followed by a surface pore, as explained above. The fifth sense organ also lies in the frontal bone, but differs from the others in that it is enclosed in the wall of the tubule leading from the fifth pore to the canal.

Sense organs one, two, three, and four of the operculo-mandibular canal are situated in the dentary bone between pores one, two, three, four, and five respectively.

The first sense organ of the body canal has its position in the squamosal part of the canal, anterior to the junction of the body and operculo-mandibular canals. The second sense organ is near the posterior part of the squamosal and the third in the extrascapular between pores two and three. The fourth and fifth

sense organs in lateral line ossicles one and two respectively, while the remaining ones are distributed one in each segment throughout the rest of the canal as it courses below the epidermis, though not protected by scales as in *Amia*.

(e) Innervation of the Canals.

It is a well-known fact that all the sense organs belonging to the canals are innervated by branches of the cranial nerves, and in *Amiurus* as elsewhere, the entire lateral line system is innervated by the branches of three cranial nerves; the facialis, the glossopharyngeal, and the vagus. Four branches of the facialis innervate all the branches in the head region as shown in figure 1 (Plate I). A short ganglionated branch of the glossopharyngeal innervates the second sense organ of the body canal; and the remaining sense organs of the body canal are innervated by the lateralis branch of the vagus nerve. After innervating the sense organs, the nerves terminate anteriorly in terminal buds, described for *Amiurus* by Wright and Herrick.

The sense organs of the supraorbital canal are innervated by the opthalmicus superfacialis branch of the facialis nerve, a separate twig being sent from the main branch to each sense organ. Each twig pierces the osseous ring surrounding the canal and proceeds to the base of the sense organ. In all of the canals there is a similar punctuation of the osseous envelope by the twig. Sense organ one is innervated by short twig which passes downward from the main nerve to the base of the sense organ between the anterior and posterior nares. The twig for sense organ two arises from the opthalmicus superfacialis where the nerve crosses to go below the canal. The twig for sense organ

three arises above the middle of the eye. After the nerve has crossed to below, innervating sense organ four as it crosses, a twig is given off to sense organ five. Some distance further back this branch enters the ganglionic complex of the facialis nerve without giving off any other twigs.

The sense organs of the infraorbital canal are innervated by the buccalis branch of the facialis nerve, which passes median to the orbit and innervates the sense organs by longer twigs than those of the ophthalmic branch. The twig to the first sense organ is given off in the transverse plane of the posterior naris and continues forward to its connexion with the base of the sense organ. The main nerve proceeds beyond the sense organ into the snout, where it innervates some of the terminal buds. The twig to sense organ two arises just anterior to the eye. Sense organ three is innervated by a twig which has its origin back of the eye and which runs forward and downward to its termination. The twig to sense organ four crosses the posterior ventral half of the orbit, emerging about the middle of its lower surface to run to the adjacent sense organ. The twig to sense organ five arises above and behind the eye and runs obliquely forward and downward to the corresponding organ below the eye. The twig to sense organ six, which is the shortest twig of this nerve arises just above the union of the supraorbital and infraorbital canals.

The sense organs of the operculo-mandibular line are innervated by the mandibular externus branch of the facialis nerve. Arising dorsal to the complex of the other two branches, this one crosses them and extends almost perpendicularly downward in the opercular region until it gives off a branch to the sixth sense

organ. Then it bends and pursues a course almost at right angles to its previous direction, nearly parallel to the canal in the lower jaw. The twigs to sense organs one to five are short, that to sense organ six is longer than the others. It arises at the point of strongest curvature of the nerve. The twig to sense organ seven arises above it, while the twig to sense organ eight arises a little below the beginning of the body canal.

The first sense organ of the body canal is innervated by a short branch of the ramus oticus of the facialis nerve. The second sense organ is innervated by a short ganglionated branch of the glossopharyngeal nerve. The remaining sense organs of the body canal are innervated in regular sequence by twigs from the lateralis branch of the vagus nerve.

III. Larval Forms.

Solger and Allis say that the canals and their sense organs in bony fishes and in *Amia*, are formed in the following manner: at first the sense organs are independent, differentiated hill-ocks of ectoderm connected to each other by the white cord of sensory cells. Each sense organ sinks into a pit, carrying the basal layer of the epidermis with it as in figure 2, (Plate I) ; the pit now elongates, the sides rise above the sense organ and fuse along the middle line, leaving an opening at each end. These are half pores and each unites with the half pore of the adjacent sense organ to form a whole pore and make a complete canal. The whole pore in *Amiurus* never divides dendritically, but remains simple in the adult as in the larva ; differing in this respect from *Amia*.

In a young *Amiurus catus* ten millimeters long, the pores

already formed were edged with white. The sense organs were just beginning to be enclosed and some which were not yet enclosed were visible. They lie in grooves or pits just below the outer surface of the epidermis, are white and are connected to the other sense organs of the same canal by a white cord of cells. In figure 2, (Plate I) the canals are shown in process of formation in a specimen ten millimeters long, and may be described as follows:

The first pore of the infraorbital canal, always a half pore as it can unite with no other, lies posterior to the anterior naris. Pore two is in process of formation by the union of the posterior half pore of sense organ one and the anterior half pore of sense organ two. The two half pores forming it are elongated and the posterior of the two, is connected with the succeeding half pore by the line of closure, which was the result of the division of the primary pit of sense organ two. The pit of sense organ two has its sense organ at the bottom, still visible from the exterior. No division has yet begun, and the same holds true for all the other pits of this line. When this pit of sense organ three divides, the anterior of the two resulting pores will move forward to unite with the posterior half pore of sense organ two, mentioned above. The pit of sense organ three and the succeeding pits are connected by a white cord of cells, and at this stage supraorbital and infraorbital canals are not connected.

The first pore of the supraorbital line, really a half pore, is fully formed and circular in outline and lies in front of the anterior naris. The second pore also completed in the same

way as described for pore two of the infraorbital and is situated behind the anterior naris. Pore three is very near completion, as the half pores which form it have almost coalesced. The posterior half pore of sense organ three lies above the eye on the lateral edge of the cranium and the anterior pore of sense organ five is just separating from pore five, also a half pore in the adult. There is no trace of a frontal cross-commissure in this stage of development.

The first, second, and third pores of the operculo-mandibular canal completely developed at this stage and occupy the same positions as they do in the adult. The fourth pore is almost formed and the fifth is a little behind this in development. Pore six is also near completion. One half pore of sense organ six, the posterior one, is connected to sense organs seven and eight by the white sensory cord. The first sense organ of the body canal is being enclosed and the half pores from its pit are separating. The same is true of sense organs two, three, and four; these are all the parts yet formed of the body canal.

On the whole, the canals at this stage are not very far developed and there is no connexion between the canals such as exists in the adult. The sense organs are in the same position as in the adult, and when the canal is formed by the division of the pit, lie between two pores. The plan of formation is the same as that described in bony fishes and the condition in this larval form is similar to that of the adult *Esox lucius*, where the canals are not connected with each other.

IV. Comparisons With Other Forms.

A comparison of the arrangement of the lateral line system

in *Amiurus catus* and that described for *Clarias* and *Auchenaspis*, African and South American Siluroids, shows a general morphological agreement. There is, however, a difference in the details of the arrangement of the sense organs and the pores. In *Clarias*, there is a frontal cross-commissure, such as I have found in *Amiurus*, and there are sense organs in certain parts of the canals, which are not followed by peripheral pores, as is true in *Amiurus*. These differences can be better studied by comparing the figures of Pollard and figure 1 (Plate I) of this paper. The canals traverse the same bones in both forms and the innervation is similar. The supraorbital canal has five surface pores and six sense organs in *Clarias*, while in *Amiurus* there are five pores and five sense organs. If we assume that primitively there was one more pore than there were sense organs, then in *Clarias* two pores have disappeared in this canal and in *Amiurus*, one. In *Amiurus* there is a pore just anterior to the frontal cross-commissure, but this pore is absent in *Clarias*; instead, however, there is a pore posterior to the commissure not found in *Amiurus*. The other canals of this system are the same as those of *Amiurus* and the sixth sense organ of the supraorbital canal in *Clarias*, which corresponds to the first sense organ in the body canal of *Amiurus*, is followed by a union with the operculo-mandibular canal. Neither of these forms have any pores which branch dendritically and both agree with the very ancient form of *Chaetostomus*.

Amiurus catus agrees with *Amiurus melas* in the structure, distribution and innervation of the lateral line canals, in all but one point, as the frontal cross-commissure is lacking in *melas*. In some of his specimens of *Amiurus melas*, Herrick found

an absence of union between the operculo-mandibular and body canals, but he thinks that this is due to incomplete growth. The conditions in other specimens bear out this assumption, as the canals have united in all cases.

In *Amiurus catus* and *Amia calva* the general course of the canals and their innervation are similar, except that there are more pores and sense organs, and a dendritically branching system in *Amia*. A detailed comparison shows that the canals are developed in the same way in larval forms of both species and that, with subsequent growth, the three canals of the head become connected to the main canal of the body. In both forms certain pores unite and close over, so that sense organs occur in the canals which are not followed by peripheral pores. In the supraorbital canal of both *Amiurus* and *Amia*, there is a short horizontal tubule containing a sense organ, anterior to the union of the infraorbital and supraorbital canals. In *Amia* the canals of the two sides are connected in the extrascapular and ethmoid bones, and in *Amiurus*, only in the frontals. The bones above the operculum, which Allis calls the suprascapula and supraclavicle, are termed in my figure, lateral line ossicles, following the terminology used by Herrick. The body canal after passing through these bones, in *Amia*, courses the rest of the body in the scales, there being a pore and sense organ in each one; in *Amiurus* there are no true scales and the canal passes below the epidermis, having a pore and sense organ in each segment of the body. Taking *Amia* as a type of the development of the lateral line system in the Ganoid fishes, it appears that it is much more highly developed than in the Teleosts of which *Amiurus* is

a type. This would make the Teleosts nearer in the phylogenetic arrangement to the Dipnoi and the Amphibia, where the lateral line canals have degenerated gradually.

In the Dipnoi, the canals have degenerated further and only a few of the sense organs are enclosed in canals, the remainder lying in open furrows in the skin. The number of lines of sense organs on the ventral side of the head has increased, so that besides the regular infraorbital and supraorbital lines of the dorsal surface, there is a jugular and gular line on the ventral surface of the head. Kingsbury (1895) gives a detailed description of the condition in Protopterus and the Urodele Amphibia. In these latter forms the sense organs occur in groups and the only lines whose homology with those in the Teleosts is unmistakable, are the lateral lines and the lines above and below the eye.

V. General Summary.

(1) The lateral line system in *Amiurus catus* has the arrangement of the canals and peripheral pores, common to the Siluroid fishes.

(2) There are three canals on each side of the head ; the infraorbital, the supraorbital, and the operculo-mandibular canals, and a main canal on each side of the body.

(3) These canals open to the exterior by peripheral pores, of which there are five in the supraorbital canal, seven in the infraorbital, and nine in the operculo-mandibular canal. In the main canal there is a pore for each myotome of the body.

(4) Between every two pores there is a specialized sense organ within the canal wall, innervated by a branch from either

facialis, glossopharyngeal, or vagus nerves.

(5) The only point of connexion between the canals of the two sides is by the frontal cross-commissure, which extends from the supraorbital canal of one side to that of the other.

(6) In the adult the main canals of the head are enclosed in the bones of the skull.

(7) A tubule going to an external pore is given off wherever the main canal passes from one cranial bone to another, but additional tubules in some cases, find their exit through the bone.

(8) The sense organs in the head lie in those parts of the canal which are enclosed in the bones. In the trunk there is a sense organ for each myotome.

(9) The head, gill covers, and gular plates are covered with superficial sense organs, the so-called terminal buds, which are innervated by the facialis, glossopharyngeal, or vagus nerves.

(10) The development of the canals in *Amiurus* is similar to that of *Amia* and of the other bony fishes, as far as described.

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Explanation of Plates.

Abbreviations.

A., articular bone.

a.n., anterior naris.

Arabic numerals used in figure 1, (Plate I) to denote sense orgs.

b., barbel.

B.C., body canal.

Ce., cerebellum.

C.H., cerebral hemispheres.

cl., clavate cells.

c.t. connective tissue.

D., dentary bone.

E.S.C., extrascapular bone.

F., frontal bone.

F.C., frontal cross-commissure.

f.l., fibrous layer of epidermis.

g.VIIIn., ganglionic complex of the facialis nerve.

I., Roman numerals denote peripheral pores in figure 1, plate I.

i.c., indifferent or supporting cells.

In.O., infraorbital canal.

IX. n., glossopharyngeal nerve.

L.L.O., lateral line ossicle.

L.T., lobus trigemini.

L.V., lobus vagi.

m., mucous pore.

m.l., Malpighian layer of epidermis.

N., nasal bone.

n., nerve.

O.M., operculo-mandibular canal.

O.L., optic lobes.

o.r., osseous ring.

P.F., postfrontal bone.

p(In.O)., pore of infraorbital canal in figure 2, (Plate I).

p.n., posterior naris.

p(O.M)., pore of operculo-mandibular canal in figure 2,(Plate I).

P.O.P., preoperculum.

p(Su.O)., pore of supraorbital canal in figure 2,(Plate I).

p.l., pigmentary layer of the epidermis.

1/2 p., a half pore.

R.bucc.VII.n., ramus buccalis of the facialis nerve.

R.L.X.n., ramus lateralis of the vagus nerve.

R.M.E.VII.n., ramus mandibularis externus of facialis nerve.

R.O.,ramus oticus of facialis nerve.

R.O.S.VII.n., ramus ophthalmicus superfacialis of facialis nerve.

s.h.,sensory hairs.

So., suborbital bones.

S.O.(B.C).,sense organ of body canal.

S.O.(In.O)., sense organ of infraorbital canal.

S.O.(O.M)., sense organ of operculo-mandibular canal.

S.O.(Su.O)., sense organ of supraorbital canal.

Su.O., supraorbital canal.

t.b., terminal bud.

Plate I.

Fig. 1. Diagrammatic reconstruction of the pores,sense organs, canals and innervation of same,in one side of head of *Amiurus catus*.

Fig. 2. Surface of head of *Amiurus catus*, ten millimeters long, greatly enlarged.

Plate II.

Fig. 1. Transverse section through skin and lateral line sense organ, in head region of *Amiurus catus*.

Fig. 2. Brain of *Amiurus catus* (after Wright) with addition of frontal commissure.

Plate I .

Plate II.

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