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THE LATERAL LINE SYSTEM
OF
BATRACHUS TAU

A DISSERTATION

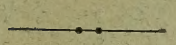
Submitted to the Faculties of the Graduate Schools of Arts,
Literature, and Science, in candidacy for the degree of

DOCTOR OF PHILOSOPHY

(Department of Zoölogy)
May, 1896

BY

CORNELIA MARIA CLAPP



BOSTON, U.S.A.

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THE LATERAL LINE SYSTEM OF BATRACHUS TAU.

CORNELIA M. CLAPP.

CONTENTS.

	PAGE		PAGE
Introduction	223	Innervation	232
I. ADULT FORM.		General Considerations	237
General Description	225	II. LARVAL FORMS.	
Topography of the Lateral Line		Origin of the Lateral Line System	238
System	226	(1) Lateral line sense organs.....	238
(1) Infraorbital line	226	(2) Lateral line nerves	242
(2) Supraorbital line	227	(3) Formation of canals.....	244
(3) Operculo-mandibular line.....	227	(4) Connecting strand.....	245
(4) Body lines.....	228	Comparison with other teleosts.....	249
Canals	228	Comparison with ganoids.....	250
(1) Pores	229	Comparison with selachians	250
(2) Relation of canals to cranial		Comparison with dipnoids	250
bones	230	Comparison with cyclostomes	250
Number and position of organs.....	231	Comparison with Amphibia	251
Variations	232	General Summary	251

INTRODUCTION.

IN a recent contribution to the "Skin and Cutaneous Sense Organs of Teleosts," Leydig (1) says: "Every one who has worked in this field shares the conviction that there is need of the coöperating participation of many observers before any conclusive presentation of the subject is possible."

As the discoverer of the true nature of the so-called "lateral line" of fishes, Leydig's words have weight, when, after nearly fifty years of investigation, he is obliged to confess that "the points still obscure outnumber by far those well ascertained."

Kupffer maintains that we are still on the very threshold of a history of the development of the peripheral nervous system. It is therefore the task of the investigator to furnish data for the future work of generalization.

In the following pages an attempt has been made to describe the lateral line system of the toadfish, both in the adult and developmental stages, for, as Mr. Allis (2) has well said, the "purely descriptive part of the subject" has been too much neglected.

Frequent reference will be made to the conditions existing in *Amia*, and the nomenclature employed by Allis will be adopted.

Ryder (3) describes the appearance of the lateral line organs in the young toadfish at the time of the formation of canals on the head, and speaks of the lines of free organs on the body as *canals*! It is evident that his observations, though in many ways valuable, were incomplete. So far as I am aware, this preliminary "notice" contains all we have on the subject of the lateral line system of the toadfish.

In Jordan's "Synopsis of Fishes of North America" (4) the only mention of this system is the statement that in *Batrachus* there is "*no lateral line*, nor conspicuous pores."

My study of the lateral line system of *Batrachus* was begun in the summer of 1888, under the direction of Prof. C. O. Whitman, at the Marine Biological Laboratory of Woods Holl, Mass., and completed at the University of Chicago.

I wish to express my deep feeling of obligation to Professor Whitman for the interest he has taken in the supervision of my work; and for the many courtesies and suggestions received from instructors and associates, I wish here to make acknowledgment.

For assistance in obtaining material at Woods Holl I am greatly indebted to Mr. G. M. Gray, the Collector of the Marine Biological Laboratory; for specimens of *Acanthias* I wish to thank Dr. A. D. Mead and Prof. A. D. Morrill.

The drawings for this paper were made after my sketches by the following draughtsmen at the Marine Biological Laboratory:

Figs. 1-3 and 7-11 were made by Mr. Crosby.

" 4-6	" "	" Mr. Tokano.
" 12	" "	" Mr. John Walton.
" 22, 23, 24	" "	" Mr. Hayashi.

I. ADULT FORM.

General Description.

There is something singularly grotesque in the appearance of the toadfish; and, as its name would imply, there is a superficial resemblance to the familiar batrachian. The sluggish disposition, the mottled brown and gray of the wrinkled, scaleless skin, the depressed head and toadish eyes do not suggest the typical teleost. The young fish also are tadpole-like in their form and motions.

From Pl. XVII, Figs. 1-3, it will be seen that there are quite conspicuous projections of the skin on the head. Besides the paired flaps found in connection with the sense organs, there are other single, often longer projections to be found, which become lacinated in the older fish. These are especially prominent about the mouth, fringing the margin of the lower mandible and opercular regions, while over each eye rises a broad conspicuous flap, giving an owl-like facial expression. The goosefish (*Lophius*) and the sea raven (*Hemitripterus*) also possess these somewhat ornamental appendages about the mouth. The function of these skinny tentacles seems evidently to be for protection, as they strikingly resemble both in color and form the seaweed (*fucus*) that abounds near their favorite haunts.

The toadfish frequents the shallow water of bays and inlets of the sea, ranging on the Atlantic coast from Cape Cod to Florida.

It is abundant at Woods Holl, Mass., and is easily obtainable in the month of June, during the spawning season. At this time the fish resort in pairs to large stones, usually near low watermark, and scooping out a cavity beneath, remain for days in their retreat. The toadfish of the Eel pond near the laboratory seem to prefer the *débris* of civilization to the excavation beneath the rock; for example, tin cans, old boots, broken jugs, etc. After depositing the eggs, the female departs, while the male remains to guard the nest.

The young fish do not "attach themselves by a ventral disc which soon disappears," as has been supposed, but at the time

of oviposition each egg is securely glued to the rock by means of a secretion on the egg membrane at the pole of the egg opposite the micropyle.

After hatching, the embryo fishes still remain attached to the rock by the adhesion of the yolk sac to the inside of the egg membrane over the disc area, until the yolk material has been entirely absorbed — a period of three or four weeks.

The largest toadfish seldom reaches a length of more than twelve inches.

Dr. Goode (5) gives the following facts about the toadfish: "In general appearance it resembles a sculpin. It possesses the power of changing its color to lighter or darker shades when exposed to light in shallow vessels with dark or light colored bottoms. It probably becomes torpid in winter in the more northern regions, is very hardy, and utters a loud croaking sound when handled."

In Storer's description of *Batrachus tau* one finds certain statements which are hardly correct. For example, he speaks of the eggs as being "not larger than very small shot," as "increasing in size" after deposition, also as adhering by a "disc acting as a sucker," and finally he says of the fish which remains to guard the eggs, that "it is in all cases the mother of the young ones."

Topography of the Lateral Line System.

1. *Infraorbital line.* — The first six organs of this line are found on a semicircular fold of the skin, anterior to the nasal tube (Pl. XVII, Fig. 2). These organs constitute the antorbital portion of the infraorbital line. They are free organs protected by a pair of flaps of the skin, representing in their position the sides of a canal. Each organ occupies a depression in the skin, and on opposite sides are developed the pointed flaps which arch over this depression, the tips of the flaps almost meeting over the center of the organ (Fig. 1).

There is no anterior commissure between the infraorbital lines of the two sides of the head as seen in *Amia*.

At a point midway between the anterior and posterior nares the infraorbital line branches. One division extending along the border of the maxillary may therefore be called the maxillary branch, the other being the suborbital portion of the main line (Fig. 1). There are seven organs in this maxillary branch, five being free organs and two enclosed in a short canal (Pl. XX, Fig. 22). The suborbital portion consists of eight free organs, bordering the lower half of the orbit (Figs. 22 and 23).

At the outer angle of the eye there are two free organs (9, 10) continuing the line of the infraorbital and corresponding to the otic portion (15, 16) as seen in *Amia*. (Compare Pl. XX, Figs. 21 and 22.) In the temporal portion of the line there is a single organ (11) enclosed in a canal (Fig. 22). The infraorbital line is continued on to the body as the dorsal line of free organs (Figs. 22 and 24).

2. *Supraorbital line.* — There are seven organs in this line. The first, a free organ, is situated near the median line, a little anterior to the opening of the posterior nares (Pl. XX, Fig. 22). Organs 2–6 are enclosed in a canal, while the seventh is a free organ occupying a position apparently outside the line and on the top of the head (Pl. XVII, Fig. 2 ; Pl. XX, Fig. 22). There is evidence of the presence of the supra-temporal cross-commissure, although the canal seen in *Amia* is wanting in *Batrachus*. In one specimen, 12 cm. in length, the line was conspicuous, as two extra organs were present in this region of the head. In Pl. XX, Fig. 22, *st.com.*, the position of the line is indicated. The middle pit line of *Amia* may be represented in *Batrachus* by the organ just dorsal to the temporal canal (Fig. 22, *m.l.*).

Four organs on the top of the head, extending on to the trunk each side of the first dorsal fin, constitute what is designated by Allis as the dorsal body line in *Amia*. (Compare Figs. 21–23.)

3. *Operculo-mandibular line.* — The first organ of this line is found on the lower side at the symphysis of the mandible. There is no commissural connection here between the two sides of the head. Four organs, which never become enclosed in a canal (Fig. 3), occupy a depression which appears as an

open groove in the bone (Fig. 5). The succeeding organs, 5-7, are within a canal in the articular bone (Fig. 5). At the angle of the jaw the opercular division begins, and consists of four enclosed organs (8-11) with one (12) free organ near the temporal region (Fig. 22). Outside of these twelve organs of the operculo-mandibular line there are accessory lines of free organs. On the mandible there is a short line of three organs (Pl. XVII, Fig. 3, *ac.md.l.*) anterior and parallel to the canal. Near the pore at the junction of the two portions of the operculo-mandibular line there are two free organs (*mdl.*) (Figs. 1, 3, and 22), while on the operculum two lines of free organs diverge at right angles to the canal in the preoperculum, the more dorsal (*d.o.l.*) having four, and the other (*v.o.l.*) three organs (Fig. 22).

4. *Body lines.* — There are three lines of free organs on the side of the body (Fig. 24); the most dorsal, of twenty-seven organs, being a continuation of the infraorbital, the middle line appearing as a branch from this line, represented by only a few scattered organs, usually eleven, and the ventral line, of twenty-seven organs, extending from a point in front of the ventral along the border of the anal fin. Continuations of these lines are found on the caudal fin, but the organs are somewhat diminished in size toward the posterior end of the body. The usual number on the caudal fin is four.

Canals.

The canals enclosing lateral line organs are found only on the head, and these present a rudimentary, perhaps vestigial condition in *Batrachus*.

From Fig. 22 it appears that the infraorbital line throughout its extent has only two short canals, one on the maxillary branch containing two organs, and the other in the temporal region enclosing only one. The supraorbital line, on the other hand, exhibits the opposite condition, in that all the organs of the line are enclosed in a canal with the exception of a free organ at each end of the line. The operculo-mandibular canal is well developed, only five of the twelve organs being super-

ficial. There is a direct union of the canals of the two sides of the head between the eyes, but no organ is developed in this commissural portion (Fig. 23; also Fig. 4).

Pores.

For a complete understanding of the relation of the pores to the canals, a knowledge of their mode of development is necessary. Each organ becomes enclosed in a short canal (Cut 1), the two openings of which are called by Allis terminal or half pores. By the union of these half pores, the so-called primary pores of the young *Amia* are formed.

In the case of *Amia* there is a subsequent process of division of these primary pores, resulting in the dendritic systems of the adult fish. The pores in *Batrachus* correspond to the terminal and primary pores of Allis, as shown in the diagram



CUT 1. — Diagrammatic representation of the formation of a primary pore: *a*, *b*, and *c*, two terminal pores approaching each other and fusing; *d*, primary pore.

representing the post-larval stage of *Amia*. (Compare Figs. 21 and 22.) In the supraorbital line of *Batrachus* the *primary pores have become fused*, so that only the two terminal pores are present, and no pore marks the union of the canals between the eyes, as seen in *Cottus gobio*. These pores, in process of fusion, may be observed during the development of the canals in the young fish.

It seems all-important that the term *pore* be restricted in its application to the *openings into the canals*. In consequence of the indiscriminate use of this word, it is often difficult to understand the statements of some writers. A puzzling case is presented in a description of the canals of *Polyodon* by a writer (6) on the Sensory System of Ganoids, where the "*cluster pores*" are described as *openings of canals, and figured as sense organs!*

A recent writer (7) in alluding to this subject says: "The word *pore* is inappropriate in *Amphibia* if used in the same

sense as in fishes," as may be easily understood when it is known that *no canals exist in the Amphibia*.

Relation of Canals to Cranial Bones.

From an examination of the skull (Fig. 4) it appears that grooves or open channels in the bones serve as protection for the organs. In *Batrachus* the only cranial bones which become modified to give protection to the lateral line organs are the frontal, dentary, and articular bones, the preoperculum, and an accessory membrane bone in the maxillary branch of the infraorbital. The curious T-shaped arrangement of the upper surface of the frontal bones where the canals of the two sides of the head unite, has given the specific name (tau) to the species under consideration. These channels are spaces between ridges of bone projecting from the surface and partially surrounding the membranous tube containing the sense organs. They vary in diameter in the different regions of the head. In the opercular region this membranous tube occupies the space (Fig. 4) between the outer edges of the two lamellae of bone forming the preopercle. In the canal of the maxillary branch the accessory membrane bone appears as though folded together to enclose the canal (Fig. 4, *ac.b.*). In the mandible there is the nearest possible approach to a closed bony canal (Fig. 5), while in the case of the temporal canal there is no cranial bone involved. This short canal lies outside the muscles which cover the squamosal and occipital bones, and consists of a tough fibrous or semi-cartilaginous covering within which is the lining epithelial layer (Fig. 22, T.C.). Leydig (8) figures a similar formation in *Chimaera*. The supporting substance is described as consisting of incomplete rings, one behind the other, comparable to the rings of the trachea, and the free ends of these rings are represented as branching. In cross-sections of the temporal canal in *Batrachus* a very similar structure is seen.

At the anterior end of the supraorbital canal there is a scale-like cartilaginous formation, by means of which the canal is extended across between the two openings (Fig. 22) of the

nasal tube. This scale bears some resemblance to the cartilaginous tube of the temporal canal, yet is unlike it, and seems to be a peculiar structure found in no other part of the canal system of *Batrachus*. Something very similar is found in the canal of the trunk in *Cottus gobio* (Cut 2), as described and figured by Bodenstein (9).

The nasal tube itself is a canal belonging to this system which never becomes surrounded by any bony formation. In this connection it may be stated that there



CUT 2.—Scale from trunk canal of *Cottus gobio*.

is good reason for regarding the semicircular canals of the ear as belonging to the lateral line system, although shut off entirely from the surface of the body. This view has been advocated by Ayers (10) and other writers.

Number and Position of Organs.

In *Batrachus* the organs in canals are identical with the so-called free organs, the only difference being the fact that the free organs, being situated on dermal papillae, have a slightly different form.

The number of organs on the head is 128, and on the body 140, making a total of 268 organs on the entire surface of the head and body. The number enclosed in canals is only 30, making the number of free organs 238. There is no indication that the number of organs increases by multiplication during the life of the fish, and the "nerve ridges" described by Allis (2) have never been found in *Batrachus*. The "pit organs" of *Amia*, assigned to the same general class of nerve hillocks, are yet said to differ greatly from the canal organs in "shape, arrangement, and methods of multiplication." From the description, however, there seems little evidence of greater difference than between the enclosed and free organs of *Batrachus*, except, possibly, in the size. It seems quite impossible to arrange them in two separate groups in the case of *Batrachus*, as they replace so constantly the regular canal organs. The enclosure of organs within a canal seems quite incidental and secondary. The absence of accessory lines of pit organs is

quite noticeable in *Batrachus*, as also the numerous "surface sense organs" (terminal buds) described by Allis (2) on the head of *Amia*.

Variations.

Frequent variations in the number and position of the organs have been noted. There may be five, six, or seven organs in the antorbital portion of the infraorbital line. The number in the suborbital may be eight or nine. In the mandibular line at the place of union of the opercular and mandibular divisions one organ is often wanting.

Two extra organs — one on each side of the head — occurred in the case of one specimen, confirming the opinion that the free organs of this region are homologous with those of the commissural canal in the occipital region of *Amia*. (Compare Figs. 21 and 22.)

On the body the variation is still more marked, the two sides seldom having exactly the same number or arrangement of organs.

On one large specimen there was the following arrangement :

In the dorsal body line of the right side, 25, left 29.

" " middle " " " " " 11, " 8.

" " ventral " " " " " 26, " 27.

At the anterior end of the ventral line in another specimen one organ was lacking on each side. The number may be four, five, or six on the caudal fin.

Innervation.

The method most successfully employed for determining the course of the nerves was maceration of the adult fish in nitric acid. After being kept for some time in a weak solution, not only the large nerve trunks could be easily followed, but the bundles composing these trunks could be separated, the connective tissue sheath having been dissolved. It thus became possible to demonstrate the course of the different components of nerves enclosed in the same sheath.

By reference to the diagrams (Figs. 22 and 23) which represent the side and dorsal view of the head and anterior part of the body of an adult toadfish, the course of the nerves may be traced after their exit from the skull. Fig. 21 is reproduced from Allis's plate for purposes of comparison, as it is of interest to note the general resemblances and slight differences which appear in comparing the teleost *Batrachus* with the ganoid *Amia*. As may be observed, the number of organs in the different lines and their mode of innervation correspond in a surprising manner.

The lateral line system in the head of *Batrachus* is innervated by dorsal branches of the VII and X cranial nerves.

The VII Nerve.

The supraorbital line is innervated by the R. ophthalmicus superficialis facialis (Fig. 22). This branch arises from the ganglion lying above the Gasserian ganglion (Fig. 13), and runs along the inner margin of the orbit in close association with the ophthalmic branch of the trigeminus. There is an evident interchange of fibres in one place, and the two nerves are included in the same sheath for a short distance near their peripheral termination. Each organ is supplied by a short branch, which enters the bony canal immediately below the organ. Organ No. 7 being a free organ, and on the top of the head, yet belongs to this supraorbital line of organs, as may be seen by tracing its development and its innervation. As Allis has shown in *Amia*, the supraorbital line is widely separated, at an early period of development, from the infra-orbital, at the point where later there is a union of the two canals.

Infraorbital line. — The organs in the pre-auditory part of the infraorbital line are innervated by the R. buccalis facialis (Figs. 22 and 23, *buc.f.*). This branch arises from the facial (Fig. 13), lying above the Gasserian ganglion, and immediately divides, sending a comparatively small number of fibres (Fig. 13, *buc.f.*²), to the outer angle of the orbit to supply the eight organs of the suborbital portion of the infraorbital. The

main portion of the buccalis passes directly downward to the floor of the orbit (Fig. 13, *buc.f.*¹) enclosed for some distance in the same sheath with the maxillaris of the fifth. It then again divides, one branch being directed toward the median line supplying the six antorbital organs, while the other sends branches to the seven organs which constitute the maxillary portion of the infraorbital line (Fig. 23). The two organs (9, 10) of the infraorbital line, corresponding to those innervated by the otic branch in *Amia* (Fig. 21), are in *Batrachus* supplied by a branch from the R. buccalis facialis (Figs. 22 and 23).

Operculo-mandibular line.—The organs of this line are innervated by the R. mandibularis externus facialis. Organ 12, —a free organ,—together with the most dorsal of the two branch lines of free organs on the operculum (Fig. 22, *d.o.l.*), are innervated by a branch of the hyoideo-mandibularis facialis, before the externus has separated from it. It leaves the main trunk through the foramen at the base of the opercular spine.

Organs 8–11 are supplied by branches which pass from the externus between the bony lamellae of the preoperculum to the canal occupying the space between the outer edges of these lamellae. Between organs 9 and 10 a branch is given off to the three free organs forming the ventral line on the operculum (Fig. 22, *v.o.l.*).

There are two free organs situated near the large pore which marks the union of the opercular and mandibular portions of the line, and which seem to correspond to the mandibular pit line of *Amia* (Fig. 21, *m.d.l.*), which are innervated by branches from the externus. In the same way the two free organs at the angle of the mouth in *Batrachus* may easily be identified with the vertical cheek line in *Amia* (Fig. 21, *c.l.*), also supplied by a branch from the externus.

The three canal organs of the mandible are innervated by the externus, as also the four organs in the groove at the anterior part of the mandible (Fig. 3), while the three superficial organs in a line parallel with them are also supplied by a branch of this same nerve (Fig. 22, *ac.md.l.*).

There seems to be an interesting peculiarity in the innervation of the body lines of *Batrachus*. The N. lineae lateralis does not supply the line of sense organs continuous with the infraorbital of the head, but it does send branches to some of the scattered organs of the middle line. The dorsal and ventral lines of the body are innervated, in part at least, by the R. recurrens facialis. This nerve emerging from the *ventral* branch of the dorsal VII (Fig. 13) turns directly backward within the cranial cavity; it passes obliquely through the cranial wall and through a loop in the glosso-pharyngeal, beyond which it forms an anastomosis with an ascending branch from the posterior root of the vagus, at a point just behind the auditory capsule. The position of the R. recurrens facialis is superficial to the N. lineae lateralis, and it extends on to the body just underneath the skin. It divides immediately (Fig. 22), sending one branch toward the dorsal region supplying the organs of the anterior portion of the dorsal line, while the ventral branch curves around behind the base of the pectoral fin innervating the anterior organs of the ventral line.

The X or vagus nerve.—The anterior root of the vagus nerve arising from the dorsal region of the medulla (Fig. 12, *X an.r.*), does not possess any distinct ganglion. It runs backward and outward, crossing the main root of the vagus, with which it is connected by a few fibres, and after leaving the cranium by the foramen in the occipital is continued on the body as the N. lineae lateralis. It courses deeply underneath the muscles for some distance, becoming superficial at the posterior portion of the body.

Although this is the main lateral line nerve, *it seems to innervate only a few of the organs on the body of Batrachus.*

The supratemporal branch of the vagus is composed mainly of anterior root fibres (Fig. 13, *st.v.*¹). It arises intracranially, passing upward and leaving the skull through a foramen in the supraoccipital (Fig. 4, *o.c.f.*). It then turns forward, supplying the canal organ of the temporal region (Figs. 22 and 23) and three other organs on the top of the head. The most anterior of the three organs may be considered as representing the middle dorsal line of pit organs, which in *Amia* are innervated

by branches of the IX, while the two others are probably homologous with the organs forming the cross-commissure of *Amia*. (Compare Figs. 21 and 23.)

Another branch (*v.*²), arising from the anterior root of the vagus just outside the cranium, and taking a course upward and backward, innervates the four organs of the dorsal line (Fig. 22, *dl.*).

Fig. 13 shows an intracranial commissure between the VII and X. The branch from X which anastomoses with the R. *recurrens facialis* (Fig. 13) arises from the *posterior root* of the vagus. It is also evident that the fibres of the R. *recurrens facialis* emerge with the *ventral root fibres* of the VII. It is probable that the components of this nerve have a different central termination in the medulla from the dorsal branches of the VII and the anterior root of the X. The innervation of the body lines in *Batrachus* presents a somewhat puzzling problem, which can only be solved by a careful study of the terminations or origin of the fibres in the medulla. The *apparent* course of the nerves is often deceptive, as fibres having *different central connections* are enclosed in the *same sheath* outside of the medulla, or, the central connections being the same, the fibres follow different pathways to their destination. A case in point is that of the glosso-pharyngeal, which seems to take no part in the innervation of sense organs in *Batrachus*, although in *Amia* one canal organ and a line of pit organs are supplied by that nerve.¹ It is probable that the fibres innervating the organs are enclosed sometimes with the IX and sometimes with the X nerve.

The attempt to homologize the body lines of *Batrachus* seems useless until a better knowledge of the components of the so-called R. *recurrens facialis* is obtained. It seems probable that this nerve is identical with the R. *dorsalis recurrens trigemini* (Stannius), which is said to innervate a line of end buds at the base of the dorsal fin in Siluroids, but the dorsal body line of organs in *Batrachus* would hardly seem homologous with this line of end buds.

¹ In a recent paper (*Journal of Morphology*, vol. xii, p. 747) Allis has shown that the "so-called dorsal root" of the IX is composed of fibres from the lateral line root of X.

General Considerations.

If one may judge from the contributions to this subject by various investigators, it is becoming evident that the lateral line system may take rank among the organs of special sense.

The connection of the olfactory, optic, and auditory organs with the central nervous system is effected by means of special pairs of cranial nerves originating in definite centers within the brain. On the other hand, the sensations of touch are mediated by cutaneous nerves which seem to be so universally distributed as to suggest the idea that the skin itself may be regarded as an immense sense organ and its innervation correspondingly general.

The system of the lateral line has usually been regarded as composed of organs of the more *generalized* type. Their wide distribution over the entire head and body would favor this conclusion, but the study of the cranial nerves of Amphibia brings into view several significant facts. In his recent paper, Strong (11) calls attention to a "most beautiful extirpation experiment in nature." The tadpole has the sense organs found in fishes and the Urodeles, and these organs are innervated by certain dorsal branches of the cranial nerves. When the tadpole becomes a frog, and these organs disappear from the skin, the dorsal branches supplying them become atrophied. As regards the innervation of the lateral line organs, there seems to be a remarkable agreement between the Urodela, larval forms of Anura, and the fishes. In general, the arrangement seems to be the same, inasmuch as dorsal branches of the VII and X cranial nerves supply these organs. This has been shown in the case of amphibians (11), selachians (12), two ganoids and one dipnoid (13), but among teleosts the matter has been in doubt. *Batrachus* is certainly one teleost in which the dorsal branches are present and innervate the lateral line organs.

In his analysis of the cranial nerves of Amphibia, Strong gives a description of the different nerve components distinguishable by the nature of their fibres, peripheral distribution, and internal origin.

He describes a *general* cutaneous component and a *special* cutaneous or lateral line component, the dorsal branches of which innervate the organs of the lateral line. These branches are coarse fibered and therefore distinguishable in sections, while their internal origin or termination is the tuberculum acusticum, a portion of the medulla which is greatly developed in fishes. If the lateral line component has its origin in the tuberculum acusticum, we have good reason to conclude that the localization of function in the medulla is as definite for these widely distributed organs as it is for the more circumscribed patches of sensory epithelium seen in the case of the ear, eye, or olfactory organ.

The ear furnishes a fine illustration of this subject, and seems like a connecting link between the system of lateral line organs from which it has probably originated, and the most highly modified sensory structure in Vertebrates—the eye. Ayers (10) has shown that the auditory organ is in reality a series of canal organs innervated by two distinct cranial nerves which he regards as possibly dorsal roots of VII and IX.

II. LARVAL FORMS.

Origin of the Lateral Line System.

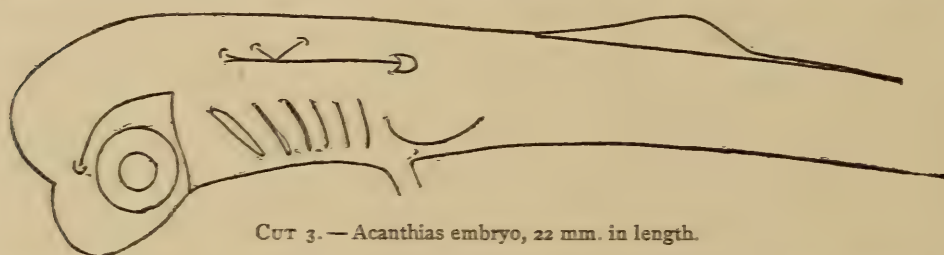
1. *Lateral line sense organs.*—Sections of early stages in the development of *Batrachus* show thickenings of the ectoderm in the region behind the eyes. In sections of later stages these areas of thickened ectoderm have become invaginated to form the auditory vesicles. Immediately after the closure of the auditory pits, thickenings of the lower layer of the ectoderm are observed on each side of the head in the pre-auditory region. From this thickened area two cords extend, one above and another below the eye. These cords are the rudiments of the supraorbital and infraorbital lines of sense organs.

Simultaneously in the post-auditory region there appear similar thickenings of the ectoderm which extend rapidly backward on to the trunk. In very young embryos this line advances along the side of the body with an enlargement at the growing end.

These thickenings of the ectoderm are described by H. V. Wilson (14) as "sensory tracts," and he maintains that in the bass, unlike what has been observed in selachians, in *Amia* and in the trout, the lateral line originates in the form of "sensory sacs," which later on become flattened out into the "patches" described by other authors. There is no dissent from the view that the auditory region is the place where the lateral line system originates, but the occurrence of these "sensory sacs" appears to be peculiar to the bass. Wilson states that the ear, branchial organ, and the first of a series of organs extending on to the body, are derived from this "common sensory furrow." In *Batrachus* there is no definite furrow present, and the "branchial sense organ" described as "functional in the later stages of embryonic and during larval life" is certainly not "histologically differentiated" as in the bass. There is no sign of an organ composed of "sense cells with short stiff hairs," as described by Wilson in an embryo of fifty-nine hours.

Fig. 17 shows the growing end of this line as seen in a preparation of the skin of an embryo 5 mm. in length. After fixing in picro-sulphuric acid and slight maceration in water, if the skin is removed, stained in alum cochineal, and mounted in glycerine, the proliferating cells in the lower layer of the ectoderm may be clearly seen. A horizontal section of this is shown in Fig. 18, at the time when the growing point has reached only a short distance behind the pectoral fin. A more highly magnified view of a portion of the same is seen in Fig. 19. A comparison of the lateral line of *Batrachus* at this stage with the same structure in an *Acanthias* embryo is of interest (Fig. 14). In *Acanthias* the lateral line is quite conspicuous. In an embryo of 22 mm. (Cut 3) it is easily seen with a hand lens, as a prominent, somewhat flattened ridge, extending backward above the branchial region and along the sides of the body. There is a curious fold of the epidermis, the so-called "pocket," which covers the growing end of the line. Pl. XIX, Fig. 14, shows a horizontal section of an embryo 17 mm. in length, from which it is evident that the "pocket" consists of a reduplication of the skin accompanying the enlarged growing point.

The branches of this system on the head also show this peculiar fold (Cut 3), the significance of which it is hard to discover. In connection with this fold, Mitrophanow (15) describes the formation of canals, but gives no figures that illustrate the manner of their formation. Behind the dorsal fin, as seen in older embryos, the "pocket" becomes greatly elongated, and suggests the existence of a canal in that region, but furnishes no clue to the condition that is supposed to exist in the anterior part of the body of the adult *Acanthias*. Cut 4 is a cross-section of the anterior part of the line at this stage.



CUT 3.—*Acanthias* embryo, 22 mm. in length.

This subject has not been sufficiently investigated to afford a satisfactory basis for comparisons. Beard (16) mentions this growing end of the line as "plowing its way backward through the indifferent ectoderm." The appearance of the structure in *Acanthias* would suggest this idea.

Balfour (17) describes the lateral line of *Syllium* as appearing "in the form of a linear thickening of the inner row of cells of the external epiblast on each side, at the level of the notochord." He says that at this time it shows no segmental character, and he also notes the interesting fact of the "broadening at the growing point." He probably has reference to this remarkable fold of the epiblast when he speaks of the "perfectly abrupt" termination of the line. He also mentions the contrast between the narrow anterior and the broad terminal portion of the line. This thinning out of the anterior portion of the lateral line is noticeable in *Batrachus*. Allis describes and gives figures of surface preparations showing the same appearance of the line in *Amia*. "The ends of these lines are enlarged, that of the lateral line sometimes forming a large and prominent swelling."

Hoffmann (18) regards the sense organs as arising segmentally, and gives no account of the growth of the rudiment

of sense organs on the side of the body. H. V. Wilson (15) has evidently found the line only in the form of a slender cord on the posterior part of the body, and makes no mention of any enlargement at the growing end. From figures in a recent paper on *Necturus*, by Miss Platt (19), this enlarged growing point is shown as quite conspicuous. In selachians, ganoids, and amphibia we have evidence of this mode of growth of the sense organ rudiment, but no figures or descriptions of the enlarged growing point of the lateral line of any teleost have been published, so far as I am aware.

Fig. 6 represents the condition of a *Batrachus* embryo about the time of hatching and when the embryo is still attached to the yolk sac. The principal organs of the different lines can now be distinguished in surface preparations, but a more satisfactory showing of the exact number and position of the organs, as well as of the connecting strand, can be obtained from preparations of the skin, as previously described.

Regarding the canal and free organs as identical, the development may be briefly outlined as follows: In *Batrachus*, as in *Amia*, the growing line of sensory epithelium begins to present the appearance indicated in Fig. 15, which is a camera drawing from a preparation of the skin at a stage somewhat earlier than that shown in Fig. 6. The cells destined to form the sensory portion of the organ begin to elongate and arrange themselves in a definite manner, suggesting the name "hillock" given by Merkel (20) to this class of organs. At the summit there soon appears a clear vacuolar space toward which the upper portion of the cells is directed. The "hillock" formed in the lower layer of the skin soon pushes its way to the surface and gradually takes on the characteristics of an adult organ. This process has been fully described by Allis (2).

The sensory and supporting cells are very much alike in the organs of *Batrachus*, although the cells in the center of the "hillock" are pear-shaped and somewhat shorter than those of the peripheral part of the organ. From Fig. 16, which is a section of a side organ of a fish of one year old, the shape of the adult organ is evidently that of a cone hollowed at the base.

Soon after the organ has reached the surface, there appears on the summit a structure known as the "hyaline tube" or "cupola." This was seen on specimens 2 cm. in length, being easily observed with low magnifying power on the living fish, some chloroform being added to the water to quiet the fish during the observation. This tube measured .10 mm. in length and .01 in breadth. From sections through the canal organs of older fish, it is apparent that this "hyaline tube" is present after the enclosure of the organs in canals. There is little doubt in regard to the nature of this hyaline structure. The cells of the organ, in common with other epidermal cells, may secrete a cuticular substance on the free ends of the cells. In the case of the hair cells this secretion is in the form of hairs or bristles. These hairs may coalesce, forming a continuous membrane, surrounding the central portion of the hillock, thus forming the so-called tube, which is frequently present. The hairs of the most central cells may remain separate within this tube, as Leydig (1) observes in his most recent paper on this subject.

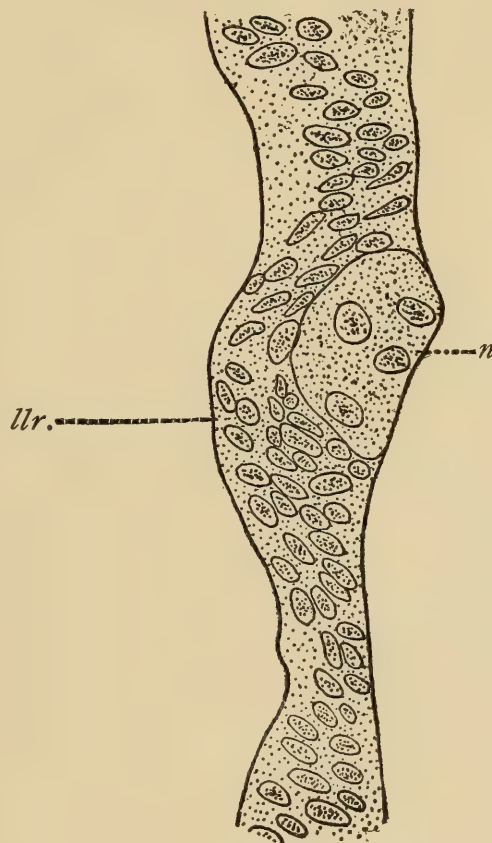
The "terminal buds" of Merkel or "end buds" of other writers are not found on the surface of the head or trunk of *Batrachus*, but they occur in the mouth and branchial cavities. These organs are much smaller than the hillocks on the surface of the body, and very little is known in regard to their innervation.

2. *Lateral line nerves*. — In his "Elasmobranch Fishes" Balfour (17) says that, in considering the subject of the lateral line system, we are dealing with two distinct structures, (1) the modified epidermis seen in certain lines along the sides on the head and body, and (2) the accompanying nerves.

The origin of the organs from the modified ectodermal cells has been demonstrated, but the mode of origin of the accompanying nerves is not so well understood. Balfour (17), following what he believed to be the analogy of cranial nerves in general, held that the dorsal branches which supply the sense organs grow out from the brain to these organs. On the other hand, Götte (21), Semper (22), van Wijhe (23), and Beard (16) consider it certain that the cells from the ectoderm contribute

to the formation of these branches. According to Hoffmann (18), the lateral nerve in *Salmo* arises from a string of cells in the nervous layer of the ectoderm some time previous to the development of the organs. This string gradually moves out of the ectoderm, coming to lie at some distance internal to it, but connected at intervals by short side branchlets with the locality where the future segmental sense organs are to arise. Hoffmann's (18) observations were made on embryos of a teleost, which he regards as a less favorable form than the selachian, in which, according to Semper (22), it is uncommonly easy to show the origin of the lateral nerve.

In the section of the *Acanthias* embryo (Fig. 14), there is an evident extension of nerve fibres from the vagus ganglion accompanying the lateral line rudiment. In cross-section these fibres are seen to constitute at this stage a part



CUT 4. — Cross-section of lateral line of *Acanthias* embryo.

of the lateral line (Cut 4). It will be necessary to study the changes taking place in the later stages before a final conclusion can be drawn, but it would appear that the thickened ectoderm forming the lateral line and the extension of the outgrowths of the ganglion cells were associated during the early history of the structure.

Hoffmann's (18) description of the origin of the nerve becomes more intelligible after the study of the selachian embryo, although in both the case of *Salmo* and *Acanthias* the *exact mode of origin of the sense organs remains uncertain*. In *Batrachus*, on the other hand, the origin of the sense organs

is easily demonstrated, while the *origin of the nerves and their connection with the organs becomes the great problem, as in the case of other teleosts.*

In stages represented in Fig. 18 it is impossible to detect any *nerve fibres* accompanying the growing line on the side of the body. The whole line has the appearance of being an *extension of the mass of ganglion cells.* This seems the more striking as the entire string of cells constituting the rudiment of the lateral line in *Batrachus* seems to occupy the same relative position as the extension of *ganglionic fibres* in *Acanthias.*

Wilson (14) states that he has been unable to trace the origin of nerves in the Bass. He says in regard to the lateral branch of the vagus, that he could not distinguish it "during embryonic life" nor "in the larvae of two or three days."

It is difficult to reconcile Hoffmann's (18) observations on *Salmo* with the facts brought out by Wilson (14) or with the conditions existing in *Batrachus.* That the origin of the sense organ rudiment precedes the appearance of the nerve in both the Bass and *Batrachus* can hardly be doubted, while from the description of the "growing sensory tissue" in the skin of *Amia*, Allis (2) surely conveys the idea of the early appearance of the sense organ rudiment.

3. *Formation of canals.* — Figs. 7-11 represent the appearance of the head of *Batrachus* during the period of the enclosure of the organs in canals. The plates of Allis show in detail the different steps of this process of canal formation, and a very full account of the same is to be found in the admirable paper on the development of the lateral line organs of *Amia.* Previous to this paper, we have the accounts of canal formation in *Cottus gobio* by Bodenstein (9), and in *Plateria* by Schulze (24) and Solger (25), but the illustrations of the subject, as well as the accounts, are not so full and clear as in the case of *Amia.*

The appearance of the head during these stages is almost identical in *Amia* and *Batrachus.* At the time of hatching, the organs are not apparent on the surface, but after treatment with picro-sulphuric acid they may be seen below the surface as whitish spots or irregular lines (Fig. 6).

The canals are formed in sections, as described by Allis (2): "After a developing canal organ has reached the surface, it begins to sink, carrying with it the surrounding tissues, thus forming a small pit at the bottom of which the organ lies. Lips grow upward and inward from the edges of the pit, and meeting above the organ, form a short canal, the openings of which are inclined to the general surface and give to the canal a tunnel-like appearance." In Figs. 7 and 8 the organs have begun to sink below the level of the surface and form linear areas of depression.

In Figs. 9, 10, and 11 the process has been continued and the organs are partially enclosed by the approaching lips of the canal, but complete fusion has not taken place. This condition is permanent in some forms, as *Chimaera* and *Polyodon*, open grooves taking the place of canals in the adult. The process of enclosure goes on unequally; the most anterior organs are the first to become enclosed. In Fig. 10 the line of fusion of the nasal tube is distinctly seen, and the two half pores which are formed constitute the anterior and posterior nares. In the supraorbital line the process of fusion is carried out most completely, the short canals coalescing and therefore no primary pores formed, the terminal or half pores only being present (Figs. 2 and 23). A comparison of the commissural canal between the eyes, so prominent at this stage (Fig. 10), with the bony channels on the frontal bones (Fig. 4) is instructive, as showing the effect of the flattening of the head and the closer approximation relatively of the eyes in the adult.

In the case of the operculo-mandibular line (Fig. 9) the opercular portion is seen to form independently of the mandibular division, and the double or primary pore which marks their union remains larger than the others of the line (Fig. 22). In the mandibular portion of the line the four anterior organs are never enclosed in a canal, but retain the open groove condition in the adult (Fig. 3).

4. *Connecting strand*.—While examining adult specimens of *Batrachus* which were partially macerated in nitric acid my attention was attracted by a very well-defined strand connecting the organs on the side of the body. This structure had the

appearance of the commissures connecting the ganglia of the sympathetic system, and from the fact that it resisted the action of nitric acid I inferred that it was nerve tissue. In direct sunlight, by aid of an ordinary lens, this cord was plainly to be seen, and its connection at either end with the cells near the summit of the sense organs was evident.

The appearance of this structure in connection with a free organ is shown in a section from the side of the body of a specimen 10 cm. in length (Fig. 16, *com.st.*). As may be seen, the strand near the organ has a diameter greater than that of the nerve supplying the organ, and it extends in a sort of festoon from the summit of one organ to that of the next in the line, becoming narrower midway between the organs. It extends below the skin into the thick felt-like layers of connective tissue occupying the space between the skin and the muscles. This cord is also found connecting the organs of the supra- and infraorbital lines in the head, as well as those of the operculo-mandibular line, and even where free organs seem quite disconnected, as in case of organs on the top of the head, there is at least a short extension of this cord on each side of the organ. In Figs. 22 and 23, the strand is represented in blue. A cord of cells is found on the floor in the epithelial

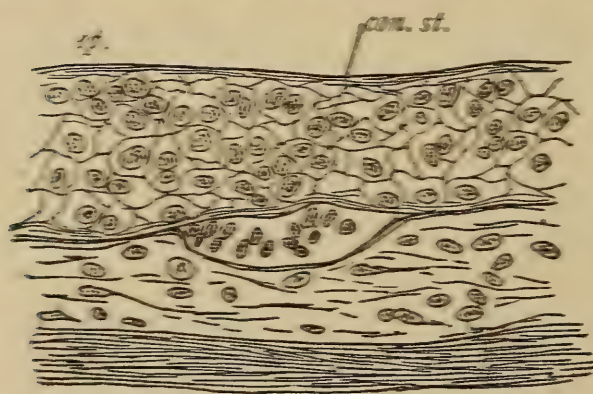


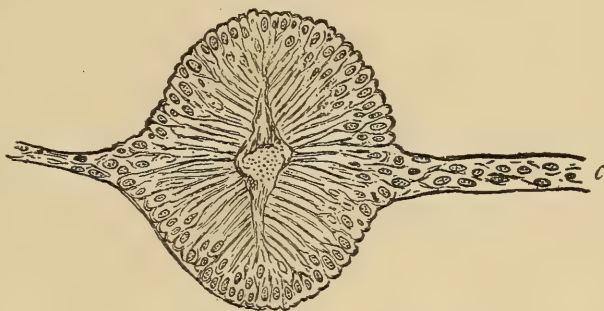
FIG. 3. — A cross-section of temporal canal of *Batrachus*, showing the strand in floor of canal.

lining of the canals (Figs. 22 and 23). It therefore becomes evident that in the case of *Batrachus tau* the connecting strand constitutes a prominent feature throughout the lateral line system in the adult fish (Cut 5). Bodenstein (9) describes

this structure in the adult *Cottus gobio*, and says that the strand extends from the *center* of one organ to the next. This is hardly the case in *Batrachus* (Fig. 16), as the cord evidently terminates at the *summit* of the organ, among the supporting

cells, having no connection with the nerve, as suggested by Bodenstein, when he speaks of the possibility of its forming anastomoses with the nerves in the series of sensory hillocks. Emery (26) describes what he calls "epithelial canals" in the adult *Fierasfer*, and

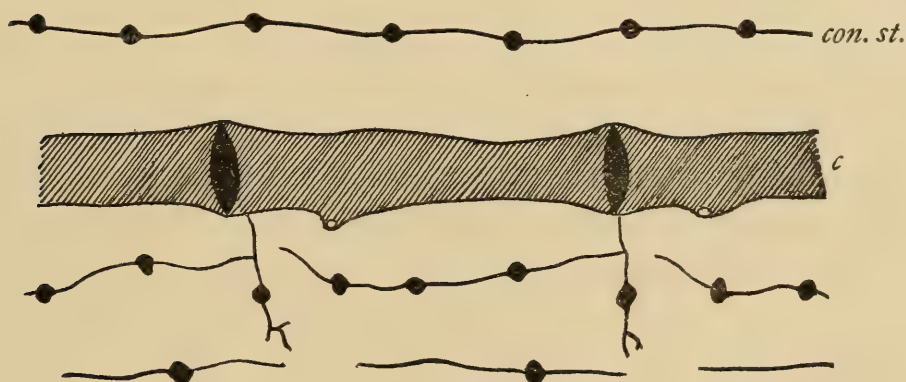
his figures leave no doubt as to their homology with the connecting strand of *Batrachus* (Cuts 6 and 7). No mention is made of any connecting canals between the *canal*



CUT 6. — Copied from Fig. 58, Emery (26).

organs, but they are evidently well developed between the "nerve buttons" (pit organs) of the accessory lines.

The fact that these "canals" sometimes branch and end blindly (Cut 7) is a peculiar characteristic if these canals are functional. Exactly similar peculiarities are noticed in the case of the strand in *Batrachus*. The free organs situated in a line parallel with the canal on the mandible have the strand



CUT 7. — Copied from Fig. 6, Emery (26).

directed at right angles to the canal, and in one case the end of the cord was branched in a similar way to that figured by Emery. In a series of cross-sections the irregular outline of this strand in *Batrachus* becomes evident (Cut 8). There is some indication of its being fibrous in structure, and

often near the organ a suggestion of a lumen is noticed, especially in longitudinal sections.

According to Leydig (1), Feé (27) seems to have figured this connecting strand, but makes no allusion to it. Solger (25) refers to the "side organ chains," in the case of *Acerina cernua* and *Lota vulgaris*, and speaks of the chain as consisting of "marrowless nerve fibres enclosed in a nucleated sheath." Merkel (20) speaks of "modified (cutis) epithelium" and suggests that the connecting strand may be the vestige of a canal! The presence, however, of both the canal and the connecting strand, one found within the other, as in *Batrachus*, would overthrow any such supposition.



Cut 8. — Cross-section of strand between organs 9 and 10 of infraorbital line of *Batrachus*.

Carrière (28) thinks there is no possibility that this "chain" is composed of nerve fibres. Ryder (29) speaks of "faint filamentous prolongations" from the organs. In a figure of Savi's (40) vesicles there is a connecting cord shown and described as "filament anastomotique," which suggests the same structure.

Leydig (1) has examined this peculiar structure in *Gobio*, *Rhodeus*, *Salmo*, and *Anguilla*, and although reaching no conclusion as to its significance, says that the strand does not consist of nerve elements, but principally of epithelial cells which enclose a space that may be considered a lymph passage, or, in some cases, no lumen being present, the strand presents a fibrous or ligamentous appearance. He regards the "epithelial canals" of Fierasfer as lymph channels. Leydig (1) further observes that although he has not seen the epithelial thickenings out of which the sense hillocks arise, it is probable that the strand is derived from these thickenings. From this point of view the strand would be a remnant of an epithelial growth which separates from the epidermis and forms the foundation of the sense hillocks. Leydig (1) utterly discards the idea that this structure is in any way connected with the later forming canal.

In regard to the origin of the strand, my observations on the embryos and larval forms of *Batrachus* would tend to confirm the opinion expressed by Leydig. Whatever the function may be, *its origin from the sense organ rudiment is not to be doubted*. In very young embryos the growth of the sensory tissue is easily demonstrated, as shown elsewhere. In the larval fish 15 mm. long, just after the yolk has become absorbed, the strand is distinctly seen in preparation of the skin, the cells of the strand between the organs still retaining much the same appearance as in earlier stages (Fig. 15, *con.st.*). Later, however, the cells undergo a change so that the tissue appears as seen in Fig. 16, *con.st.*

Comparison with Other Teleosts.

1. *Lophius piscatorius*. — The goosefish resembles the toadfish in being destitute of scales and in having similar tentacular appendages in various parts of the body (Guitel, 30). The sense organs are not enclosed in canals, but are protected by projections of the skin, as in the case of the free organs of *Batrachus*. The maxillary portion of the infraorbital line of organs is greatly developed and the suborbital is wanting. The innervation is quite similar in the two forms, the dorsal branches of the VII being quite distinct from the V.

2. *Cottus gobio*. — Bodenstein (9) has described the "connecting strand" in the adult *Cottus* and represents it in his figures as on the floor of the canals. From his description of the skin and the appearance of the canal organs, there is a striking similarity between the two forms.

3. *Amiurus*. — *Batrachus* and this common fresh-water form have several characteristics in common. The naked skin, closely studded with gigantic gland cells, the depressed head, and general shape of the body is the same, but the sense organs of the trunk in *Amiurus* are, for the most part, in canals. The interesting comparison is in respect to the course of the R. dorsalis recurrens facialis, which has been wrongly called "*trigemini*." In *Amiurus*, according to Wright (31) and Pollard (32), this arises from a "posterior dorsally placed gangli-

onic extension and passes upwards intracranially to the parietal bone," and from thence on to the body innervating a dorsal line of sense organs. This nerve is undoubtedly homologous with the R. recurrens of *Batrachus*, although taking a somewhat different course. It receives a branch from the vagus, and in this respect resembles the R. recurrens facialis of *Batrachus*.

4. *In Fierasfer* the "connecting strand" is well developed, and although Emery (26) describes this structure as an "epithelial canal," still the evidence is hardly conclusive from his figures.

5. *Ganoids*. — As already shown, *Batrachus* and *Amia* have many of the same characteristics, but in *Batrachus* the canals are never entirely enclosed within the bones of the skull, nor is the elaborate system of branching canals with their numerous groups of pores to be found. Allis (2) has shown that the trigeminus takes no part in the innervation of the canal organs of *Amia*. The terminal buds found in such abundance on the surface of the head of *Amia* are not present in *Batrachus*.

6. *Selachians*. — The comparison between the lateral line of *Acanthias* and *Batrachus*, which has already been made, shows the differences that will probably be found to exist in the mode of origin of this system in the two groups of fishes. So far as the innervation is concerned, there is great similarity between *Batrachus* and selachians. Ewart (12) has shown that the lateral line organs are supplied by the dorsal branches of the VII and X cranial nerves.

7. *Dipnoïds*. — Pinkus (13) has shown that the commissure connecting the VII and X is quite prominent in *Protopterus*. He does not describe this nerve as connecting with the branches extending on to the body, but shows its union with the vagus ganglion. This commissure is undoubtedly homologous with the R. recurrens facialis of *Batrachus*. A few of the sense organs of *Protopterus* are enclosed in canals, but they are, for the most part, on the surface of the body, as in *Batrachus*.

8. *Cyclostomes*. — The commissure between the VII and X has been found in *Petromyzon* and figured by Ahlborn (33). Stannius (34) speaks of the N. lateralis as "*formed partly by a recurrent branch from the facialis passing around outside the auditory capsule, a thing which does not occur in the N. lateralis*

in higher forms." This is a complete description of the course of the *R. recurrens facialis* in *Batrachus*.

9. *Amphibia*.—While *Batrachus* is a true teleost, there are certain superficial resemblances to the Urodeles, the sense organs of both having much the same appearance and arrangement on the body.

As regards the course of the cranial nerves, Strong (11) has pointed out the remarkable homologies that are presented in the tadpole and the teleost; the dorsal branches corresponding to those of teleosts being present in the tadpole but becoming aborted in the adult frog.

General Summary.

Development of organs and canals.—The sense organs of the lateral system in *Batrachus* arise from special cords of cells formed in the lower layer of the epidermis. These cords originate from certain thickenings which make their appearance in the auditory region of very young embryos, and proliferate along definite lines on the head and trunk. The enlarged growing end of one of these cords pushes its way from the auditory region to the extreme posterior part of the body, the swollen appearance remaining conspicuous for some time in the region of the caudal fin.

These thickenings of the ectoderm give rise to the sense organs; each organ arising as a "local proliferation" of cells along the cord (Fig. 15). These cells push through the overlying epidermal cells and gradually take on the form and character of the adult organ, having the hair cells well developed, and the so-called "cupola" structure surmounting the organ.

In a later stage each organ sinks slightly below the surface, and a pointed fold of the skin projects on either side of it. This is the permanent condition of the majority of the sense organs of *Batrachus*. On each side of the head, however, four short canals are formed. They enclose organs identical with those remaining on the surface, and the canals may be regarded as a fusion and extension of the paired flaps which serve to protect the free organs. In the adult the canals lie in open

channels of the dermal bones and only primary pores are present.

Innervation. — The dorsal branches of the VII and X cranial nerves supply the lateral line system. The supraorbital line of organs are innervated by the R. ophthalmicus superficialis; the infraorbital by the R. buccalis facialis; the operculo-mandibular by the R. mandibularis externus; while the vagus sends branches to the single canal organ in the temporal region, as well as to the organs on the top of the head.

The anterior organs of the trunk are supplied by the R. recurrens of the VII, which forms an anastomosis with a branch of the vagus just outside of, and posterior to, the auditory capsule, and extends on to the body, occupying a position directly superficial to the N. lineae lateralis. The R. recurrens in *Batrachus* is probably the same as the R. dorsalis recurrens facialis (trigemini) of the Siluroids, or of the cutaneous quinti in *Gadus*, although following a different course on the side of the body.

It remains for future investigation to determine the exact innervation of the organs on the body of *Batrachus*.

The complexity of the peripheral nervous system grows more apparent with every step of advance in methods of investigation. In Kupffer's words, "The researches of the last decade in comparative embryology have shown that the development of the peripheral nervous system is a far more complicated process than it was formerly supposed to be" (36). This is especially true in the case of the vertebrate head, as the recent work on *Amphioxus* by Hatschek (37), and the important investigations by Kupffer (38) on *Ammocetes* clearly show.

In the views of Hatschek (37) we encounter a slightly modified form of Balfour's hypothesis in regard to the origin of both cranial and spinal nerves from a type of segmental nerves which had only dorsal, yet *mixed* dorsal roots. According to Hatschek the spinal nerves have lost certain elements, while the cranial nerves have retained more of the primitive characteristics. In *Petromyzon*, Kupffer (38) has shown that the "dorsal spinal nerve root" and the "mixed head nerve root" exist together side by side as coördinate components of a typical head nerve.

In the researches of Kupffer (36), we gain important additions to our knowledge of the development of the cranial ganglia in connection with the thickenings of the ectoderm which have long been recognized, but little understood. Since Beard's (16) and Froriep's (39) simultaneous discovery of "branchial sense organs" in the embryos of sharks, and the corresponding transient structures in embryos of higher forms, there has been much controversy in regard to the question of the ectoblast elements entering secondarily into the formation of the cranial ganglia and nerves. There has been much hesitation on the part of investigators in accepting this fact, for, as Froriep (39) has said, "It would certainly bring about a fundamental change in our views, were we to be convinced that during a long period of embryonic development, the whole ectoblast possessed the capacity to act as 'Nervenkeim.'"

It is now settled beyond dispute that these "placodes" in *Ammocetes* do furnish material to the processes growing down from the neural ridge, and subsequently forming the cranial ganglia and nerves. The peripheral portion of the "placodes" may become the "foundations of the primary sense organs." The sense organs of the lateral line, although distributed over the entire length of the trunk, are connected with ganglia formed in the head region, and are therefore innervated by cranial nerves. There seems every reason for considering the system as belonging with the more highly specialized sense organs.

In his admirable paper on "The Cranial Nerves of Amphibia," Strong (11) has shown the extensive modification which takes place in the nervous system of *Rana*, due to the disappearance of the lateral line organs in the adult, and suggests "the importance of taking into full consideration, as a factor, the *cutaneous sense organs* in the attempt to obtain a philosophical understanding of the changes undergone by the peripheral and central nervous systems. The development and specialization of these structures have probably played an important part in the changes leading to the organization of the vertebrate peripheral and central nervous systems."

BIBLIOGRAPHY.

33. AHLBORN, F. Ueber den Ursprung und Austritt der Hirnnerven von Petromyzon. *Zeit. f. wiss. Zool.* Bd. xl. 1884.
2. ALLIS, EDWARD PHELPS, JR. The Anatomy and Development of the Lateral Line System in *Amia calva*. *Journ. of Morph.* Vol. ii, No. 3. 1889.
10. AYERS, HOWARD. Vertebrate Cephalogenesis. II. A Contribution to the Morphology of the Vertebrate Ear, with a Reconsideration of its Functions. *Journ. of Morph.* Vol. vi, No. 1. 1892.
17. BALFOUR, F. M. Elasmobranch Fishes. 1877.
16. BEARD, JOHN. The System of Branchial Sense-Organs and their Associated Ganglia in Ichthyopsida. *Q. J. M. S.* Vol. xxvi, N.S., No. 101. 1885.
9. BODENSTEIN, EMIL. Der Seitenkanal von *Cottus gobio*. *Zeit. f. wiss. Zool.* Bd. xxxvii, Heft 1. 1882.
28. CARRIÈRE, G. Postembryonale Entwicklung der Epidermis des *Siredon pisciformis*. *Arch. mikr. Anat.* 1884.
6. COLLINGE, W. E. The Sensory Canal System of Fishes. Part I. Ganoidei. *Q. J. M. S.* Vol. xxxvi, N. S. 1894.
26. EMERY, C. Le Specie del Genere *Fieras* nei Golfo di Napoli e Regimi limitrofe. *Fauna und Flora des Golfes von Neapel*. II. Monographie. 1880.
12. EWART, J. C. The Lateral Sense-Organs of Elasmobranchs. I. The Sensory Canals of *Laemargus*. II. The Sensory Canals of the Common Skate (*Raia batis*). *Trans. Roy. Soc. Edinb.* Vol. xxxvi, Part 1. 1892.
27. FÉÉ. Recherches sur le nerf pneumo-gastrique chez les poissons. 1869.
39. FRORIEP, AUGUST. Entwicklungsgeschichte des Kopfes. *Merkel und Bonnet's Anat. Hefte*. Bd. i. 1891.
5. GOODE, G. BROWN. Natural History of Useful and Aquatic Animals. 1884.
21. GÖTTE, ALEXANDER. Die Entwicklungsgeschichte der Unke. 1875.
30. GUITEL, F. Recherches sur la ligne laterale de la Bandroie (*Lophius piscatorius*). *Arch. de Zool. ex. et Gen.* Sér. 2. Tome ix. 1881.
37. HATSCHEK. Die Metamerie des *Amphioxus* und des *Ammocoetes*. *Verh. d. anat. Gesell., Sechste Versammlung*. 1892.
18. HOFFMANN, C. K. Zur Ontogenie der Knochenfische. *Arch. f. mikr. Anat.* Bd. xxviii, Heft 1. 1883.
4. JORDAN AND GILBERT. Synopsis of the Fishes of North America. *Bull. U. S. Nat. Mus.* No. 16. 1883.
7. KINGSBURY, B. F. The Lateral Line System of Sense-Organs in Some American Amphibia and Comparison with the Dipnoans. *Proc. Am. Micr. Soc.* Vol. xvii. 1895.

36. KUPFFER, C. VON. Entwicklungsgeschichte des Kopfes. *Merkel und Bonnet's Anat. Hefte*. Bd. ii. 1892.
38. KUPFFER, C. VON. Studien zur vergleichenden Entwicklungsgeschichte des Kopfes der Kranioten. Heft 2. Die Entwicklung des Kopfes von Ammocœtes Planeri. München und Leipzig. 1894.
1. LEYDIG, F. Integument und Hautsinnesorgane der Knochenfische. Weitere Beiträge. *Zool. Jahrb.* Bd. viii, Heft 1. 1894.
8. LEYDIG, F. Zur Anatomie und Histologie der Chimaera monstrosa. *Müller's Archiv f. Anat. u. Phys.* 1851.
20. MERKEL, FR. Ueber die Endigungen der Sensiblen Nerven in der Haut der Wirbelthiere. Rostock. 1880.
15. MITROPHANOW, PAUL. Étude embryogénique sur les Selaciens. *Arch. de Zool. ex. et Gen.* Sér. 3. Tome i. 1893.
13. PINKUS, F. Die Hirnnerven des Protopterus annecteus. *Schwalbi's Morph. Arbeiten*. Bd. iv, Heft 2. 1894.
19. PLATT, J. B. Differentiations of Ectoderm in Necturus. *Q. J. M. S.* Vol. xxxviii, Part 4. 1896.
32. POLLARD, H. B. The Lateral Line System in Siluroids. *Zool. Jahrb.* Bd. v. 1892.
3. RYDER, JOHN A. A Preliminary Notice of the Development of the Toadfish (*Batrachus tau*): *Bull. of U. S. Fish Comm.* 1886.
29. RYDER, JOHN A. Embryography of Osseous Fishes. *Report of U. S. Fish Comm. for 1882*.
40. SAVI, PAUL. D'études anatomiques sur le système nerveux et sur l'organe électrique de la Torpille.
24. SCHULZE, FRANZ EILHARD. Ueber die Sinnesorgane der Seitenlinie bei Fischen und Amphibien. *Arch. f. mikr. Anat.* Bd. vi. 1870.
22. SEMPER. *Merkel und Bonnet's Anat. Hefte*. Bd. i, p. 592. 1891.
25. SOLGER, B. Neue Untersuchungen zur Anatomie der Seitenorgane der Fische. *Arch. f. mik. Anat.* Bd. xvii, Heft 1, iv, and Bd. xvii, Heft 3.
34. STANNIUS, H. Das peripherische Nervensystem der Fische, anatomisch und physiologisch untersucht. Rostock. 1849.
11. STRONG, OLIVER S. The Cranial Nerves of Amphibia. A Contribution to the Morphology of the Vertebrate Nervous System. *Journ. of Morph.* Vol. x. 1895.
23. VAN WIJHE, J. W. Ueber die Mesodermsegmente und die Entwicklung der Nerven des Selachierkopfes. 1882.
14. WILSON, H. V. The Embryology of the Sea Bass (*Serranus atrarius*). *Bull. of U. S. Fish Comm.* Vol. ix. 1891.
31. WRIGHT, R. RAMSAY. On the Nervous System and Sense-Organs of *Amiurus*. *Proc. Can. Inst.* Vol. ii, Fasc. No. 3. Toronto. 1884.

REFERENCE LETTERS.

- A.* = anal fin.
ac.b. = accessory membrane bone.
ac.md.l. = accessory mandibular line.
a.l. = anterior pit line of head (*Amia*).
an.r. = anterior root.
an.na. = anterior nasal aperture.
ar. = articular.
buc.f. = ramus buccalis facialis.
cb. = cerebellum.
C.H. = cerebral hemispheres.
c.l. = cheek line.
com.VII-X = commissure between *VII* and *X*.
con.st. = connecting strand.
d. = dentary.
d.b.VII = dorsal branch of *VII* nerve.
d.b.ll.n. = dorsal branch of nervus lineae lateralis.
d.b.rec.f. = dorsal branch of recurrens facialis.
d.l. = dorsal line.
d.o.l. = dorsal opercular line.
ep. = epiphysis.
F.R. = frontal.
f.g. = facial ganglion.
g.l. = glossopharyngeal nerve (*Amia*).
g.g. = Gasserian ganglion.
h.l. = horizontal pit line of cheek (*Amia*).
I.O.C. = infraorbital canal (*Amia*).
ll.r. = lateral line rudiment.
m. = muscles.
MX.C. = maxillary canal.
md.l. = mandibular line.
m.e.f. = ramus mandibularis externus facialis.
m.l. = middle dorsal pit line of head.
n.ll. = nervus lineae lateralis.
n.c. = noto chord.
oc.f. = supraoccipital foramen.
oll. = olfactory lobes.
OM.C. = operculo-mandibular canal.
OP. = operculum.
op.f. = ramus ophthalmicus superficialis.
op.l. = optic lobes.
O.S. = opercular spine.
ot.n. = otic nerve (*Amia*).
p. = pore of canal.
P. = pectoral fin.
pigm. = pigment.
pl. = posterior pit line of head (*Amia*).

- p.n.a.* = posterior nasal aperture.
P.OP. = preoperculum.
p.r. = posterior root.
rec.f. = ramus recurrens facialis.
s.or. = sense organ.
SO.C. = supraorbital canal.
sp.c. = spinal cord.
st.com. = supratemporal cross-commissure.
st.v' = supratemporal branch of vagus.
T.A. = tuberculum acusticum.
T.C. = temporal canal.
V. = ventral fin.
v.b.rec.f. = ventral branch of recurrens facialis.
v.o.l. = ventral opercular line.
v.g. = vagus ganglion.
v.² = second branch of vagus.
wd. = wolffian duct.

EXPLANATION OF PLATE XVII.

FIG. 1. Side view of head of *Batrachus tau*, one year old. $\times 6$. Showing the appearance of the lines of sense organs in the adult, also the position of the paired flaps and other projections of the skin on the head.

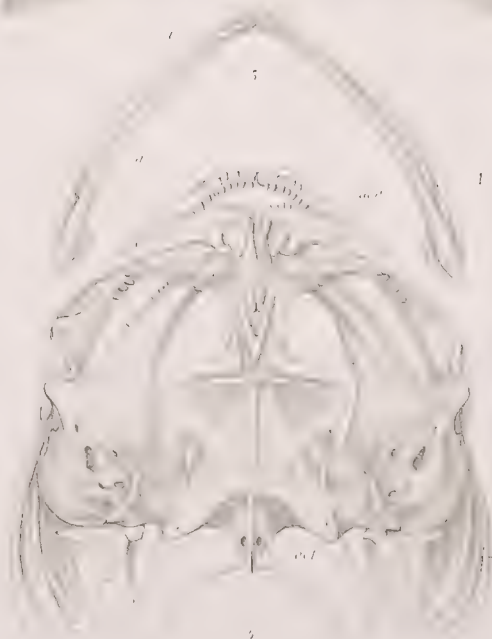
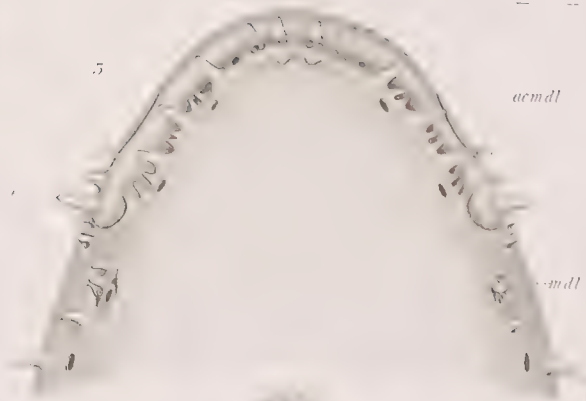
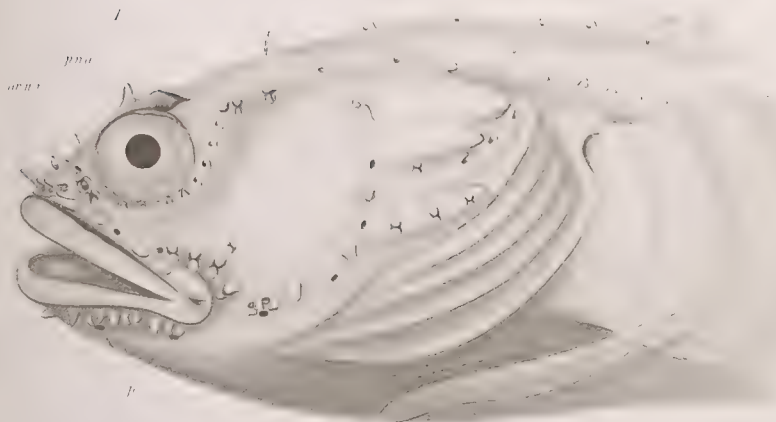
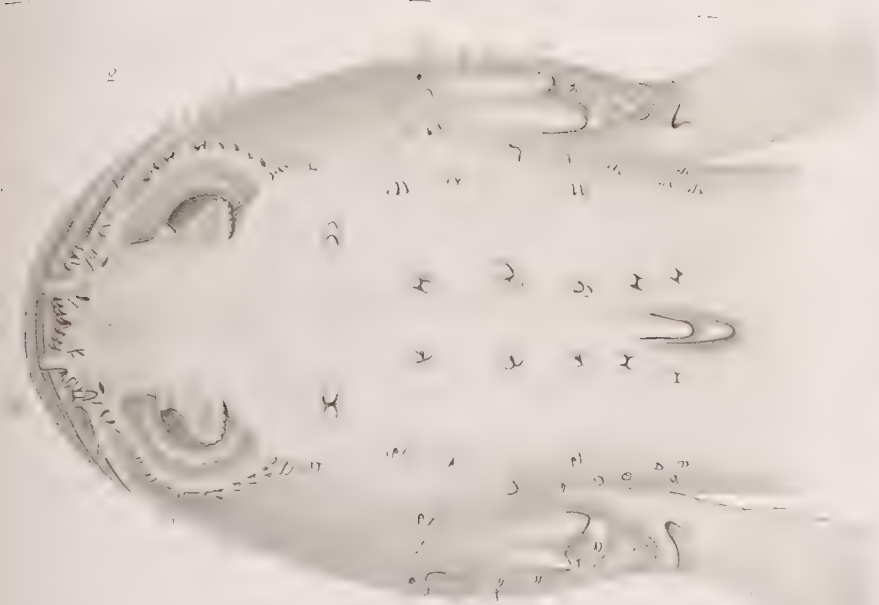
FIG. 2. Dorsal view of same. $\times 6$.

FIG. 3. Ventral view of same. $\times 6$.

FIG. 4. Dorsal view of skull. Natural size.

FIG. 5. Ventral view of mandible. Natural size. The grooves show the position of the lateral line organs.

In Fig. 4, for *JR* read *FR*.



EXPLANATION OF PLATE XVIII.

FIG. 6. Embryo of *Batrachus* at time of hatching, showing the different lines of organs well defined. $\times 15$.

FIG. 7. Side view of head of larva, showing sense organs on the surface. $\times 6$.

FIG. 8. Front view of same.

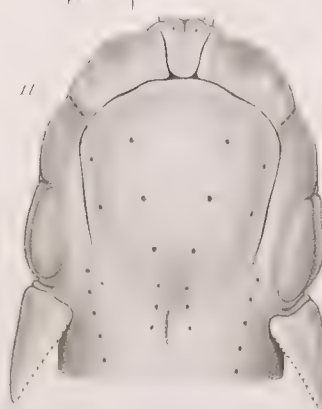
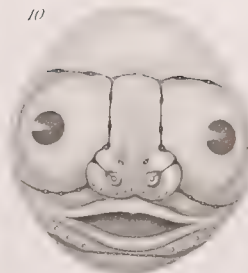
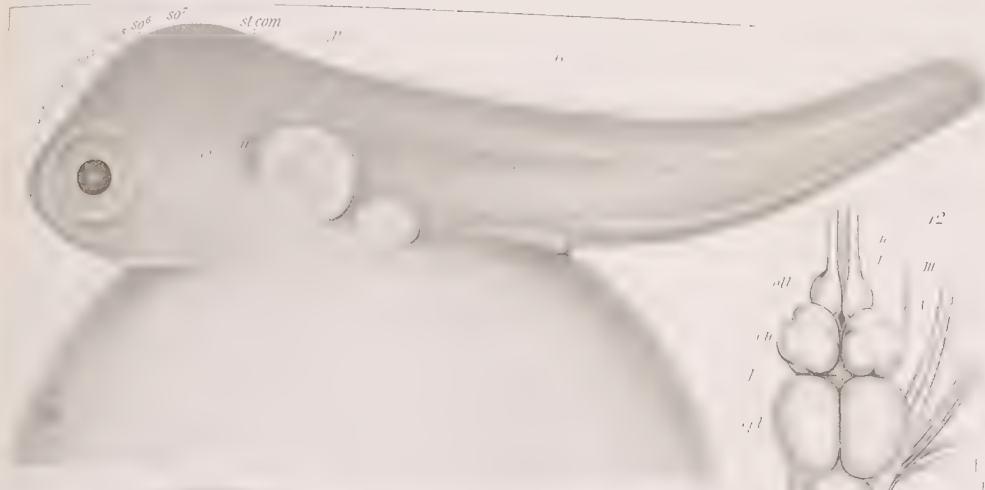
FIG. 9. Side view of head, a few days later, showing canals in process of formation. $\times 6$.

FIG. 10. Front view of same.

FIG. 11. Dorsal view of same.

FIG. 12. Dorsal view of brain, showing roots of cranial nerves. $\times 6$.

FIG. 13. Diagram showing connections between the *VII* and *X*. The intracranial commissure, and the anastomosis of the *recurrens facialis* with a branch from the *X*. The *VIII* has been omitted, as also the portion of the *X* innervating the branchial region.



EXPLANATION OF PLATE XIX.

FIG. 14. A horizontal section of an *Acanthias* embryo 17 mm. long, showing the growing point of the lateral line with its "pocket" and the nerve. Cam. Z. 16, oc. 3.

FIG. 15. Drawn from a preparation of the skin, showing the appearance of the cells of the organs at an early stage of their development. Cam. Z. 4, oc. 3.

FIG. 16. A vertical section through a sense organ, showing the relation of the connecting strand to the organ. Cam. Leitz 7, oc. 3.

FIG. 17. Preparation of skin showing the appearance of the rudiment of the lateral line organs with its enlarged growing end. Cam. Z. 4, oc. 3.

FIG. 18. A horizontal section of an embryo of *Batrachus* 7 mm. long, showing the position of the growing point of the line in its relation to the outer layer of ectoderm and to the muscles. Cam. Z. 16, oc. 3.

FIG. 19. View of same magnified. Cam. Z. 4, oc. 3.

FIG. 20. Cross-section through the enlarged portion of the line. Cam. Leitz 7, oc. 3.

In Fig. 16, for *m* read *n*.



EXPLANATION OF PLATE XX.

FIG. 21. Diagram showing the innervation of the lateral line organs of *Amia*. *Journ. of Morph.*, Vol. ii, No. 3, Pl. XLII (reduced).

FIG. 22. Diagram showing innervation of the lateral line organs of *Batrachus*. The lines in blue indicate the sense organ with the connecting strand.

FIG. 23. Diagram showing dorsal view of the same. The course of the nerves is shown on the right, and the position of the connecting strand, in blue, on the left. The short lines on each side of the organ represent the position of the paired flaps.

FIG. 24. View of left side of body of *Batrachus* one year old. Showing position of sense organs in adult. Natural size.

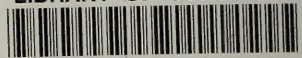
In Fig. 21, for *st.cbm.* read *st.com.*

In Fig. 22, in supraorbital line, supply 1, 2, 3, 4, 5, 6, as indicating the organs of that line.

For *d.b.nec.f.* read *d.b.rec.f.*

For *b.n.ll.* read *d.b.n.ll.*

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