

THE PHOSPHORESCENT ORGANS IN THE TOAD-FISH, PORICHTHYS NOTATUS GIRARD.

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I. INTRODUCTION.

FISHES described as possessing phosphorescent organs belong almost without exception to the deep-sea fauna. They live at depths where the light of the sun rarely if ever penetrates, and this fact is supposed to account for the process of evolution which has brought about the phylogenetic development of light-producing organs. It lent interest, therefore, to the study of phosphorescent organs in fishes when in 1889 a paper appeared, describing phosphorescent organs in *Porichthys*, a shore fish. The study of these organs was made on unfavorable material, as the author states, and as the structures described were so obviously different from phosphorescent organs in other fishes, it seemed desirable to reinvestigate the question.

It is my purpose in this paper to present the distribution, structure, and development of the phosphorescent organs in *Porichthys*, together with their surface relations to the lateral-line system of sense organs.¹ In the future I hope to follow with a second paper on the morphology of the lateral-line system, work now partially completed.

The results presented in this paper were obtained chiefly from the study of *Porichthys notatus* Girard. But I have also some material from *Porichthys nautopedium* Jordan and a new species of *Porichthys* kindly furnished me by Prof. C. H. Gilbert.

Porichthys notatus is found abundantly along the Pacific coast from Sitka to Panama. It is taken in early spring and summer at tide water where it comes to spawn. The eggs are cemented in a single layer to the under surfaces of stones, and, as the male remains with the brood until the young become free-swimming (when they are about one inch in length), it is comparatively easy to secure adults together with young. Adults are also taken in large numbers in the trawls on the fishing banks north of San Francisco in spring and summer. In winter they are very scarce on the banks.

In a surface view, the phosphorescent organs appear as bright silvery spots distributed in lines or rows over the surface of the body of the fish. The average number of organs is about 350 on each side of the fish, 700 organs in all. Of these, 275 on either side are located in eight lines on the ventral and ventrolateral surface of the body. In this region the rows are very conspicuous (Pl. XXXVIII, Figs. 1 and 2), but more obscure

¹ The material for this study was collected and the work begun at the Hopkins Seaside Laboratory, Pacific Grove, Cal., in the summers of 1892 and 1894. I am deeply indebted to the directors, Dr. O. P. Jenkins and Dr. C. H. Gilbert, for the privileges of the laboratory and for advice and encouragement. I wish also to express my indebtedness to Dr. C. O. Whitman for the privileges of a table at the Marine Biological Station, Woods Holl, Mass., during the summers of 1896 and 1897; also to thank the members of the instructing corps for suggestive criticism and advice. Miss Clapp has kindly allowed me to examine her manuscript on the Lateral-Line System of *Opsanus tau*, and has criticised my manuscript, as well as given me many suggestions as to methods of making preparations. And, finally, I am especially indebted to my wife, whose invaluable criticism and enthusiastic interest have been my constant support.

or sometimes entirely absent over the dorsal aspect of the body. Each organ, viewed from the surface, appears as a silvery spot more or less circular in outline and varying in size from a point scarcely visible with the unaided eye to .8 mm. in diameter. The larger organs are found on the ventral surface of the fish, the less conspicuous ones on the dorsal surface—a fact to be again referred to later in the paper. They are often surrounded by, or bordered on one side by, an increased amount of pigment. This is especially noticeable in organs on the sides of the body where the pigment is much increased in amount on the side of the organ away from the mid-ventral line.

The structures, indiscriminately designated by Test as “lateral-line organs,” “slime glands,” “mucous pores,” or “pores,” are in reality lateral-line sense organs of the kind designated as nerve hillocks by Merkel. Such an organ, viewed from the surface, presents a point on the epidermis free from pigment, the end of the sense organ itself with its immediately surrounding supporting cells. It is too distinct and characteristic in appearance to be mistaken by even the most casual observation.

The lines of phosphorescent organs and lateral-line organs are so closely associated in their distribution in the skin of the fish that they may be most economically mapped out together. Test did not discriminate between these two sets of organs. Terms he introduced, referring to lines of organs, will be indicated by quotation.

II. DISTRIBUTION OF THE PHOSPHORESCENT ORGANS AND THE LATERAL-LINE SENSE ORGANS.

The organs of both systems are arranged in lines or rows and are very constant in their relation to each other in any given row, also the rows are constant in their relative positions in different individual fishes. The number of organs in a given line of either phosphorescent organs or sense organs may, however, vary much in different individuals (see Table). The average number only will in most instances be given in the general description.

The lateral-line organs are located free on the surface with the exception of certain rows on the head which are in canals. These lines of canal organs form only a small part of the lateral-line system in *Porichthys*. Unless otherwise specified, surface organs are meant.

It is impossible to determine the homologies of the parts of the complex lateral-line system without a knowledge of the development of the sensory *Anlage* and of the innervation of the system, including the origin of the nerves in the central nervous system. Such a study has been made in part for only a few fishes, while the great mass of fishes remain unknown in this regard. It is necessary, therefore, while awaiting the development of our knowledge of the origin and distribution of the lateral-line nerves, to designate the groups of lateral-line organs in particular species by some sort of descriptive terms. The intention in this paper is not so much to name the groups in *Porichthys* as to describe their location by short descriptive terms that will serve temporarily, *i.e.*, until we have a surer foundation for establishing homologies between the parts of the lateral-line system in different species of fishes, when a permanent nomenclature may be adopted.

1. *Lines of Organs on the Body.*

The lateral row, *la* (Pl. XXXVIII, Figs. 1-3), begins on the side at a point posterior to the upper border of the pectoral fin and directly below the third dorsal ray. It runs straight back along the side to the upper third of the base of the caudal, and contains both kinds of organs. This line contains an average of thirty-six sense organs with a phosphorescent organ immediately below and generally one above each sense organ. In the lower series the phosphorescent organs are well developed and large, but the organs of the upper series are quite small and rudimentary; in fact they are often wanting, there being only an average of twenty-two in the fifteen specimens tabulated. The organs in this line correspond very nearly with the segments of the part of the body along which they lie. They are found above the grooves which mark the boundary between the myomeres.

The "pleural" row, *pl*, consists of parallel lines of phosphorescent organs and sense organs. The row of phosphorescent organs begins at a point posterior to the middle of the base of the pectoral and below the anterior ray of the dorsal fin. The line curves backward and downward to a point back of the lower edge of the pectoral and above the first anal ray, thence straight back along the side, ending usually above the twenty-third anal ray. The organs of this line vary in number from forty-three to sixty-two, or an average of fifty-three, and have no relation to the body segments. The row of sense organs is located immediately below the row of phosphorescent organs and follows the same general course. This row usually extends backward only to the thirteenth anal ray, but in three specimens from Alaska (see Table, Nos. 8-10) the row extends to the base of the caudal fin. There is an average of thirty-two sense organs in the row, excluding the three exceptions mentioned. In these three there are sixty, bringing the general average up to thirty-six.

There are two caudal, *ca*, lines of sense organs on each side the fin, located on the upper and lower thirds, respectively. These rows contain only sense organs, which are well developed at the base of the caudal, but become smaller toward the extremity of the fin. There are as many as twenty-five in each line in the oldest specimens, but the number varies greatly, increasing with the age of the specimen. These rows are in line with the lateral and pleural rows of sense organs, but they are not continuous with them.

The "anal" row, *a*, runs along the body on either side of the base of the anal fin from opposite the interspace between the second and third anal rays to the base of the caudal. The phosphorescent organs of this line correspond in position to the anal rays and are in pairs, with exceptions to be mentioned. The first organ is usually single; the next twenty-eight or twenty-nine, paired; the last six or seven, single. The last four or five organs are situated under the base of the caudal and are arranged in a markedly compact row. There is an average of thirty-six organs in this row, counting the pairs but once. The outer organs of the pairs are apparently larger than

the inner, but this appearance is in part due to the fact that the inner organs are more deeply buried in the angle of the base of the fin. The posterior two or three pairs are closely united. The anal row contains a single line of sense organs. There are thirty-four of these organs in the line. The first is placed just in front of the second pair of phosphorescent organs, and each successive one bears the same relation to its corresponding phosphorescent organ, except the last two, which are placed external to and just above the four or five phosphorescent organs along the base of the caudal.

The "ventral rows, *v*, form a parenthesis on the stomach," extending from the side of the anus three-fourths the distance to the ventral fin. The anterior ends of the two rows are usually continuous with each other, and comprise thirty-four phosphorescent organs on either side. The organs present a clear, circular outline without apparent increase of pigment around them. These rows are not accompanied by sense organs.

The "gastric" line of phosphorescent organs, *ga*, begins a little below the middle of the front of the base of the pectoral, curves forward, downward, then backward, around the lower edge of the pectoral; then extends straight back along the side of the belly to a point dorsal to the anterior edge of the anal papilla. The line contains an average of thirty organs, about ten in the curved portion and twenty in the straight part of the line.

The "gular" line, *gu*, begins a little back of the isthmus and runs parallel with its fellow backward to the posterior and ventral side of the ventral fin, then curves outward and backward to a point below the anterior end of the straight portion of the gastric line. There is an average of twenty-seven organs in this row. The gular line gives off a short spur of seven organs running forward along the external border of the ventral fin.

The gastro-gular line, *ga gu*, of sense organs begins at the isthmus somewhat anterior to the end and toward the median ventral side of the phosphorescent row, runs posteriorly parallel to the phosphorescent line to its end, then backward parallel to

the gastric row, curves upward around its posterior end, and terminates in close relation to the pleural row of sense organs (see Pl. XXXVIII, Fig. 1). There are fifty organs in the entire row.

The "scapular" row, *sc*, begins just back of the posterior pore of the temporal canal, runs straight back above the pectoral fin, then curves in toward the base of the dorsal fin, where it is continued into the dorsal row at the base of the third dorsal ray. There are seventeen sense organs in this row, with an average of ten phosphorescent organs alternating with them.

The straight part of the scapular row is accompanied by a scapular accessory row, *sc ac*, of three to five sense organs, with a small phosphorescent organ above each.

The dorsal row, *d*, extends along the dorsal surface of the body at the base of the dorsal fin from the third dorsal ray to the caudal peduncle. This row contains an average of seventy-one sense organs. Rarely phosphorescent organs are found between the first three or four organs of the row, but in such exceptional specimens they are always small and rudimentary.

Outside the dorsal row is an irregular line, or accessory row, *d ac*, which contains sense organs and rudimentary phosphorescent organs arranged as in the lateral line. The number of organs in this row is quite variable, an average of sixteen in five specimens (see Table).

2. *Organs of the Lower Jaw and Head.*

The branchiostegal row, *br*, begins in front of the isthmus and extends outward over the membrane of the gill-cover to the base of the lower branchiostegal ray; then along the membrane between the first and second rays almost to the edge of the gill-cover. There are thirty-four phosphorescent organs in this line and no sense organs.

The "mandibular" row, *md*, of phosphorescent organs extends around the inner rim of the ridge formed by the dentary bones. It contains twenty-two organs on either side.

The operculo-mandibular row consists of surface organs and canal organs. It begins on the side of the head at the anterior pore of the temporal canal. It runs downward on the surface

to in front of the opercular spine, where it sinks into a canal. This canal extends along the posterior border of the preopercle, around the angle of the mouth, and forward on the ventral surface of the mandible to near its anterior end, where the line comes again to the surface and ends at the symphysis of the jaw (Pl. XXXVIII, Fig. 2). There are eight pores or openings to the canal portion. This line contains twenty-one organs, seven at the upper free end, seven in the canal, and seven at the lower free end. At the upper free end there are occasionally rudimentary phosphorescent organs between the sense organs — an average of one.

There are two "opercular" rows, an upper and a lower. The upper row, *u op*, contains ten phosphorescent organs and fourteen sense organs. These are arranged in parallel lines, the phosphorescent organs above and the sense organs immediately below them. The line begins posterior to the second pore from above of the operculo-mandibular canal, and extends in a curve backward and upward, over the operculum, to a point posterior to the opercular spine. The row of sense organs is the longer of the two.

The lower row, *l op*, contains from two to ten phosphorescent organs, on an average four, and an average of seventeen sense organs, the phosphorescent organs occurring between the sense organs at the base of the line. The row begins opposite the third operculo-mandibular pore and extends backward and upward to near the posterior angle of the opercular flap. The curvature of the lower row is a little greater than that of the upper, the two ending near each other.

The infraorbital consists of two portions, a preorbital and a suborbital, each of sense organs. The preorbital or nasal portion is made up of a row of four to six organs from the posterior nasal opening to the base of the anterior nasal papilla, two pairs of organs between the anterior nasal papillae, and two to three more in a transverse line at the posterior base of the tube. The suborbital extends from the posterior nasal opening around under the eye to the anterior pore of the temporal canal. It contains fourteen sense organs and one large phosphorescent organ below the posterior border of the eye.

The temporal canal (Pl. XXXVIII, Fig. 3, *t*) corresponds to the squamosal of Allis in *Amia*. It contains a single canal organ. Above this canal are two free organs. The infraorbital, temporal, scapular, and dorsal form a continuous series of sense organs.

A short maxillary canal, *mx*, with two organs, extends along the maxillary bone below the posterior nasal opening. At its lower end are two free organs with a small phosphorescent organ above each in very old specimens.

A malar row of sense organs, *ma*, extends downward from the suborbital across the cheek to the angle of the mouth, thence along the mandible over the operculo-mandibular canal to its anterior end. There are thirty-one organs in this row, thirteen in the malar portion and eighteen in the mandibular. Two spurs are connected with this line, a short anterior spur of two organs from the middle of the cheek portion of the line and a second posterior one of four to five organs from the angle formed at the mouth.

The supraorbital line, *sup o*, is enclosed in a canal which begins by a pore at the median border of the posterior nasal opening, runs backward and inward toward the median line of the head, where it anastomoses with its fellow of the opposite side at a point in a transverse line drawn through the posterior border of the lens of the eye. Here the canals diverge and each runs to a point behind the eye a distance equal to half the diameter of the latter. This canal opens at its ends only. Five sense organs are found in the canal — three in the anterior part and two in the posterior limb.

The "frontal" group, *fr*, consists of two rows of organs. It is located over the posterior end of the frontal bone, about midway from the median line of the head to the outer edge of its flat top. The outer row of each group consists of an average of six sense organs, with five phosphorescent organs, alternating in a longitudinal row. The inner row is a shorter one, parallel with the posterior part of the outer row, and consists of from four to five sense organs with phosphorescent organs at the inner and outer edge of each sense organ. The phosphorescent organs of this group, like those of other dorsal groups, are especially variable in number and rudimentary.

The "occipital" row, *oc*, contains from nine to twelve sense organs, sometimes with a pair of rudimentary phosphorescent organs on the inner and outer side of each sense organ, sometimes with no phosphorescent organs. The row begins near the posterior edge of the spinous dorsal, curves first inward toward the median dorsal line, then outward and forward (see Pl. XXXVIII, Fig. 1).

In a species described from the Galapagos Islands, *Porichthys nautopedium* Jordan, the arrangement of phosphorescent organs and sense organs corresponds, group for group, with that given above. There are only slight variations from the average number of organs, except in the pleural row, which, like the pleural row of three specimens from Alaska (Table, Nos. 8-10), is continued back to the base of the caudal.

In the new species of *Porichthys* previously referred to, obtained recently at Panama by Dr. Gilbert, the location of the lines of phosphorescent organs and sense organs corresponds very closely with that in *Porichthys notatus*. Also the number of both kinds of organs, as will be seen by a reference to the appended table, Nos. 16 and 17, is very similar to the number in the common form. It may be noted, however, that on the dorsal surface, where in *Porichthys notatus* rudimentary organs are found, phosphorescent organs are wholly absent. The phosphorescent organs on the ventral surface of this species are not more than half as large as in the common species.

In general, we may say that the phosphorescent organs of the three species of *Porichthys* studied are always well developed and prominent along the ventral and ventro-lateral surfaces of the body, while along the dorsal surface they are markedly small and rudimentary, and are very variable in their development in the different specimens of the same species.

The sense organs, on the other hand, are quite constant both in their presence and the extent of their development in the different regions. The sense organs are accompanied by dermal papillae, two for each organ. These dermal papillae differ very much in the extent of their development, being most

marked in the nasal, dorsal, anal, and mandibular lines. In these lines they often reach a length of 2 mm., and are three and four parted at their ends.

III. STRUCTURE OF THE PHOSPHORESCENT ORGANS.

Organs from different parts of the body have a common general structure, differing only in minor details. It will, therefore, be sufficient to describe a typical organ in detail and later compare with it those organs which have a specialized form or structure.

The epidermis of *Porichthys* has no scales and is richly supplied with large, club-shaped mucous cells in all stages of development. The dermis is quite a thick layer of dense connective tissue bearing blood vessels, nerves, and pigment cells. The phosphorescent organs are imbedded in the deeper portion of this dermis.

Each organ consists of four parts (Pl. XXXVIII, Fig. 4, and Pl. XXXIX,^a Figs. 5 and 9), the lens, the gland, the reflector, and pigment.

1. *The Lens.*

In a typical organ, from the anal or ventral row, for example, the outer or more superficial portion of the organ consists of a group of cells, the lens (Pl. XXXIX,^a Fig. 5, 4). The surface of the lens directed toward the exterior, the distal portion, is oval or spherical in outline, while the deeper or proximal portion is projected into a more or less pronounced subconical form. The cells of the lens are polygonal in form in the center of the structure, becoming flattened toward the surface. At the distal surface the cells are quite regular and form a pavement-like layer (Pl. XXXIX,^a Figs. 5 and 9), but in the deeper conical portion the cells are very irregular in form, often with processes which interlace in a confused mass at the extreme proximal part. The lens cells have a small oval nucleus which is very sharply defined in contrast with the modified cytoplasm. The cell body is very dense, homogeneous, and highly refractive. The coagulation of this dense substance by reagents often slightly

separates the cells, thus rendering their outlines in sections very distinct.

The lens has no capillaries distributed to its substance. In Golgi preparations nerve fibers were found distributed to the superficial part of the lens and terminating among its cells in small free varicose ends. The number was, however, not greater than that found in the surrounding connective tissue of the skin and seems, therefore, of no special significance (Pl. XXXIX,^a Fig. 8).

2. *The Gland.*

The gland forms a shallow cup surrounding the proximal two-thirds of the lens. It is composed of cells varying greatly in size and shape (Pl. XXXIX,^a Figs. 5-7). The gland cells are held in a mesh of connective tissue and capillaries and in part by processes from the cells of the base of the lens. They have their long diameters placed vertical to that portion of the surface of the lens along which they lie. These cells have large round nuclei which are often vacuolated. The cytoplasm of the cells is very granular and is stained with the greatest difficulty. In alcoholic material these gland cells present an appearance which indicates that their granular constituents are largely dissolved out. In fact it is impossible to gain a true idea of the character of these cells from such material, as I found after many trials. On the other hand, the cells are beautifully preserved in Flemming's fluid and present in such preparations the structure shown in Pl. XXXIX,^a Figs. 6 and 7.

The gland is richly supplied with blood vessels, which enter around the distal border and also by puncturing the reflector below. The capillaries form a network among the gland cells and are in sections generally filled with red and white corpuscles.

3. *The Reflector.*

The reflector forms one of the most striking structures of the organ. It also is a cup-shaped mass which encloses the gland and the proximal portion of the lens, extending up around

the latter for over two-thirds of its surface (Pl. XXXVIII, Fig. 4, and Pl. XXXIX, Fig. 5). The reflector is composed of connective tissue, the matrix of which is modified into peculiar fine strands or fibrils, called spicules. These spicules very strongly reflect light. This property is very manifest even in the thinnest of sections where the reflector is dark gray or brown by direct light but bright silvery by reflected light. The spicules form a dense mass of fibrils somewhat regularly parallel with the surface of the lens. Small oval nuclei are scattered throughout the reflector, also a certain number of ordinary connective-tissue fibrils are scattered among the spicules, especially toward the periphery of the cup. That these fibrils are not "calcareous spicules," as von Lendenfeld describes for phosphorescent organs of *Scopelus* and other deep-sea forms, is evident, since they are not altered by nitric acid, nor, in fact, by any of the numerous fixing reagents used in their preparation.

Small blood vessels are found in the reflector, but only as they pierce the structure to reach the gland within.

4. *The Pigment.*

The pigment mass is composed of the large, many-branched type of cells characteristic of the pigment cells of the skin of fishes and amphibia generally. The cells are located around the outer and deeper surface of the reflector and vary in number in different organs. They are sometimes so numerous as to form dense masses, and again, as in the ventral or anal rows, there may be only three or four such cells to the organ.

IV. NERVE SUPPLY OF THE PHOSPHORESCENT ORGANS.

A most diligent and persistent effort was made to demonstrate the presence of a special nerve supply to the phosphorescent organs. Numerous preparations of the skin containing the organs were prepared by the methods which give specific nerve staining. By the iron-haematoxylin method and by the gold-chloride method, no nerves could be distinguished in the organs. By the Golgi method beautiful preparations were

obtained showing the distribution of nerves to the skin and to the epidermis, but in only two sections were nerves shown to have direct relation to the phosphorescent organ. The better one of these sections (Pl. XXXIX,^a Fig. 8) showed nerves branching over the surface of the lens. Whole mounts of the skin were made by the methylen-blue method of Bethe. These showed the most detailed network of nerve fibers lying in the connective tissue of the skin. Preparations containing both phosphorescent organs and lateral-line sense organs showed branches of the lateral-line nerve coming off the main stem and ending in the sense organs with almost diagrammatic regularity. Nerve fibers or bundles of nerve fibers were found in the skin above or below the phosphorescent organs, but no nerve bundles penetrated the phosphorescent organs and ended there. Two organs out of a very large number prepared contained each a single nerve fiber which entered the organ and terminated there. In one or two others single fibers seemed to terminate in the organ, but the fact could not be determined with certainty.

The facts set forth above, based on very favorable preparations, justify the conclusion that *the phosphorescent organs of Porichthys possess no specific nerve supply*. The few individual nerve fibers demonstrated to enter the organ may be considered as branches from the general nerve supply of the skin.

V. ORIENTATION OF THE ORGANS WITH REFERENCE TO THE SURFACE OF THE BODY.

A line passing through the middle of the three parts of the phosphorescent organ may be taken as its axis, and the position of this axis with reference to the body surface as the direction or position of the organ. In the ventral rows of the body the organs are directed downward, that is, the axes of the organs are almost or quite vertical with the surface of the body of the fish. The organs on the sides of the body and the lower part of the head are directed downward and slightly outward, and the axis of each organ thus makes quite a wide angle with the vertical to the surface. In the pleural row this angle is from

30° to 40°, while in the lower series of the lateral row it is often 80° or more ; in fact the axis is sometimes quite tangent to the surface of the body at that point. In this class of organs a variation from the typical arrangement of the parts may be noted. In a transverse section of such an organ, say from the pleural row, the deeper part of the cup of the reflector extends inward and upward (Pl. XXXIX^a, Fig. 10) ; that is, toward the dorsal part of the fish. It forms a somewhat deeper pocket than is formed by organs on the ventral surface. In such specimens the pigment is amassed around the upper or dorsal portion of the reflector. In these organs on the side of the body the conical base of the lens is relatively longer and is always in the axial line of the organ. The cells of the gland in such organs are arranged radially around the conical part of the lens.

The organs on the dorsal surface of the body and head have their axes vertical to the surface of the body. All these organs are small and rudimentary and irregular in their development, as shown by the fact that the lens is small and irregular in form, that the gland and reflector have more ordinary connective tissue in their structure, and especially by the inconstancy in the presence of the dorsal organs in different individual fishes.

VI. DEVELOPMENT OF THE PHOSPHORESCENT ORGANS.

The phosphorescent organs arise quite late in the development of the embryo. In skins of embryos 8.5 to 8.9 mm. in length, and in a transverse serial section of an embryo not measured but probably of about the same length, I find the first or incipient stages in the development of the rows of phosphorescent organs on the ventral surface of the body. The organs appear first in the ventral, gastric, branchiostegal, and apparently also in the anal rows at the same time. In the anal row it is not easy to determine their first appearance, owing to the changes accompanying the development of the fin.

In embryos 8 mm. in length the sensory Anlage of the lateral-line system is complete and the sense organs are sufficiently

well differentiated to be counted in skins. But the ventral and branchiostegal rows are not accompanied by sense organs, and, therefore, furnish a crucial test as to the origin of the organs. In the serial sections of the embryo mentioned above, the basal layer of cells of the epidermis of the ventral side of the body is slightly thickened in the region occupied by the adult ventral line (Pl. XL^a, Fig. 13). The thickening is produced by a more rapid increase in the number of the epidermal cells in the particular area.

In the gastric row of the same specimen there is a similar multiplication of cells just above the accompanying sensory Anlage (Pl. XL^a, Fig. 14). In this case the multiplication of cells shows a sort of center toward which the surrounding nuclei perceptibly converge. This is the beginning of a cell aggregation which soon proliferates into well-marked centers or groups, the antecedents of the individual organs of the line. In this incipient stage of the gastric organs the cells lie immediately against the cells of the sensory Anlage of the gastrogular row of sense organs, but they show no other evidence of origin from it. In skins it happened in one instance that the sensory Anlage of this row was torn free of the epidermis, and the cells along its upper border were apparently undisturbed. They were slightly increased in number, however, indicating a stage comparable to that from the ventral line figured in cross-section in Pl. XL^a, Fig. 13, or in the corresponding line in Pl. XL^a, Fig. 14.

Although it would seem impossible to affirm that the origin of the phosphorescent organs in the gastric row is independent of the sensory Anlage which has arisen by migration of cells, yet I am convinced that such is the case. The above facts, especially the independence of the origin of the rows above mentioned not associated with sense organs, form the basis of my belief that *the phosphorescent organs arise by local proliferation of cells from the epidermis in the region which they permanently occupy.*

The further progress in the development of the phosphorescent organ consists in the rapid multiplication of cells, giving rise to a distinct nodule which projects as a small papilla from

the inner surface of the epidermis (Pl. XL,^a Figs. 15 and 16). The orientation of the organ is determined in this very early stage. Organs of the ventral line are vertical to the surface of the skin, while organs of the ventro-lateral surfaces are oblique (Pl. XL,^a Figs. 15-20). In embryos 13 mm. long this papilla, in vertical section of ventral organs, presents the general outline of a finger-tip. It has a diameter of about six cells and is four to five cells deep. Pigment cells now appear in the connective tissue beneath the organ and are found in almost every section. In skins they show as the much-branched type of pigment cell spreading over the inner surface of the papilla. In specimens 14 mm. long there are from three to six such cells around each organ.

The next stage consists in the gradual separation of this papilla from the epidermis. The papilla becomes constricted where its sides are continuous with the general epidermis, the constriction continuing until complete separation occurs. At the same time a new layer of columnar cells forms in the epidermis and all evidence of the former union is obliterated. The separated mass now has a diameter of about .04 mm. and is found in embryos 18 to 20 mm. in length.

Soon after separation from the epidermis occurs, in fact before in some instances (Pl. XXXIX,^a Fig. 12, and Pl. XL,^a Fig. 21), the structure elongates slightly in the line of the axis of the developing organ and a differentiation occurs near the base, enabling one to distinguish in the mass two parts, an outer to become the lens and an inner the gland. No separation occurs between the two portions, yet the cells of each become more and more specialized in the direction of the cells of the adult lens and gland, respectively. By the time the embryo becomes free swimming, a length of about 25 mm., the organs possess the general characters of adult organs. Later growth consists in a great increase in size, due to the multiplication of the cells in the lens and gland, respectively.

Accompanying the differentiation of the lens and the gland there is a corresponding differentiation of the capsule. The connective-tissue cells of the dermis first form a cup-shaped aggregation around the base of the epidermal portion of the

developing organ (Pl. XL,^a Figs. 21, 23, and 24). The matrix of these connective-tissue cells is gradually converted into the modified fibrils which characterize the adult reflector (Pl. XXXIX,^a Figs. 9-11, and Pl. XL,^a Fig. 24). These fibrils are at first intermixed with a large amount of ordinary connective-tissue strands but ultimately form almost the entire mass. The pigment cells likewise increase in number and form masses of cells about the reflector, especially in organs on the side of the body.

Organs in different rows do not appear at the same time. Those on the mandible and ventral surface of the body appear first, and since they reach the highest development are taken as types. The lower series of the lateral line at 20 mm. is not farther advanced than organs of the ventral line at 11 to 12 mm. Those organs above the lateral line appear later and are always very rudimentary. In fact, such organs as I have designated rudimentary are never present above the lateral line and on the dorsal surface of the body up to the time when the embryos become free-swimming, a length of at least 25 mm.

VII. FUNCTION OF THE PHOSPHORESCENT ORGANS.

I have kept specimens of *Porichthys* in aquaria at the Hopkins Seaside Laboratory, and have made numerous observations on them with an effort to secure ocular proof of the phosphorescence of the living active fish. The fish was observed in the dark when quiet and when violently excited, but, with a single exception, only negative results were obtained. Once a phosphorescent glow of scarcely perceptible intensity was observed when the fish was pressed against the side of the aquarium. Then, this is a shore fish and quite common, and one might suppose that so striking a phenomenon as it would present if these organs were phosphorescent in a small degree would be observed by ichthyologists in the field, or by fishermen, but diligent inquiry reveals no such evidence.

Notwithstanding the fact that *Porichthys* has been observed to voluntarily exhibit only the trace of phosphorescence mentioned above, still the organs which it possesses in such num-

bers are beyond doubt true phosphorescent organs, as the following observations will demonstrate.

A live fish put into an aquarium of seawater made alkaline with ammonia water, exhibited a most brilliant glow along the location of the well-developed organs. Not only did the lines of organs shine forth, but the individual organs themselves were distinguishable. The glow appeared after about five minutes, remained prominent for a few minutes, and then for twenty minutes gradually became weaker until it was scarcely perceptible. Rubbing the hand over the organs was followed always by a distinct increase in the phosphorescence. Pieces of the fish containing the organs taken five and six hours after the death of the animal became luminous upon treatment with ammonia water.

Electrical stimulation of the live fish was also tried with good success. The interrupted current from an induction coil was used, one electrode being fixed on the head over the brain or on the exposed spinal cord near the brain, and the other moved around on different parts of the body. No results followed relatively weak stimulation of the fish, although such currents produced violent contractions of the muscular system of the body. But when a current strong enough to be quite painful to the hands while handling the electrodes was used, then stimulation of the fish called forth a brilliant glow of light from apparently every well-developed organ in the body. All the lines on the ventral and lateral surfaces of the body glowed with a beautiful light, and continued to do so while the stimulation lasted. The single well-developed organ just back of and below the eye was especially prominent. No luminosity was observed in the region of the dorsal organs previously described as rudimentary in structure. I was also able to produce the same effect by galvanic stimulation, rapidly making and breaking the current by hand.

The light produced in *Porichthys* was, as near as could be determined by direct observation, a white light. When produced by electrical stimulation it did not suddenly reach its maximal intensity, but came in quite gradually and disappeared in the same way when the stimulation ceased. The light was

not a strong one, only strong enough to enable one to quite easily distinguish the apparatus used in the experiment.

An important fact brought out by the above experiment is that an electrical stimulation strong enough to most violently stimulate the nervous system, as shown by the violent contractions of the muscular system, may still be too weak to produce phosphorescence. This fact gives a physiological confirmation of the morphological result stated above that no specific nerves are distributed to the phosphorescent organs.

I can explain the action of the electrical current in these experiments only on the supposition that it produces its effect by direct action on the gland.

The experiments just related were all tried on specimens of the fish taken from under the rocks where they were guarding the young brood. Two specimens, however, taken by hooks from the deeper water of Monterey bay, could not be made to show phosphorescence either by electrical stimulation or by treatment with ammonia. These specimens did not have the high development of the system of mucous cells of the skin exhibited by the nesting fish. My observations were, however, not numerous enough to more than suggest the possibility of a seasonal high development of the phosphorescent organs.

Two of the most important parts of the organ have to do with the physical manipulation of light — the reflector and the lens, respectively. The property of the reflector needs no discussion other than to call attention to its enormous development. The lens cells are composed of a highly refractive substance, and the part as a whole gives every evidence of light refraction and condensation. The form of the lens gives a theoretical condensation of light at a very short focus. That such is in reality the case, I have proved conclusively by examination of fresh material. If the fresh fish be exposed to direct sunlight, there is a reflected spot of intense light from each phosphorescent organ. This spot is constant in position with reference to the sun in whatever position the fish be turned and is lost if the lens be dissected away and only the reflector left. With needles and a simple microscope it is comparatively

easy to free the lens from the surrounding tissue and to examine it directly. When thus freed and examined in normal saline, I have found by rough estimates that it condenses sunlight to a bright point a distance back of the lens of from one-fourth to one-half its diameter. I regret that I have been unable to make precise physical measurements.

The literature on the histological structure of known phosphorescent organs of fishes is rather meager and unsatisfactory. Von Lendenfeld describes twelve classes of phosphorescent organs from deep-sea fishes collected by the *Challenger* expedition. All of these, however, are greater or less modifications of one type. This type includes, according to von Lendenfeld's views, three essential parts, *i.e.*, a gland, phosphorescent cells, and a local ganglion. These parts may have added a reflector, a pigment layer, or both; and all these may be simple or compounded in various ways, giving rise to the twelve classes. Blood vessels and nerves are distributed to the glandular portion. Of the twelve classes direct ocular proof is given for one, *i.e.*, ocellar organs of *Scopelus* which were observed by Willemoes Suhm at night to shine "like a star in the net." Von Lendenfeld says that the gland produces a secretion, and he supposes the light or phosphorescence to be produced either by the "burning or consuming" of this secretion by the phosphorescent cells, or else by some substance produced by the phosphorescent cells. Furthermore, he says that the phosphorescent cells act at the "will of the fish" and are excited to action by the local ganglion.

Some of these statements and conclusions seem insufficiently grounded, as, for example, the supposed action of the phosphorescent cells, and especially the control of the ganglion over them. In the first place, the relation between the ganglion and the central nervous system in the forms described by von Lendenfeld is very obscure, and the structure described as a ganglion, to judge from the figures and the text descriptions, may be wrongly identified. At least it is scarcely safe to ascribe ganglionic function to a group of adult cells so poorly preserved that only nuclei are to be distinguished. In the second place, no structural character is shown to belong to the

"phosphorescent cells" by which they may take part in the process ascribed to them.¹

The action of the organs described by him may be explained on other grounds, and entirely independent of the so-called "ganglion cells" and of the "phosphorescent cells."

Phosphorescence as applied to the production of light by a living animal is, according to our present physiological-chemical notions, a chemical action, *an oxidation process*. The necessary conditions for producing it are two — an oxidizable substance that is luminous on oxidation, *i.e.*, a photogenic substance on the one hand, and the presence of free oxygen on the other. Every phosphorescent organ must have a mechanism for producing these two conditions; all other factors are only secondary and accessory. If the gland of a firefly can produce a substance that is oxidizable and luminous on oxidation, as shown as far back as 1828 by Faraday, and confirmed and extended recently by Watasé, it is conceivable, indeed probable, that phosphorescence in *Scopelus* and other deep-sea forms is produced in the same direct way, that is, by direct oxidation of the secretion of the gland found in each of at least ten of the twelve groups of organs described by von Lendenfeld. Free oxygen may be supplied directly from the blood in the capillaries distributed to the gland which he describes. The possibility of the regulation of the supply of blood carrying oxygen is analogous to what takes place in the firefly and is wholly adequate to account for any "flashes of light" "at the will of the fish."

In the phosphorescent organs of *Porichthys*, the only part the function of which cannot be explained on physical grounds is the group of cells called the gland. If the large granular cells of this portion of the structure (Pl. XXXVIII, Fig. 4, and Pl. XXXIX,^a Figs. 5-7) produce a secretion, as seems probable from the character of the cells and their behavior toward reagents, and this substance be oxidizable and luminous

¹ The cells which von Lendenfeld designates "phosphorescent cells" have as their peculiar characteristic a large, oval, highly refracting body imbedded in the protoplasm of the larger end of the clavate cells. These cells have nothing in common with the structure of the cells of the firefly known to be phosphorescent in nature. In fact, the true phosphorescent cells are more probably the "gland cells" found in ten of the twelve classes of organs which he describes.

in the presence of free oxygen, *i.e.*, photogenic, then we have the conditions necessary for a light-producing organ. The numerous capillaries distributed to the gland will supply free oxygen sufficient to meet the needs of the case. Light produced in the gland is ultimately all projected to the exterior, either directly from the luminous points in the gland or reflected outward by the reflector, the lens condensing all the rays into a definite pencil or slightly diverging cone. This explanation of the light-producing process rests on the assumption of a secretion product with certain specific characters. But comparing the organ with structures known to produce such a substance, *i.e.*, the glands of the firefly or the photospheres of *Euphausia*, it seems to me the assumption is not less certain than the assumption that twelve structures resembling each other in certain particulars have a common function to that proved for one only of the twelve.

I am inclined to the belief that whatever regulation of the action of the phosphorescent organ occurs is controlled by the regulation of the supply of free oxygen by the blood stream flowing through the organ; but, however this may be, the essential fact remains that the organs in *Porichthys* are true phosphorescent organs.

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August 13, 1898.

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EXPLANATION OF PLATE XXXVIII.

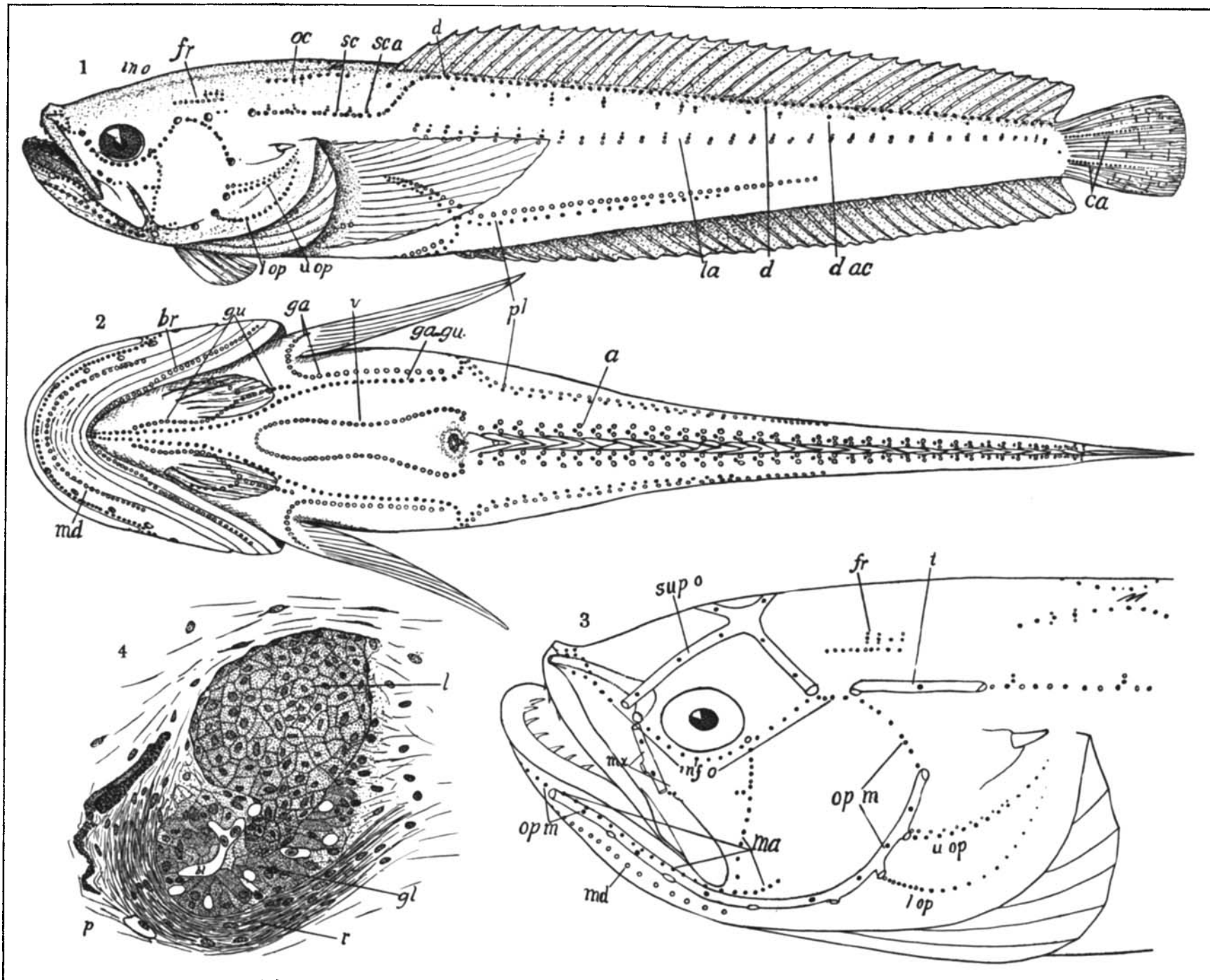
FIGS. 1 and 2. Lateral and ventral view of the lines of phosphorescent organs and lateral-line organs in the adult of *Porichthys notatus*. The representation of organs is diagrammatic. Small circles show the location of phosphorescent organs, and the dots the lateral-line organs. I am indebted to my friend, Edward Hughes, for the outlines upon which these two figures are constructed.

<i>a</i>	anal.	<i>md</i>	mandibular.
<i>br</i>	branchiostegal.	<i>mx</i>	maxillary.
<i>ca</i>	caudal.	<i>oc</i>	occipital.
<i>d</i>	dorsal.	<i>op m</i>	operculo-mandibular.
<i>d ac</i>	dorsal accessory.	<i>pl</i>	pleural.
<i>fr</i>	frontal.	<i>sc</i>	scapular.
<i>ga</i>	gastric.	<i>sc ac</i>	scapular accessory.
<i>ga gu</i>	gastro-gular.	<i>sup o</i>	supraorbital.
<i>gu</i>	gular.	<i>t</i>	temporal.
<i>la</i>	lateral.	<i>u op</i>	upper opercular.
<i>l op</i>	lower opercular.	<i>v</i>	ventral.
<i>ma</i>	malar.		

FIG. 3. Lines and canals on the head. For explanation, see Figs. 1 and 2.

Figs. 4 to 24 are drawn with camera lucida. Figs. 4 to 8 represent the structure of adult phosphorescent organs, and Figs. 9 to 24 show the stages in the development of the phosphorescent organs of *Porichthys notatus*. The orientation of each organ with reference to the dorso-ventral plane of the fish is indicated by a short arrow pointing ventrally. Every section of epidermis shows numerous large mucous cells, many of which are empty.

FIG. 4. Cross-section of an adult organ in a new *Porichthys* from Panama. The gland shows several capillaries, all in cross-section but one. *l*, lens; *gl*, gland; *r*, reflector; *p*, pigment; *bl*, blood vessel.



EXPLANATION OF PLATE XXXIX.²

FIG. 5. Cross-section of a ventral organ in *Porichthys notatus* Girard. *l*, lens; *g'*, gland; *r*, reflector; *bl*, blood vessels. In this section only a small amount of pigment shows to the left.

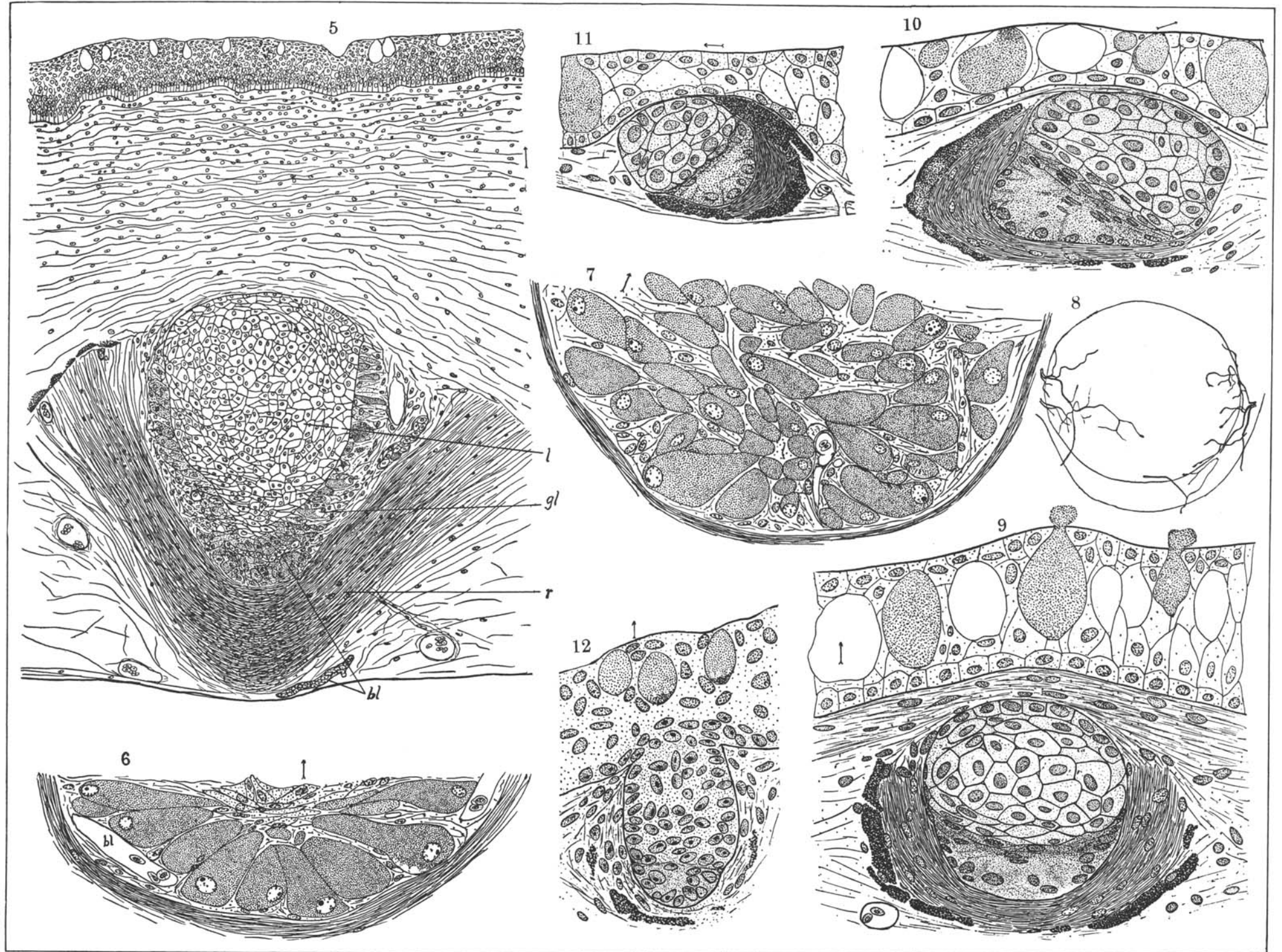
FIG. 6. Section of the deeper portion of a phosphorescent gland highly magnified to show the character of the cells. Flemming preparation.

FIG. 7. A somewhat oblique section of the deeper portion of a gland a little to one side of the center of an organ. Flemming preparation.

FIG. 8. The nerves distributed around the lens. Lens in outline. Golgi preparation.

FIGS. 9-11. Sections through a ventral, a pleural, and a lateral organ, respectively, of an embryo just before becoming free-swimming. The orientation of the organ with reference to the epidermis varies according to the position on the body. These three figures should follow in stage of development that shown in Fig. 24.

FIG. 12. Section of an embryonic organ just separating from the epidermis. This organ shows a differentiation even before it is cut off from the epidermis. Compare with Figs. 21 to 23.



EXPLANATION OF PLATE XL^a

FIG. 13. Cross-section of a ventral organ at its first recognizable stage. Only a slight aggregation of cells in the basal layer of the ectoderm has appeared. This row is not associated with a lateral-line sense-organ Anlage. Embryo about 9 mm. long.

FIG. 14. Cross-section of gastric organ associated with sense-organ Anlage, *san*. From the same embryo as Fig. 13.

FIG. 15. Cross-section of a pleural organ of an embryo 14 mm. long. The sensory Anlage shows to the left of organ.

FIG. 16. Section of a gular organ just external to the base of the ventral fin. Same embryo as Fig. 15.

FIG. 17. An organ from the same region as Fig. 16, but associated with a sense-organ.

FIG. 18. A pleural organ slightly older but from the same embryo as Fig. 15. *san*, sensory Anlage.

FIG. 19. An inner anal organ beginning to separate from the epidermis. Same embryo as Fig. 15.

FIG. 20. Section through a pair of anal organs, showing a different degree of development. Same embryo as Fig. 15.

FIGS. 21 and 22. Organs in process of separation from the epidermis. Compare with Fig. 12.

FIGS. 23 and 24. Organs separated from the epidermis. The lens, *l*, and the gland, *gl*, are distinguishable, and the reflector, *r*, is forming from the connective tissue. Pigment cells, *p*, are arranged around the outside of the reflector.

