

AN ABSTRACT OF THE THESIS OF

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Myctophids of the Genus Lampanyctus

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A comparative study was made of the morphology and histology of three major groups of light organs in the genus Lampanyctus of the family Myctophidae for the species, L. leucopsarus, L. ritteri, L. nannochir, and L. regalis. The species can be divided according to their ranges in depth, the first two named above coming to surface waters at night, the other pair remaining at greater depths. The organs studied included complex organs on the trunk ("Schusselformigie" organs) and in the lower jaw (branchiostegal organs), and less specialized organs on the caudal peduncle (infra- and supracaudal organs). The morphology of the three groups was found to vary with species and depth, in size and form of the constituent elements, but otherwise supported and supplemented previous observations made for other genera of the family. The elements of the most complex organs (Schusselformigie" organs) consisted of a lens, photogenic gland, vascular and connective tissue, and an inner scale and reflector backed by pigment. The lens and inner scale were lacking in the branchiostegal organs.

The less specialized caudal organs consisted mainly of glandular tissue interspersed with blood vessels and connective tissue. Changes in morphology of the trunk organs of the deeper animals were found. Included were a marked decrease in the size of the organs in L. regalis and a lessening in amount of glandular tissue in L. nannochir. The most significant histological difference was the unusually large capillary bed found in the trunk organs and branchiostegal organs of L. nannochir which contrasts with a very sparse blood supply to these organs in L. regalis. However, the caudal organs of these species did not manifest this divergence in structure, suggesting a difference in function between the two groups of organs. This interpretation was supported somewhat by the observed difference in luminescence of the two groups. The branchiostegal and trunk organs produced a continuous low intensity luminescence while the caudal organs displayed a more brilliant intermittent flashing. An additional histological difference was the prolific supply of nerves to the caudal organs and the conspicuous lack of nerves to the complex trunk organs. Large nerve branches to the branchiostegal organs, however, did not support a correlation between intensity and character of light produced and the degree of innervation. A further study of physiological mechanisms controlling luminescence in these species is needed.

THE COMPARATIVE HISTOLOGY OF LIGHT
ORGANS IN FOUR PACIFIC MYCTOPHIDS
OF THE GENUS, LAMPANYCTUS

by

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THE COMPARATIVE HISTOLOGY OF LIGHT ORGANS IN
FOUR PACIFIC MYCTOPHIDS OF THE GENUS, LAMPANYCTUS

INTRODUCTION

The upper oceanic depths off the coast of Oregon are inhabited by a phylogenetically diverse community of animals associated with the mesopelagic environment of the open sea. Many of these forms undergo regular diurnal migration from the surface waters at night to deeper water in the daytime. Many members of these group have the ability to produce light of varying degrees of intensity and luminescence. Among the mesopelagic fish, the lantern fish have developed highly specialized groups of organs, the photophores, for the emission of light. The genus Lampanyctus is representative of a large cosmopolitan family of lantern fish, the Myctophidae, of the Order Inioi.

The sub-family, Myctophinae, which includes Lampanyctus, is conspicuous in the possession of numerous photophores arranged in complex patterns over the ventral and lateral surfaces of the body. Their patterns of distribution and structural features are characteristic of the subfamily (Frazer-Brunner, 1949). The majority of the organs are discrete circular organs shallowly embedded in the skin and underlying muscle. Other less specialized organs may also be present, but they are not as constant in their appearance throughout the subfamily.

A classification of photophore types was constructed by Brauer (1908) after a general survey of a large number of myctophid species. He divided them into the following six groups:

- 1) Bowl-formed or "Schussselformigie" Organs.
- 2) Light Plates or "Leuchtplatten".
- 3) Light Scales or "Leuchtschuppen".
- 4) Branchiostegal Organs.
- 5) Orbital Organs.
- 6) Numerous less developed organs about the head and trunk.

The histology of light organs in Myctophidae has been previously investigated by numerous investigators: Ussow; Leydig (1881); Guppy (1882); Emery (1884, 1879); von Lendenfeld (1887, 1905); Gatti; Brauer (1908); and Oshima (1911). Only two myctophid species have been described by modern workers: Nicol (1958), and Iwai and Okomura (1960). Of the early studies, only the works of Brauer and Gatti deal extensively with this family. Gatti (discussed by Brauer) describes the major classifications of organs in most of the Mediterranean species (Brauer, 1908). Still more monumental in scope and detail is the work of Brauer himself in which he describes all major classifications of organs in eighteen species of myctophids from the Mediterranean, Atlantic, and Indian Oceans.

Four species, belonging to the genus Lampanyctus, commonly occur off the coast of Oregon. Two species, L. regalis and L. nannochir, are predominantly deep, seldom being taken above five hundred meters. The two remaining species, L. ritteri and L. leucopsarus display regular diurnal migration from below five

hundred meters in the daytime to the upper two hundred meters at night (Pearcy, 1964). The bathymetric range of closely related species is complimentary in each case. L. leucopsarus, a predominant form in surface waters at night, has as its closest relative, L. nannochir, which typically remains below five hundred meters in the water column. Likewise L. ritteri, a little deeper in the upper two hundred meters at night than L. leucopsarus, is more closely related to L. regalis which rarely appears above two hundred meters.

A survey of the literature reveals that the histology of none of the four species of Lampanyctus located off Oregon has previously been described in any detail.

The question of function of photophores has been variously speculated. The possibility of more than one function is suggested from the observations of Beebe, in which he observed small crustacea attracted to the ventral lights of Myctophum cocci, "whereupon the myctophid twisted around and seized several of the small beings" (Beebe, 1944). The brilliant flashes of the caudal organs (light plates) are considered by Beebe to be either of sexual significance, or of importance in escape and defense. A similar function of caudal organs has been suggested by Bolin (1961).

The most recent theory on the function of ventrally located photophores characteristic of many pelagic teleosts, crustacea, and cephalopods, has been proposed by Clark (1963). Based on the similarity in structure of photophores in these diverse groups, the quality of light emitted (Nicol, 1960), and the diurnal migratory habits of so many pelagic animals, Clark has suggested that ventral

photophores serve as a "counter-shading mechanism" which aids in the concealment from predators coming up from below.

It is the purpose of this study, then, to make a histological comparison of the major types of light organs of these four species of Lampanyctus having differences in bathymetric range. In addition it is hoped that such observations as can be made of size, luminescence, and innervation of photophores will reveal more information regarding mechanism and function of light organs in this family.

METHODS AND MATERIALS

The material for the following study was collected aboard the R/V Acona by the author between the dates of December, 1963 and July, 1964.

The four species selected for the study were:

Lampanyctus (Stenobrachius) nannochir Gilbert, 1891.

Lampanyctus (Stenobrachius) leucopsarus Eigman and Eigman, 1890.

Lampanyctus (L.) ritteri Gilbert, 1915.

Lampanyctus (L.) regalis Gilbert, 1891.

Identifications were made with the aid of Bolin (1939) and Frazer-Brunner (1949).

Live fish were taken immediately from samples collected with a six foot Isaacs-Kid Midwater Trawl, having either a half meter, "0-mesh" cod end, or a "multiple sampling" device gathering samples at three different depth intervals. The fish ranged in length from 50 mm to 113 mm. Whole fish were fixed in Bouin's Fixative or in neutral formalin (10%). It was reasoned that adequate fixation of the desired organs occurred because of their integumentary position immediately below the epidermis.

Difficulty in obtaining suitable material was encountered, especially with the deeper species. In many cases the swirling action of the net completely stripped fish of their scales and underlying photophores. Also the relatively less common occurrence of the deeper species made it difficult to obtain good specimens.

Of the six groups of photophores, only three were selected on the basis of possible differences in function. The organs included were 1) the branchiostegal organs, 2) the "Schussselformigie" organs of the body and trunk, and 3) the infra- and supracaudal organs of the caudal peduncle. The positions of these organs have been referred to by letter and number designations that were first introduced by Brauer (1908), and have been carried on by Bolin (1939) and others. By this system the branchiostegal organs have been referred to as the Br, the infra- and supracaudal organs as the Inf and Suc respectively, etc. The supraorbital organs, and the organs of the operculum were not included because of their less obvious prominence.

Material was embedded in paraffin (melting point, 56-58° C) using standard embedding procedures. Sections were cut 7-10 microns for general work and 5-7 microns for the study of nerves. Longitudinal and transverse serial sections were prepared for each of the three groups of organs studied for each species.

One general and two specific stains were used in the course of the study: Harris' Hematoxylin, for general work; Masson's Trichrome, for collagenic fibers; and Foote's Reticular Stain, for reticular connective tissue.

In some instances Von Ebner's Fluid was used to decalcify surrounding bone prior to embedding.

OBSERVATIONS

OBSERVATIONS ON BIOLUMINESCENCE

Observations of bioluminescence have been at times unreliable and not too clear. They have not been particularly elucidated in this study. The extreme stress provoked by the methods of sampling undoubtedly altered the typical luminescent reaction. Thus these observations cannot be considered a good index to the actual luminescent activity that occurs in the environment. It appears that there is a difference between the stimulus required to invoke luminescence in the infra- and supracaudal glands, and that required to invoke response in the branchiostegal organs and the "Schussselformigie" organs on the trunk. This disparity is supported by the observations of Beebe (1944), and especially by the observations of Oshima (1911) who has noted the same kinds of phenomena that will be described here.

Direct observations were made of actively swimming L. leucopsarus. It has not been possible to obtain specimens of the other three species for comparable recordings. Freshly caught animals were placed individually into trays and allowed to swim about freely. A dim reflection was perceived from the bottom of the tray which appeared to be brighter toward the head end of the fish. In no case did the ventral organs flash. However, periodical spontaneous flashes were emitted from the caudal organs. The intensity of this illumination was greater than the general glow mentioned. The unhampered fish at first produced a more intense illumination which gradually

extinguished. Replacing of the sea water brought about a renewed continuous glow from the ventral photophores.

Various methods of inducing luminescence, in freshly caught animals, were tried at sea for this work. Injections of adrenalin had no effect in eliciting response. The same held true for the use of dilute solutions of formalin or ammonia. The application of a gentle mechanical stimulation caused a progressive continuous glow to spread out from the center of stimulation. The reaction was not one of intermittent flashing as reported by other investigators (Oshima, 1911; Beebe, 1944), nor was there an immediate response from the caudal glands. Continued stimulation, however, eventually evoked a series of brilliant flashes from the caudal organs that contrasted severely with the continuous dim glow of the other organs.

ANATOMICAL ARRANGEMENT OF PHOTOPHORES

The arrangement of light organs is similar in each of the four species studied. Variations that exist are minor but serve as important landmarks in identification. The distribution of photophores is adequately described in keys to the species (Bolin, 1939; Frazer-Brunner, 1949). The following descriptions, given for orientation, are for Lampanyctus.

"Schussselformigie" Organs. These constitute the majority of the organs found on the fish and are all located below the lateral line.

The most ventral of these organs exhibit an obvious paired linear arrangement to either side of the mid-ventral line. The organs show a regular periodic spacing which is interrupted at various places dividing them into groups (Brauer, 1908) as follows (Figure 1, p. 12):

Maculae pectorales (PO)

Maculae ventrales (VO)

Maculae anales anteriores (AOa)

Maculae anales posteriores (AOp)

Maculae praecaudales (Prc)

The PO are the most anterior group. They lie on either side of the midline of the belly in front of the pelvic fin. There are five in all of the species studied, the fourth being positioned slightly above the others.

The next group, the VO, lie posterior to the base of the pelvic fin and extend almost to the anal pore. The number may

vary from four to five depending on the species.

The AO group continues behind the anus, on either side of the anal fin, toward the tail, almost to the caudal fin. The posterior end of the anal fin divides the AO into the more anterior AOa and the more posterior AOp. The number of AO may vary, depending on the species, from five to eight for the AOa, and from six to nine for the AOp.

The fourth group, the Prc, originates at about the level of the first caudal fin ray, and may or may not be continuous with the AOp series. These extend in a sharp arc toward the lateral line and differ in number from three to five according to species.

Above the ventral series the organs are more scattered in their arrangement. These have also been divided into groups. They are the following:

Maculae posterolateralis (Pol)

Maculae supra-anales (SAO)

Maculae suprapectoralis (PLO)

Maculae subpectorales (PVO)

The Pol exist as one or two organs which form a steep angle, toward the lateral line, with the rear AOa members. The number is one in L. nannochir and L. leucopsarus, and two in L. ritteri and L. regalis.

The SAO are three in number in all four of the species and form various angular arrangements above the more ventral VO series. The patterns are species specific.

The PLO and the PVO lie above the PO series, generally between the pectoral fin and the operculum. A single PLO is positioned above the base of the fin, while the PVO, two in number, form a steep almost vertical angle below the fin.

Branchiostegal Organs. The branchiostegal organs (Br) are three in number in all members of the family (Frazer-Brunner, 1949). They are located in elongated grooves on either side of the lower jaw within the branchiostegal membrane and are continuous with the most ventral organ series. In fixed material they are indistinct, but in life the overlying tissue is transparent and they show up readily.

Infra- and Supracaudal Glands. The infra- and supracaudal glands are narrow, homogeneous bands of whitish tissue on the dorsal and ventral midlines of the caudal peduncle. Both are present in all four of the species studied. The infracaudal gland lies between the paired ventral AOp series. The supracaudal gland lies by itself.

Other Light Organs. Other light organs occurring about the orbit of the eye and on the operculum are not as prominent in this genus as in others (Frazer-Brunner, 1949). These are the suborbital (Vn) and the two Maculae operculares (Op). The Op are poorly developed and therefore not readily apparent. The Vn are well developed, but deeply embedded and likewise not easily seen. In L. ritteri and L. regalis there is also an inconspicuous organ, the Ce, at the anterior end of the lateral line (Frazer-Brunner, 1949).

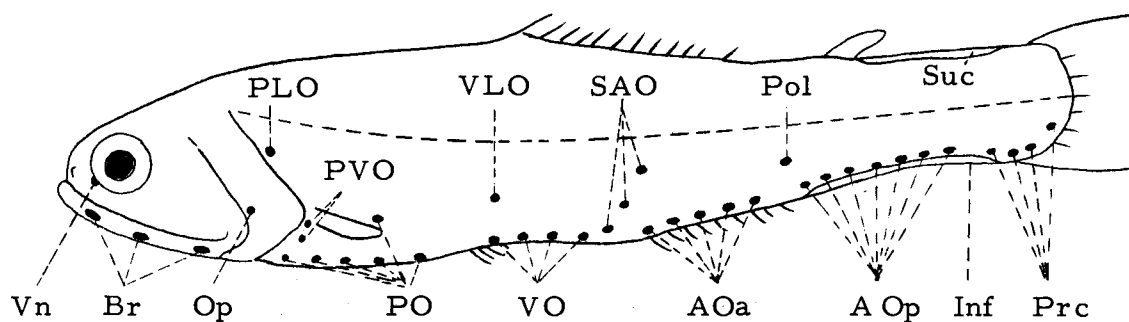
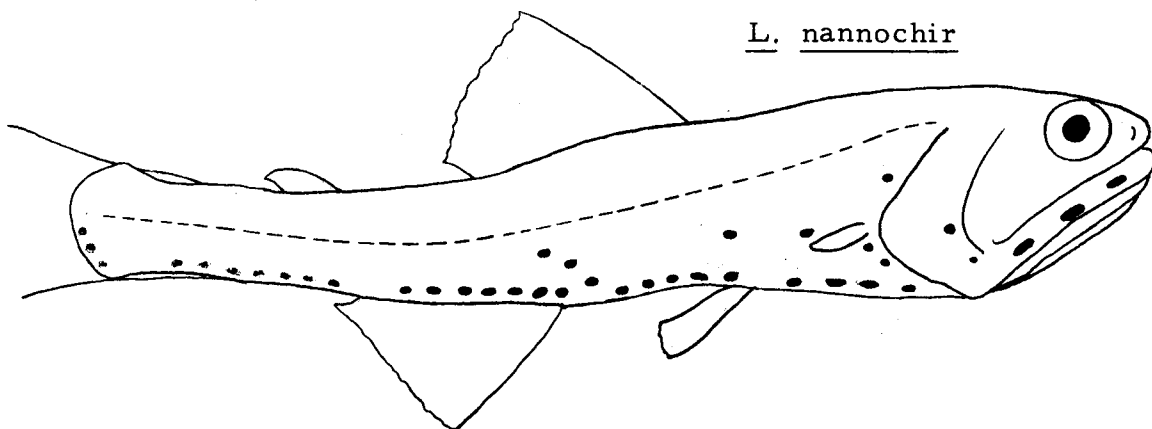
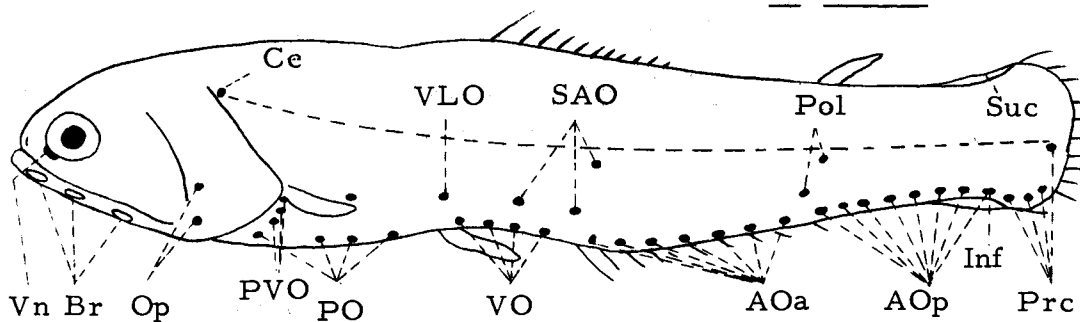
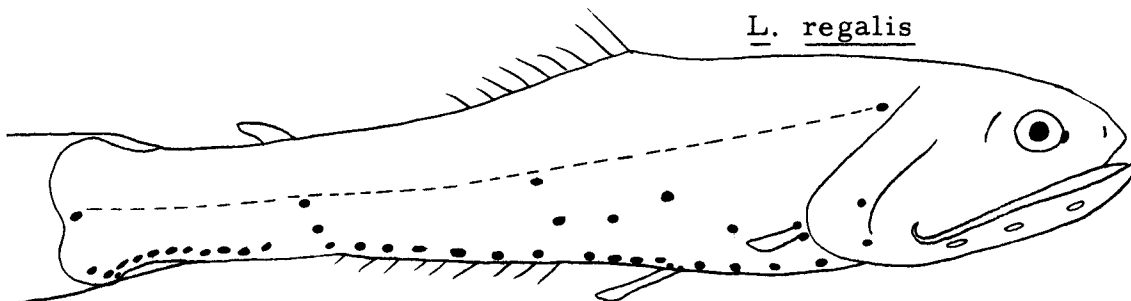
L. leucopsarusL. nannochirL. ritteriL. regalis

Figure 1. Photophore arrangements in the four species of *Lampanyctus* off the Oregon Coast. Letter designations after Bolin(1939).

PHOTOPHORE SIZE

Measurements of the diameter of the lens, the reflector, and the distance between photophores were made for each of the four species of Lampanyctus in this study. "Schussselformigie organs" from three regions of the trunk were selected; namely the AO, VO, and PO. Approximately nine or ten fish of each species were used for the measurements. A summary of the mean values of these measurements together with the standard deviation are presented in Table 1, p. 15.

The values shown in the table are average diameters and distances between photophores (in mm) calculated for a fish having a standard length (Ichthyological definition of "standard length" is the distance from the tip of the jaw to the end of the hypural plate.) of 80 mm. The actual range of length was from 44 mm to 115 mm, with the widest range being represented by L. regalis (from 44 mm to 112 mm). The measured diameters of the PO are plotted against standard length in the graph (Figure 2, p. 16). It is apparent from the graph that there is considerable scattering of points indicating a variability in size of the photophores for any particular sized animal. Oshima (1911) made similar measurements of the photophores of Myctophum watasei which ranged in length from 34 mm to 155 mm. His results showed a faster growth in size of the photophores in relation to growth in length of the body. The results obtained for L. regalis indicate otherwise, at least within the length range measured; Figure 2 indicates a direct relationship between the size of the photophore and the length of the fish.

The results in Table 1 do not show much difference in size of light organs for three of the species. The difference in size between species is not as large as the difference shown by a rostral-caudal comparison of size within a given species. The organs of L. regalis, nevertheless, are generally smaller than those of the other three species. The next largest organs are those of L. nannochir, L. leucopsarus, and L. ritteri, increasing in that order. There is some reversal in order for the latter two species, depending on whether the diameter of the reflector, or the diameter of the lens is taken as a criterion of size.

In all cases there is a gradual increase in the size of the photophores from the caudal to the rostral end of the animal. This seems to be compensated for by a parallel increase in distance between photophores, anteriorly.

TABLE I

Relative measurements of (I.) lens diameter, (II.) reflector diameter, and (III.) distance between photophores. Measurements are in millimeters based on a standard 80 mm fish.

Species:	<i>L. nannochir</i>	<i>L. regalis</i>	<i>L. ritteri</i>	<i>L. leucopsarus</i>
I. A0	0.26 \pm 0.02	*0.20 \pm 0.03	*0.33 \pm 0.04	0.27 \pm 0.03
V0	0.30 \pm 0.03	*0.28 \pm 0.06	0.45 \pm 0.04	0.42 \pm 0.06
P0	*0.33 \pm 0.20	-----	*0.50 \pm 0.04	0.51 \pm 0.08
II. A0	0.58 \pm 0.06	0.35 \pm 0.06	0.54 \pm 0.05	0.66 \pm 0.10
P0	0.66 \pm 0.03	0.52 \pm 0.07	0.74 \pm 0.06	0.66 \pm 0.11
V0	0.78 \pm 0.05	0.58 \pm 0.08	0.80 \pm 0.04	0.88 \pm 0.11
III. A0	1.84 \pm 0.16	1.84 \pm 0.24	1.60 \pm 0.08	2.00 \pm 0.16
V0	1.76 \pm 0.16	2.24 \pm 0.40	2.56 \pm 0.32	2.00 \pm 0.48
P0	4.24 \pm 0.64	3.28 \pm 0.32	3.60 \pm 0.48	3.68 \pm 0.32

* Mean value represented was determined from less than six fish.

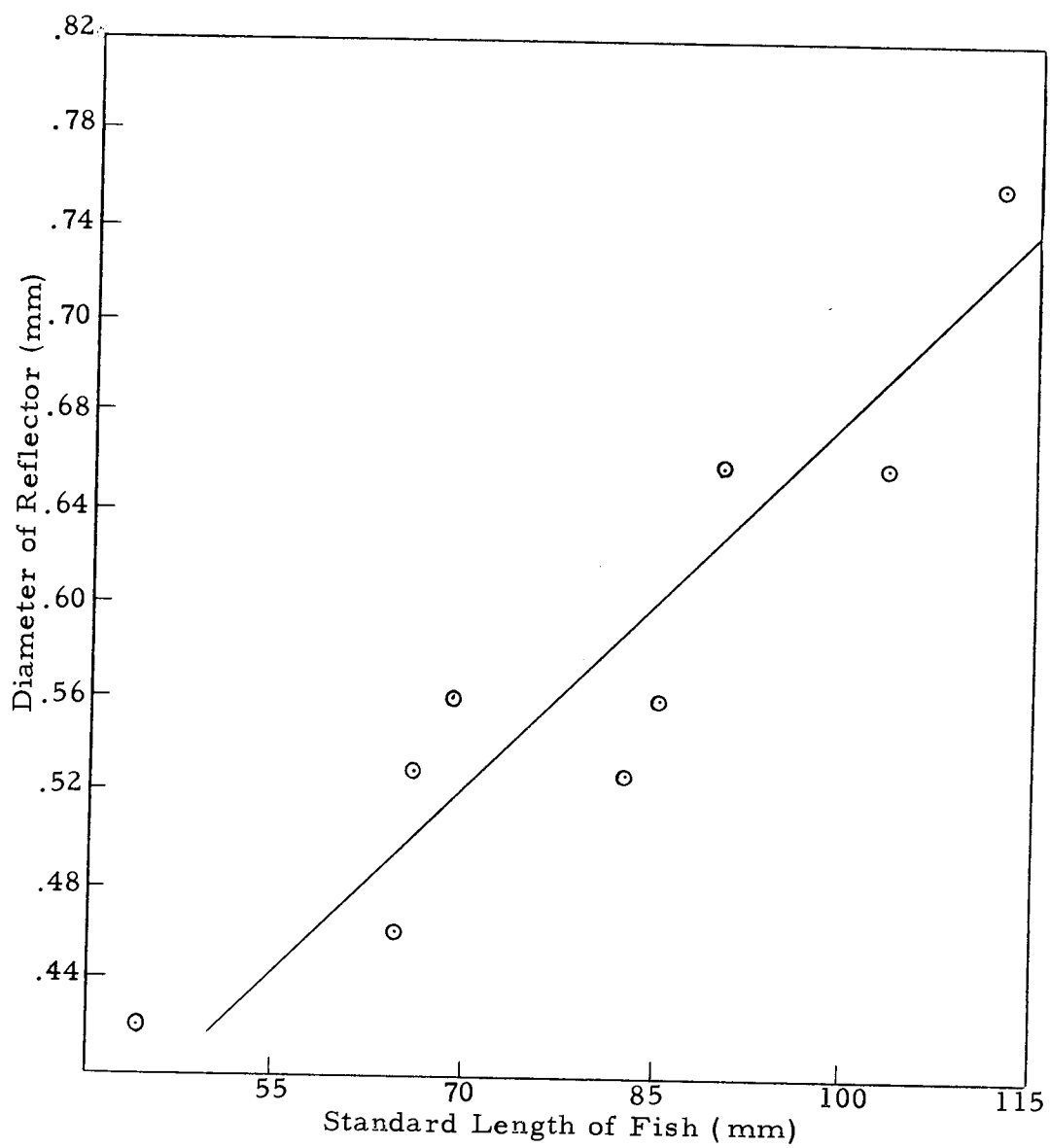


Figure 2. Reflector diameter of the PO of Lampanyctus regalis plotted against standard length of fish (from rostrum to the tip of the hypural plate).

ANATOMICAL FEATURES OF PHOTOPHORES

The large structural components encountered in the light organs of Lampanyctus are not different from the features described for the entire family (Frazer-Brunner, 1949). However, species variability in size and form of the anatomical elements was noted. The following observations were made for the four species used in this study.

"Schusselformigie" Organs.

1. Lampanyctus leucopsarus (Plate I, 1). The individual "Schusselformigie" organs lie under the center of a scale which in undamaged specimens is covered by a delicate epidermis. The scale is underlain by numerous melanophores which, under high dissecting power (60X), reveal many dendritic processes. The central part of the scale, overlying the organ itself, is free of pigment and is in the form of a clear convex lens. The lens is free of the concentric lamellar ridges clearly marking the surface of the rest of the scale.

Surrounding the lens is a more or less horse-shoe-shaped band of pigment the open end of which is directed ventrad (Plate II, 2a). The pigment is more concentrated at the sides and ends of the arms of the horseshoe. The pigment band apparently consists of two layers, one of which is adherent to the lens-containing scale and is removed with it; the other remains in the dermis as a peripheral band around the photophore. The latter appears to infringe somewhat over the ventro-lateral edges of the organ.

The glandular portion of the organ lies within a disk-shaped

plexus of vascular and connective tissue. It forms a crescentric mass of denser tissue which arches dorsally and extends five or six finger-like projections ventrally. The bulk of the tissue is homogeneously granular and translucent.

If the photophore is removed a shallow basin-shaped depression is left and a partially transparent scale is exposed. It also can be removed without disrupting its form and a lightly pigmented membrane, the reflector, lines the depression that is left.

2. Lampanyctus nannochir (Plate I, 2). The arrangement of components in the "Schussselformigie" organs of L. nannochir is similar to that of L. leucopsarus, with the exception that the pigmented band surrounding the lens is broader (Plate II, 1a). The band is approximately the width of the lens all the way around the organ except for the pigment-free cleft at the ventral edge.

Removal of the scale uncovers a homogeneous field of blood vessels and connective tissue (Plate II, 1b). The field is not entirely circular, but slightly polygonal, especially along the ventral edge. The glandular body is not visible until the organ is removed and inverted, whereupon it is seen as an irregular strand of denser tissue (Plate II, 1c).

As before, a deep scale is exposed by removal of the organ. It is polygonal in shape and maintains its form when removed. The shallow depression left is lined by a lightly pigmented reflecting membrane as in L. leucopsarus.

3. Lampanyctus ritteri (Plate I, 3). The "Schussselformigie" organs of L. ritteri deviate slightly in form from those of the

former two species in that the organ is divided horizontally by a pigmented septum into a dorsal, highly reflective portion, and a ventral portion which is overlain by the lens (Plate II, 4a). The septum, a superficial pigmented band, arches over the lens across the face of the scale and joins the marginal band of pigment which surrounds the organ as in the other species. When the scale is removed, the septum is removed with it.

As with the other species, removal of the scale uncovers a tissue complex which in this case appears to have two distinct bands (Plate II, 4b). The upper band is the gland body. It arches somewhat dorsally and is concealed by the pigment septum when the external scale is intact. Behind and beneath the gland body is a second band, not previously seen, of an unusual tortuous and perforated nature. The form of this peculiar entity is more apparent when the tissue mass is inverted (Plate II, 4c). The silvery or highly reflective portion mentioned earlier appears, on dissection, to be merely a part of the reflector showing through a region of thin connective tissue dorsal to the gland body.

An inner scale, as in other cases, can be removed leaving a shallow depression lined by a thin reflective membrane. The scale in this case is more membranous and does not hold its form well.

4. Lampanyctus regalis (Plate I, 4). As in L. ritteri, the "Schusselformigie" organs of L. regalis may also have a pigmented septum dividing the organ into upper and lower parts. In some cases it is not present at all. The organ itself is very delicate and flaccid, as is the dermis in which it lies. The lack of suitable

material for dissection has made it difficult to determine the structure of photophores in this species, and in the specimens examined the delicate nature of the organ has made it hard to discern internal detail.

As in L. ritteri, when the scale is removed, the organ appears in two parts; a thin transparent upper area with the reflecting membrane showing through, and a denser lower part with a barely perceptible glandular entity (Plate II, 3). The structure cannot be removed as readily as in other species. The inner scale is more membranous, as in L. ritteri, and is backed by the sparsely pigmented reflecting membrane.

Branchiostegal Organs. The branchiostegal photophores which outline the lower jaw occur as three long sausage-shaped organs embedded in a loose connective tissue, within the branchiostegal membrane (Plate III, 1-4). Brauer (1908) has reported no specialized lens for them; however, a pronounced thickening of the external scale is sometimes observed. Each organ is encircled by a pigment margin, such as that seen in the "Schusselformigie" organs, with a pigment free border located ventrally.

1. Lampanyctus leucopsarus. The tissue mass contained within the bounds of the pigment margin is thicker than that of the "Schusselformigie" organs (Plate III, 1). Most readily visible is the loose transparent connective tissue which fills most of the interior of the organ.

The glandular body is partially obscured by the dorsal pigment border. Its extent becomes more evident when it is dissected out.

It lies as a denser strand, approximately the width of the pigment margin, within a sausage-shaped mass of vascular and connective tissue which is also obscured by the dorsal pigment border.

The entire organ is not as readily separated from the surrounding tissue as the "Schussselformigie" organs. It is not backed by an inner scale such as occurs in the former, but instead, solely by a lightly pigmented reflecting membrane.

2. Lampanyctus nannochir. The branchiostegal organs of L. nannochir are demarcated by a wider pigmented margin than those of L. leucopsarus (Plate III, 2). This pigment band is also darker. Similarly the most visible tissue is transparent and loose. The gland similarly lies within a vascular and connective tissue plexus, the entire mass of which is hidden by the dorsal pigment margin. In contrast to L. leucopsarus the gland occupies a very small part of the entire volume of this plexus. The other features are similar to those described for L. leucopsarus.

3. Lampanyctus ritteri. The branchiostegal organs of L. ritteri lie somewhat more deeply embedded in connective tissue (Plate III, 3). The pigment margin is most concentrated at the dorsal edge, resulting in a somewhat wider cleft ventrally. The internal features are similar to those already described. The gland is oriented in the manner found in the other species, but is more closely adherent to the overlying dorsal pigment margin. Other features are the same.

4. Lampanyctus regalis. The branchiostegal organs of L. regalis differ from the other species in that they are not as

deeply embedded, nor are they as elongated (Plate III, 4). The peripheral pigment band is more closed ventrally. The interior connective tissue is especially transparent, with what appear to be a few suspended melanophores. The gland, as in other species, is found in a similar plexus. The entire mass, however, lies deeper in the organ not directly adhering to the dorsal pigment band. The reflecting membrane and other features are the same.

Infra- and Supracaudal Organs. The caudal organs of Lampanyctus are simple when compared to other genera of the family (Brauer, 1908). They consist of a series of overlapping plates, called "Leuchtplatten" by Brauer (1908), of homogeneous glandular tissue. They may be shallowly or deeply interconnected, or even separate depending on the species. The tissue may straddle the dorsal or ventral midline, or lie in a shallow trench. The overlapping plates may be separated by alternating median scales, or by both median and the lateral scales on each side, or there may be no separation by scales at all. In all cases the gland is underlain by a pigment layer which appears to be continuous with that of the dermis. The conditions summarized above vary with species.

1. Lampanyctus leucopsarus. The caudal glands consist of overlapping plates of which there are seven for the supracaudal (Suc) and nine for the infracaudal (Inf). The Suc extends from about one third of the distance from the adipose fin to the first dorsal caudal fin ray. The Inf extends from the level of the first AOp to the first ventral caudal fin ray. The light plates are separated by both a median scale and the partial infringement of the lateral

scales on each side. The plates are interconnected at the midline and become progressively thinner and more deeply separated by the scales toward the anterior end. The entire mass lies in a shallow trench which is lined by a pigmented membrane as previously described.

Lampanyctus nannochir. The caudal organs of L. nannochir also consist of overlapping plates, separated by scales, four in the Suc and six in the Inf. In this species the Suc extends one half of the distance mentioned, and the Inf originates at the level of the third AOp and extends to the first ventral caudal fin ray. As in L. leucopsarus, the plates become more deeply separated anteriorly so that the first plate is isolated entirely from the others, in both the Inf and the Suc. The light plates are shallower and thinner than in L. leucopsarus. They also are underlain by the dermal pigment layer.

Lampanyctus ritteri. The caudal organs of L. ritteri appear to be continuous strips of glandular tissue with only slight separation or plate-like formation at the lateral edges. There are six separations in the Inf and three in the Suc. The Suc extends one half to one third of the distance from the adipose fin, while the Inf originates at about the level of the second or third AOp. The lateral scales do not appear to infringe upon the gland, but merely to abutt to it. The entire organ is covered by a gelatinous membrane. The caudal organs do not lie in a trench, but instead straddle the dorsal and ventral midlines. As in the other two species, they are underlain by the dermal pigment layer.

Lampanyctus regallis. The caudal organs are similar in

structure to those of L. ritteri. The Suc extends one half to one third of the distance to the adipose fin and consists of four shallowly separated plates. The Inf originates at the level of the third or fourth AOp and consists of six plates. Other features are the same.

HISTOLOGICAL DESCRIPTION

"Schussselformigie" Organs. These are shallowly embedded in the spongiosum of the dermis which thins out, bringing the organs in to close proximity to the stratum compactum beneath. The shallow depression may or may not be imposed on the underlying muscle mass, depending on whether the dermis is thick, as in the area of the belly, or thin as on the more caudal parts of the trunk.

The most external element, the lenticular scale, is doubly convex. It is oriented in such a way that luminescence generated by the photogenic gland is directed ventrad.

Beneath the lens is a membrane, originally seen by Brauer (1908), and called the "peculiar membrane" by Oshima (1911). It has also been called the "striated membrane" by Nicol (1958). The tissue is basophilic and has large nuclei which are almost as large in diameter as the membrane is thick. Brown vertical spicules reported by Oshima (1911) as being acid soluble lend to the striated appearance. The membrane occurs in all four of the species examined and appears to be continuous with the pigmented margin. In L. ritteri it covers the dorsal portion of the organ and joins with the pigment septum below which it thins out. Brauer (1908) describes it as "adjoining the pigment septum, but lying under it, and thinning out ventrally". In L. leucopsarus the membrane is uninterrupted and covers the entire face of the organ.

Immediately beneath the membrane is a vascular and connective tissue plexus in which is embedded a strand of glandular tissue.

The plexus is continuous with the dermis at the edges of the inner scale at which point blood vessels can be seen to enter. The largest part of the tissue is composed, in varying proportions, of capillaries and gland. The interspersed connective tissue network stains lightly for collagen, but not for reticular fibers. A thin collagenic sheath surrounds the glandular body.

The entire plexus is separated from the inner scale by a layer of collagenic fibers and a looser connective tissue which has been described by Brauer (1908) as "gelatinous". In most cases there is merely a space, also noted by Brauer (1908) who attributed it to shrinkage of the gelatinous tissue due to poor fixation.

Some variation in the morphology of the gland cells exists in the four species; the cells may be elongate, sheet-like, or irregular. However, the staining reaction is the same for all. The cytoplasm is finely granular, the ground substance basophillic, and the granules acidophillic. The nuclei are long and thin in one plane and ovoid or circular in the other. They are larger than the nuclei of the neighboring tissues and are 8-10 microns in their widest diameter. There is an uneven distribution of chromatin material characteristic of the nuclei of gland cells.

The inner scale and the reflecting membrane are closely associated and probably corroborative in their function. Oshima (1911) and Brauer (1908) describe two layers; 1) a "homogeneous lamella" called a "deep scale" or "tiefe Schuppe" by previous workers, and the "chitinous layer" by Iwai and Okomura (1961), and 2) a "reflector" which is next to and not very distinct from the pigment layer.

Oshima (1911) describes the reflector as being of two types; 1) "a layer composed of hexagonal iridescent elements...made up of short and relatively thick...spicules arranged obliquely to the surface of the pigment layer", and 2) a layer "composed of bundles of spicules running parallel to the surface".

The "homogeneous lamella", referred to as the inner scale in this study, is acidophilic and definitely of a scale-like nature. In better preparations a thin monocellular layer is closely affixed to the inner concave surface. Brauer has mentioned this layer also, but it is hard to discern whether it is actually a distinct membrane, or merely a portion of the "gelatinous" connective tissue which has remained affixed to the scale.

The reflecting layer appears to be of the second type. It is very thin in all of the species studied and exists as a non-collagenic membranous layer closely adhering to the back of the inner scale and to the pigment mantle. In occasional oblique cuts it is seen to consist of large flat cells with flat ovoid nuclei. The spicules were not noticed.

The staining reactions and cellular components are the same in the four species. The most significant differences are morphological and will be discussed in the following treatment.

1. Lampanyctus leucopsarus. The glandular body takes up the greater proportion of the tissue plexus. In transverse section (Plate IV, 1) the main part of the gland is dorsal to the inner convexity of the lens with a thinner finger of material extending ventrally as discussed previously. The cells of the gland are thin

and sheet-like and stacked in rows parallel to the surface (Plate V, 1). In transverse section (Plate V; 1,2) the nuclei are long and thin, whereas in longitudinal section (Plate V; 3,4) they are round. The nuclei are 5-8 microns in diameter, and the cells 25-50 microns long. The gland is surrounded by a definite sheath. The remainder of the structure is made up mainly of blood vessels which surround but do not enter the gland itself.

2. Lampanyctus nannochir. The most obvious difference from the above species is the predominate presence of blood vessels (Plate IV, 2). The organ appears somewhat deeper in transverse section and most of the bowl-shaped depression is filled with capillary bed. The cells of the gland are sheet-like, but not nearly as orderly arranged (Plate VII, 1). The gland itself is irregular in shape and would seem to expose more of its surface area to the capillary bed. The cells vary considerably in their length and form. The nuclei are typically flat in one plane and round or ovoid in the other. The gland body is not as obviously surrounded by a connective tissue sheath.

3. Lampanyctus ritteri. The proportion of gland to blood vessels is similar to L. leucopsarus. The body of the gland is directly beneath the pigment septum, slightly dorsal to the inner convexity of the lens; and also sends a thin finger of tissue ventrally when viewed in transverse section (Plate IV, 3). The gland is fairly compact with the exception of large intercellular spaces in its interior (Plate VI, 1-3). These spaces have also been observed in some genera by Brauer (1908). The entire gland is

enclosed in a connective tissue sheath which is more pronounced than in the other species. The cellular form and arrangement is similar to that of L. leucopsarus. As in L. leucopsarus, the rest of the tissue plexus is composed mainly of blood vessels.

A prominent layer of thick collagenic fibers running parallel to the long axis of the gland lies in back of the plexus (Plate VII; 1,3). The fibers do not run exactly parallel, but cross each other to form a perforated matrix across the back of the tissue mass. The individual fibers are 2-3 microns thick.

4. Lampanyctus regalis. The "Schussselformigie" organs of L. regalis are thinner (Plate IV, 4). The tissue mass forms a tenuous disk having a high proportion of glandular tissue. The percentage of collagenic connective tissue is higher than in other species, and capillaries are more sparsely scattered. The cells of the gland are elongate and thin, and the nuclei are somewhat atypical; they are sometimes thin and twisted in section (Plate VII, 2-4). The arrangement of cells is not strictly in one direction; in some sections of the gland they are arranged vertically, in others horizontally to the surface of the organ (Plate VII, 2). There is a prominent separation of the cells by intercellular spaces as seen in L. ritteri (Plate VII, 4). The fibrous sheath surrounding the gland is not obvious.

Branchiostegal Organs. The bulk of the interior of the branchiostegal organs consists of a gelatinous or mucochondroid connective tissue which forms a wide channel to the surface. The entire mass is surrounded by a fibrous collagenic sheath. Outside

this sheath, but closely adhering to its surface, is a second thin layer, called the reflector by Brauer (1908) and others. This layer has the appearance of entwining non-collagenic fibers. Peripheral to this is the pigment mantle.

The gland body is located under the dorsal edge of the mantle. As in the "Schusselformigie" organs, it is embedded in a mass of vascular and connective tissue which is distinct from the mucochondroid channel. The relative proportion of glandular tissue and blood vessels varies with species.

The gland cells of the branchiostegal organs have the same staining properties and the same granularity of cytoplasm as in the glands previously discussed. The nuclei, too, have the same appearance. The form and arrangement of cells within the gland is modified for each species.

1. Lampanyctus leucopsarus. The capillary bed is more prominent in the Br than in the "Schusselformigie" organs (Plates VIII, 1; IX, 1). The glandular portion occupies about one third of the tissue mass, and lies very close beneath the dorsal edge of the pigment mantle. The morphology of the gland is somewhat irregular. The cells are not as obviously flattened or stacked like leaves as in the trunk organs (Plate X, 1).

2. Lampanyctus nannochir. The prominent capillary bed of the "Schusselformigie" organs is retained in the Br (Plates VIII, 2; IX, 2). The gland bodies are also very similar in appearance. The cells are short, somewhat flattened, and variable in form (Plate X, 2). As in L. leucopsarus, the gland body is close to the dorsal edge of

the pigment mantle.

3. Lampanyctus ritteri. The Br do not differ from those of the other two species except that the capillary bed is diminished considerably (Plate VIII, 3; IX, 3). The glandular cells are elongate and stacked parallel to the long axis of the organ (Plate IX, 3). In traverse plane (Plate X, 3) they are oriented about a central axis and cell boundaries are difficult to discern. Conspicuous spaces may exist in the central part of the gland as in the organs of the trunk. The heavy collagenic fibrous matrix is absent. As in the other two species the gland body lies close beneath the dorsal wall of the pigment mantle.

4. Lampanyctus regalis. The Br (Plates VIII, 4; IX, 4) of L. regalis differ in several respects:

1) The mucochondroid channel is replaced by connective tissue not greatly differentiated from the loose areolar connective tissue surrounding the organ.

2) Numerous sparsely scattered melanophores are suspended within the internal connective tissue.

3) The glandular body is embedded more deeply in the connective tissue and lies closer to the proximal wall of the pigment mantle.

Blood vessels are very sparse. Large spaces occupy the center of the gland. The cells are elongate and obliquely arranged to the long axis of the organ (Plate IX, 4). The nuclei are typical in appearance (Plate X, 4).

The Caudal Organs. These are separated from the subcutaneous tissue by the stratum compactum. They are underlain by a pigment

layer which is continuous with that of the dermis. The rest of the organ is made up of mainly glandular tissue interspersed with blood vessels and connective tissue. Numerous nerve branches supply the organs. The staining of the gland cells is typical.

In L. leucopsarus and L. nannochir the caudal organs consist of distinct overlapping plates which are separated from each other by scales (Plate XI, 1). The glandular tissue is compact, and in L. leucopsarus the cells are arranged in whorls or clumps (Plate XI, 2-3). Large vacuolated cells occupy the center of the gland. These are especially prominent in L. nonnochir (Plate XI, 4).

In L. ritteri and L. regalis the overlapping of the plates is superficial and the gland is essentially a continuous structure (Plate XII; 1,2). It is tenuous and loosely dispersed with no particular orientation of cells which are thin and net-like (Plate XII; 3-4).

INNERVATION

"Schussselformigie" Organs. One instance of possible innervation of these organs was seen (Plate XIII, 1) in L. regalis. In this instance the nerve could not be traced into the organ itself, but only into the pigment at the ventral edge where it became lost. No nerves were found to approach the "Schussselformigie" organs in any of the species.

Branchiostegal Organs. Large nerve branches were found to enter the posterior ends of the Br in L. leucopsarus (Plate XIII, 2), L. nannochir (Plate XIII, 3), and L. ritteri. Just inside the pigment mantle the nerves appeared to bifurcate with one branch entering the pigment mantle and the other becoming lost in the connective tissue of the plexus. Nerves could not be traced into the gland itself.

Caudal Organs. Nerves were found to enter the caudal organs in all four species, often in prolific number. Although terminal endings could not be found, fine branches were often found in close proximity to individual gland cells (Plate XIII, 4).

Large thick nerves were seen to enter the light plates of L. nannochir (Plate XI; 1,4) and L. leucopsarus. In L. ritteri and L. regalis the branches were smaller but more numerous (Plate XII; 1,2).

DISCUSSION

Distribution in the Water Column.

The four species of the lantern fish used in this study represent complementary pairs, with L. ritteri closely related to L. regalis, and L. leucopsarus closely related to L. nannochir. Studies of the depth distribution of two of these species have been made by Aron (1959). He found them occurring together but preferring different depths. Northern Pacific trawls to a depth of 30 meters yielded the largest number of L. leucopsarus, whereas trawls to 60 meters yielded the largest number of L. ritteri. In more southern latitudes (off the coast of Washington) L. leucopsarus was found in greatest number in trawls to 60 meters.

More recent data on the distribution of some of these species has been presented by Percy (1964). His data supplements Aron's observations by showing a predominance of L. leucopsarus, off Oregon, in tows to 25 to 30 meters at night. More information on the bathymetric ranges of the deeper species is needed. Nevertheless, the following figures give some evidence of their distributions. Of 44 specimens of L. regalis collected, 24 were taken in trawls to 500 meters, 19 in trawls to 1000 meters, and only one was taken in trawls to 200 meters. Of 41 specimens of L. nannochir collected, 39 were taken in tows to 1000 meters and only two were taken in tows to 500 meters. None was found in tows to 200 meters.

The possible relationship between bathymetric range and size of photophores has already been suggested by other workers. The

decrease in size of photophores with depth was first noted by Brauer (1908), and is mentioned by Murray and Hjort (1912) for species of Cyclothone and Myctophum. They also mention the general absence of photophores in bathypelagic forms (below 800 meters) found in warmer seas.

The size differences found in Lampanyctus tend to support these observations. L. regalis, essentially a deep form, has smaller photophores than either L. ritteri or L. leucopsarus. Histological examination of the organs of L. nannochir, which are almost as large as those of the latter two, shows that size is a poor criterion for the separation of deep and shallow forms. Consideration of the actual volume of glandular tissue, on the other hand, provides a more valid means of comparison. In the case of L. nannochir the volume is smaller than in the shallower species and is in keeping with the above diminution observations.

It is interesting that L. ritteri and L. leucopsarus, having a similar vertical range (within 30 meters), show similarities in the size and proportion of the structural elements of their "Schusselformigie" organs. L. nannochir and L. regalis, both of which can be considered deep forms, show divergent structural modifications. The large vascular plexus of L. nannochir contrasts sharply with the sparse blood supply of L. regalis. The similarities in structure in the two less closely related L. ritteri and L. leucopsarus serve to accentuate even more the differences in structure of the "Schusselformigie" organs of the two deeper species.

The contrasting differences in the two deep species raises

several questions for speculation. Is the variation due to drastic environmental differences which are not disclosed by the limited distributional data that is available? Are they a result of functional differences? Are there intrinsic physiological difference in the two animals? Or finally, should the taxonomic placement of the animals be reevaluated?

Taxonomic Relationships.

The ancestry of Myctophinae has been discussed by Frazer-Brunner (1949). Taxonomic relationships of the family can be traced almost entirely through homologies in the arrangement of their photophores. In his words, "...there is no doubt that within the Myctophidae itself, the photophores are of first rate taxonomic importance...

...photophore patterns studied together give one a graph-like, almost cinematic representation of phylogeny."

The photophore patterns in all four species used in this study are very similar. The most significant differences in photophore arrangement which distinguish L. ritteri and L. regalis from L. nannochir and L. leucopsarus are the presence of only one Pol in latter pair of species and two Pol in the former, and the positioning of the first SAO behind the last VO in the latter and in front of the last VO in the former. Other differences in arrangement and number are used to distinguish between the individual species. In L. leucopsarus the number of Prc is normally four, whereas in L. nannochir it is generally three. The number in both cases can

vary. Certain angular arrangements of the SAO are used to distinguish L. ritteri and L. regalis. There are other features used in identification such as the length of the caudal glands, the width of the orbit, body measurements, etc. Based on similarity in photophore arrangements it seems highly likely that the four species in this study are very close in their phylogenetic relationship, with L. leucopsarus and L. nannochir more closely related to each other than to the other two, and similarly for L. regalis and L. ritteri.

The structural similarities encountered in the "Schussselformigie" organs in this study would tend to support this view. Oshima (1911) has listed ten structural components comprising the luminous organs of Myctophidae; namely the 1) photogenic body (gland), 2) investing connective tissue, 3) gelatinous tissue, 4) "peculiar membrane", 5) the "Schuppenartige Lamella" or squama profunda (the inner scale), 6) layer of hexagonal iridescent elements, 7) the reflector, 8) the pigment layer, 9) the lens, and 10) nerves and blood vessels. Elements (4-9) are considered as being "accessory parts". Of the ten only number 6 was found to be missing in the "Schussselformigie" organs of Lampanyctus.

For the caudal organs, the similarities in structure are even more striking. The caudal organs have shown large modifications in structure and degree of development throughout the family. In some members of Myctophinae the caudal glands are not present at all. In others, such as Tarletonbaeanea crenularis they are present only in the male (Frazer-Brunner, 1949). In Lampanyctus there is no distinction between the caudal organs of the two sexes, and both are

present in all four of the species encountered. In still other members, according to Frazer-Brunner (1949), the caudal organs have developed into the "deep, lens-like, supracaudal gland of Notolynchus, ...apparently not covered by a scale, and apparently foreshadowing the extreme development of both supra- and infracaudal glands found in Lampandena".

The overlapping plate-like structure of caudal organs found in L. leucopsarus and L. nannochir is regarded by Frazer-Brunner (1949) as being the more primitive condition, while a tendency toward a fusion of the plates such as was encountered in L. regalis and L. ritteri is slightly more advanced. The similarities in structure within the two groups supports the relationships which have already been mentioned.

The structural variation found in the branchiostegal organs are not more significant than for the other organs. There is less difference in the structure of the Br in L. leucopsarus and L. nannochir, for instance, than there is between the "Schusselformigie" organs of the body. There is more difference in the Br of L. ritteri and L. regalis, but this seems mainly to be a difference in degree of differentiation of the internal gelatinous connective tissue.

The unusual vascularity of the "Schusselformigie" organs of L. nannochir appears then to be a difference in the degree of development of a particular element, rather than a change in relationship of total structure. The fact that parallel modifications are not found in the other organs necessarily leads one to look for

explanations other than simple species variability or a divergence in taxonomic relationship.

Possible Physiological Adaptations.

The chemical system of bioluminescence has not been characterized for fishes. From the work of Harvey (1952) and others, it seems probable that the system is analogous to that of the firefly. The system of bioluminescence in the firefly is dependent upon a rich source of oxygen which is supplied to the gland by a capillary network (McElroy, 1961) and possibly by air-transporting tracheae. The innervation of photogenic tissue is thought to control flashing by the release of acetylcholine. The histology of light organs of many pelagic fish discloses an extensive innervation of the photogenic tissue and a close association with a capillary network.

If the vascular supply observed in the organs of Lampanyctus is necessary for luminescence then it is very likely that the modifications in the amount of blood supply is either a manifestation of differences in function of photophores, or of differences in the physiology of the animals or the organs themselves.

According to Parin (1960) the layer of minimum oxygen concentration in the northeastern Pacific is from 200 meters to 300 meters in its upper limit and in the northwestern Pacific from 800 to 900 meters in its upper limit. Figures from the Department of Oceanography at Oregon State University indicate an upper limit in the northeastern Pacific which is somewhat lower than that given by Parin; around 700 meters to 800 meters. Whichever figure is used, the bathymetric

range of L. nannochir is below the region of highest oxygen concentration, and possibly very close to the region of minimum oxygen concentration. If the deeper figure is taken, it is seen from the distributional data of Pearcy (1964) that the bathymetric range of L. regalis could well be above the minimum zone, since almost half of the specimens of L. regalis collected were taken in tows to only 500 meters.

A recent study of the metabolic rates of pelagic fishes, including Lampanyctus, was made by Karinen (1965) measuring succinic dehydrogenase activity in muscle tissue. The results on a wet weight basis indicated a general decrease in metabolic activity for deeper animals. For Lampanyctus, however, the enzyme activity decreased in the following order: L. leucopsarus, L. regalis, L. nannochir, and L. ritteri. On an ash-free dry weight basis the activity of L. leucopsarus fell to the level of L. ritteri and L. nannochir, and L. regalis remained the highest. Though the activities of these four animals were actually not far separated in these results, they are not what one would expect for these four fishes with regard to their position in the water column.

In view of the similarities of the metabolic rates and the location of the zone of minimum oxygen concentration, a better explanation for the extensive capillary bed of L. nannochir may be related to the promotion of optimum oxygen concentration for the production of bioluminescence within the organ.

The function of photophores in pelagic animals is not well known. It would seem possible from the observations of Beebe (1944)

and Bolin (1961) that numerous functions exist, possibly for the same organ. The convincing evidence supporting the hypothesis of Clark (1963) suggests that light intensity controls the migratory activity of many pelagic animals which seek the level of light intensity most closely corresponding to the light emitted by their ventral photophores. Smaller photophores on deeper animals would support this hypothesis since the light reaching deeper depths would not be as intense. The smaller size of photophores in L. regalis is coincident with this idea. The unique structure of the "Schusselformigie" organs of L. nannochir, however, leaves room for additional interpretations. The fact the same modifications in structure are not carried to the other organs suggests an alternate hypothesis of a highly specialized function of the ventral organs of L. nannochir related to some peculiar aspect of this animals behavior or environment, possibly apart from Clark's hypothesis, or in addition to it.

Innervation.

The subject of innervation has been lightly touched upon but not discussed with respect to function. Large nerve branches enter the caudal organs of all four species of Lampanyctus. Similarly large nerves enter the caudad ends of the branchiostegal organs and send definite branches to the heavy dorsal pigment mantle. With regards to the "Schusselformigie" organs, there was a conspicuous lack of nerves. The single case of the nerve entering the ventral edge of the VO in L. regalis implies, however, that they may be there.

Innervation of the caudal organs was noticed by Brauer (1908),

and he likewise noted that the innervation of the "Schussselformigie" organs was sparse. Oshima (1911) described nerves into all the major organs of several myctophid species. He was specifically able to demonstrate fine nerve branches traversing the cellular lamina of the photogenic gland in the anal organs of Myctophum watasei, using a silver impregnation technique. This is the only recorded finding of nerves actually terminating in the gland cells. Ray (1950), in an anatomical study of the peripheral nervous system of L. leucopsarus, describes the light organs of the body as being innervated by the ventral rami of spinal nerves. In one instance she shows large nerves entering the Br such as were seen in this study. However, she makes no mention of the relative sizes of nerves or whether they actually terminate within the organ. She also has not traced the neural pathways involved. It is of interest that Nicol (1958), who is familiar with her work, has suggested that the organs are innervated by the autonomic nervous system.

The most significant phenomenon associated with this study was the distinctive difference between the intermittent luminescence of the caudal organs, and the continuous ~~dimmer~~ light of the ventral and lateral series outlining the form of the body. This difference was also observed by Oshima (1911). However, he also noted a flashing of the latter in fresh specimens. Although flashing of the "Schussselformigie" or the branchiostegal organs was not perceived in this study, there is no reason to exclude the possibility that they may flash under certain conditions as observed by Beebe (1944).

The production of luminescence in these and other deep sea

fishes has by no means been thoroughly characterized. The presence or absence of nerves and the difference in luminescent activity between the organs, as mentioned, are suggestive of different mechanisms of control. The low intensity luminescence observed under conditions of extreme stress is possibly indicative of a complex physiological control which varies with the conditions to which the fish is subjected. The possibility of a secondary hormonal control in situations of impending danger to the fish should not be overlooked. This then could conform to Clark's hypothesis of counter-shading in that the fish would produce a continuous light in the presence of predators. The more intense periodic flashing, such as observed by Beebe (1944), could be under nervous control and used in the attraction of prey and in the direction of schooling activity. The unusual vascularity of the organs of L. nannochir may be a functional adaptation to some special peculiarity of its environment.

There is much to be learned about the function of bioluminescence in the ocean. A more complete analysis of the physiological mechanisms controlling luminescence is needed, both in the characterization of the chemical system in fishes, and in the investigation of neural pathways and possibility of hormonal control.

SUMMARY

A comparative morphological and histological study was made of the light organs of four species of lantern fish of the genus Lampanyctus. Two species, L. regalis and L. nannochir, prevail in deep water. The other two, L. ritteri and L. leucopsarus, demonstrate vertical migration from deep water in the daytime to surface waters at night. Three major groups of organs were selected for study; namely the "Schusselformigie" organs on the ventral trunk, the branchiostegal organs on the lower jaw, and the caudal organs on the caudal peduncle. In addition, observations of luminescence and topographical measurements of the ventral photophores were made.

Luminescence observed in free swimming, freshly captured L. leucopsarus was of two types: 1) a continuous, low intensity light from the "Schusselformigie" and branchiostegal organs, and 2) more intense spontaneous flashes from the caudal organs. In less active specimens similar phenomena could be invoked by mechanical stimulation but not by chemicals such as dilute solutions of ammonia or formalin, or injections of adrenalin.

Size measurements of three groups of "Schusselformigie" organs in Lampanyctus showed the following relationships: 1) a rostral-caudal decrease in size along with a parallel decrease in distance between photophores within a given species, 2) a decrease in lens diameter with species in the following order: L. ritteri, L. leucopsarus, L. nannochir, and L. regalis.

Morphological differences between species consisted of differences in the amount and form of glandular tissue, the extent of vascularization, and minor differences in pigment distribution and character of the connective tissue. The most significant difference was the unusually large capillary bed characterizing the "Schusselformigie" organs and the branchiostegal organs of L. nannochir, and the contrasting sparse blood supply of these organs in L. regalis. A similar difference in vascularity was not found for the caudal organs.

A histological study revealed the light organs of Lampanyctus to consist of the following elements: 1) a lenticular scale, 2) a "peculiar membrane," 3) a peripheral pigment margin, 4) the glandular tissue, 5) connective tissue and blood vessels, 6) an inner or "deep" scale, 7) a reflecting layer, 8) a pigment layer, and 9) nerves. The branchiostegal organs lacked the inner scale and the lens-like thickening of the external scale. The caudal organs, being less specialized consisted mainly of glandular tissue with interspersed connective tissue and blood vessels.

Nerves were found to enter the glandular tissue of the caudal organs in great abundance. These were especially numerous in L. regalis and L. ritteri but larger and thicker in L. nannochir and L. leucopsarus. Large nerve branches were also found to enter the posterior end of the branchiostegal organs with a branch entering the pigment mantle. There was a conspicuous lack of nerves in the "Schusselformigie" organs with only a single instance of a nerve entering the pigment margin in L. regalis.

Correlations of photophore size and amount of glandular tissue with depth of the species was made. Organs were smallest in L. regalis, while in L. nannochir the larger size was compensated by a smaller volume of glandular tissue.

Differences in blood supply to "Schussselformigie" organs of L. nannochir and L. regalis posed an enigma. Since taxonomic considerations did not suggest a reconstruction of classification of these two animals, two alternate interpretations of the unusually large blood supply in L. nannochir were presented: 1) an adaptation to low oxygen availability in the environment, and 2) a possible adaptation related to some peculiar behavior of this animal, or to some other unknown aspect of its environment. The possibility of more than one function for the same organ is also speculated.

The disparity in size and clarity of nerves to the various organs together with the observed difference in luminescence activity raised questions of physiological mechanisms involved. The possibility of a secondary hormonal control, under conditions of stress, mating, etc. was presented.

BIBLIOGRAPHY

1. Aron, William. Midwater trawling studies in the North Pacific. *Limnology and Oceanography* 4:409-418. 1959.
2. Beebe, William and Mary Vander Pyl. Eastern Pacific expeditions of the New York Zoological Society, XXXIII. Pacific Myctophidae (Fishes). *Zoologica*, New York 29:59-95. 1944.
3. Bolin, R. L. A review of the myctophid fishes of the Pacific Coast. *Stanford Ichthyological Bulletin* 1:89-156. 1939.
4. Bolin, R. L. The function of luminous organs of deep sea fishes. In: *Proceedings of the Ninth Pacific Science Congress of the Pacific Science Association*, Bangkok, 1957. Vol. 10. Bangkok, 1961. p. 37-39.
5. Brauer, August. Die Tiefsee-Fische. In: *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition, 1898-1899*. Vol. 15, pt. 2. Jena, Gustav Fischer, 1908. p. 89-102.
6. Clark, W. D. Function of bioluminescence in mesopelagic organisms. *Nature* 198:1244-1246. 1963.
7. Emery, Carlo Dott. Das Leuchtorgan am Schwanze von Scopelus benoiti. *Biologisches Centralblatt* 8:228-230. 1889.
8. Emery, Carlo Dott. Intorno alle macchie splendenti della pelle nei pesci del genere Scopelus. *Mitteilungen aus der Zoologischen Station zu Neapel*, Berlin 5:471-482. 1884.
9. Frazer-Brunner, A. A classification of fish of the family Myctophidae. *Proceedings of the Zoological Society of London* 118:1019-1106. 1949.
10. Guppy, H. B. Notes on the pearly organs of Scopelus. *Annals and Magazine of Natural History* 9:201-212. 1882.
11. Harvey, E. Newton. *Bioluminescence*. New York, Academic Press, 1952. 649 p.
12. Karinen, J. F. Succinic dehydrogenase activity in mesopelagic oceanic fishes. Master's thesis. Corvallis, Oregon State University, 1965. 71 numb. leaves.

13. Iwai, Tomatsu and Osami Okamura. A study of the luminous organs of the lantern fish, Tarletonbaeania taylori Mead. Science Report of the Yokosuka City Museum 5:1-5. 1960.
14. Lendenfeld, R. von. Structure of the phosphorescent organs of fishes. H. M. S. Challenger Reports 22:278-329. 1887.
15. Lendenfeld, R. von. The radiating organs of deep sea fishes. Memoirs of the Harvard Museum of Comparative Zoology 30:169-213. 1905.
16. Leydig, F. Die augenähnlichen Organe der Fische. Verhandlungen der Preussischen Rheinlande und Westfalens, Bonn 8:31-40. 1881.
17. McElroy, W. D. and Bentley Glass (eds.). Light and life. Baltimore, John Hopkins Press, 1961. 924 p.
18. Murray, J. and J. Hjort. The depths of the ocean. London, Macmillan, 1912. 821 p.
19. Nicol, J. A. C. Observations on luminescence in pelagic animals. Journal of the Marine Biological Association, United Kingdom 37:705-752. 1958.
20. Nicol, J. A. C. Spectral composition of the light of the lantern fish, Myctophum punctatum. Journal of the Marine Biological Association, United Kingdom 39:27-32. 1960.
21. Oshima, H. Some observations on luminous organs of fish. Journal of the College of Science, Tokyo 27:1-25. 1960.
22. Parin, N. V. The distribution of deep sea fishes in the upper bathypelagic layers of the subarctic waters of the northern Pacific Ocean. Trudy Institute Okeanologii, Akademiia, Nauk S.S.S.R. 45:259-278. 1960. (Translated by L. Penny, Bureau of Commercial Fisheries Ichthyological Laboratory, U. S. National Museum, Washington, D. C. Mimeographed, 7 fig. omitted.)
23. Percy, William G. Some distributional features of mesopelagic fishes off Oregon. Journal of Marine Research 22:83-102. 1964.
24. Ray, D. L. The peripheral nervous system of Lampanyctus leucopsarus. Journal of Morphology 87:61-178. 1950.

PLATES

PLATES

Plate I

1. Lampanyctus (Stenobrachius) leucopsarus Eigman and Eigman, 1890. X1.5.
2. Lampanyctus (Stenobrachius) nannochir Gilbert, 1891. X1.5.
3. Lampanyctus (L.) ritteri Gilbert, 1915. X1.5.
4. Lampanyctus (L.) regalis Gilbert, 1891. X2.0.

Plate II

1. Lampanyctus nannochir A0
 - 1a. Lens intact. X50.
 - 1b. Scale removed. X50.
 - 1c. Organ dissected out and turned over revealing strand of luminous tissue. X50.
2. L. leucopsarus A0
 - 2a. Lens intact. X50.
 - 2b. Lens removed revealing luminous gland with ventrally projecting fingers. X50.
3. L. regalis A0
 - 3a. Without lens. X50.
4. L. ritteri A0
 - 4a. Lens intact. Note pigmented band forming septum across face of the organ. X50.
 - 4b. Lens removed, revealing band of luminous tissue and more ventral band of less dense connective tissue. X50.
 - 4c. Tissue plexus turned over, e.g. 1c. X50.

Plate III

Branchiostegal Organs

1. L. leucopsarus Ventro-lateral view. Outside scale removed. X50.
2. L. nannochir Scale removed. X50.
3. L. ritteri Ventro-lateral view. Outside scale removed. X50.
4. L. regalis Ventro-lateral view. Outside scale removed. X50.

Plate IV

AO

1. L. leucopsarus Transverse section through lens and part of caudal gland. X100.
2. L. nannochir Transverse section through center of photophore; lens removed. X100.
3. L. ritteri Transverse section through center of photophore; lens absent. X100.
4. L. regalis Transverse section through lens and center of photophore. X100.

Plate V

Lampanyctus leucopsarus

1. Transverse section through one edge of PO on belly. X430.
2. Transverse section through center of AO near tail. X430.
3. Longitudinal section through AO in region of ventral extensions of gland. X430.
4. Longitudinal section through AO, through the gland body, slightly dorsal to lens. X430.

Plate VI

Lampanyctus ritteri PO

1. Longitudinal section through at level of pigment septum. X430.
2. Transverse section through gland. X1000.
3. Longitudinal section through gland. X1000.

Plate VII

AO

1. L. nannochir Transverse section. X430.
2. L. regalis Longitudinal section. X430.
3. L. regalis Transverse section through gland. X1000.
4. L. regalis Longitudinal section through gland. X1000.

Plate VIII

Branchiostegal Organs (Transverse Section) X100

1. L. leucopsarus.
2. L. nannochir.
3. L. ritteri.
4. L. regalis.

Plate IX

Branchiostegal Organs (Longitudinal Section) X100

1. L. leucopsarus.
2. L. nannochir.

Plate IX (Continued)

3. L. ritteri.
4. L. regalis.

Plate X

Branchiostegal Organs (Transverse section through gland) X1000

1. L. leucopsarus.
2. L. nannochir.
3. L. ritteri.
4. L. regalis.

Plate XI

Caudal Organs

1. L. nannochir. Sagital section. X100.
2. L. leucopsarus. Transverse section. X100.
3. L. leucopsarus. Transverse section. X1000.
4. L. nannochir. Sagital section (enlargement of 1). X1000.

Plate XII

Caudal Organs

1. L. ritteri. Sagital section. X100.
2. L. regalis. Sagital section. X100.
3. L. ritteri. Gland cells. X1000.
4. L. regalis. Gland cells. X430.

Plate XIII

Nerves

1. L. regalis. Fine nerve branches entering ventral pigment margin of V0. Transverse section. X1000.
2. L. leucopsarus. Nerve entering posterior end of Br. X430.
3. L. nannochir. Nerve entering posterior end of Br and sending branch to pigment mantle. X430.
4. L. ritteri. Nerve in proximity of glandular cells in caudal organ. X1000.

ABBREVIATIONS

bv.	blood vessels
coll.	collagenic fibers
ct.	connective tissue
g.	gland
gc.	gland cell
is.	intercellular space
l.	lens
m.	"peculiar membrane"
n.	nerve
p.	pigment
ps.	pigment septum
r.	reflecting membrane
s.	scale

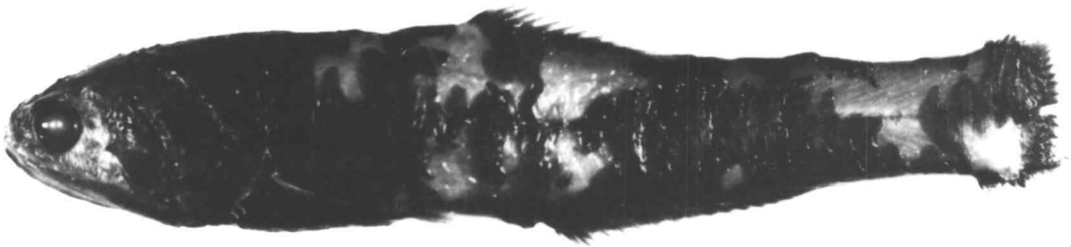
PLATE I



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PLATE II

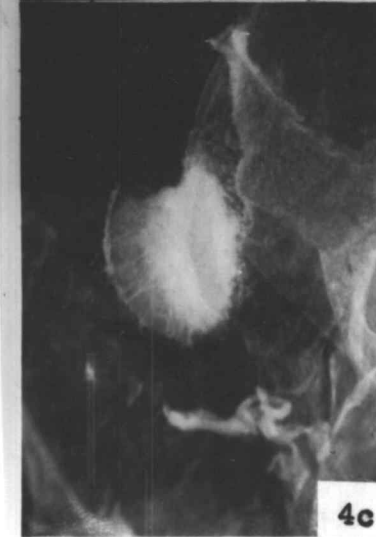
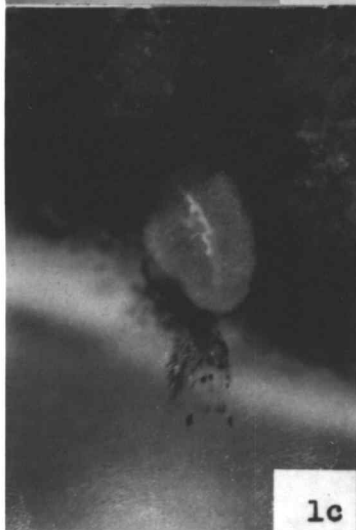
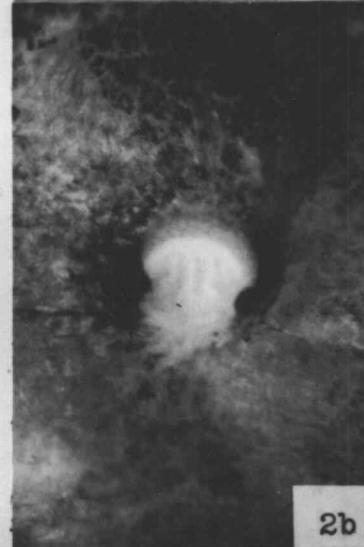
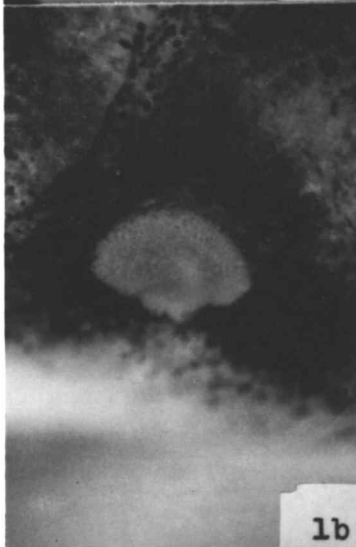
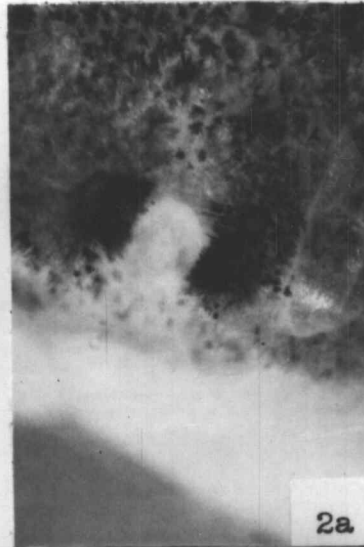
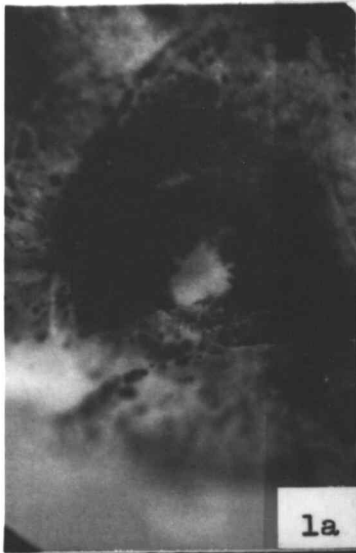


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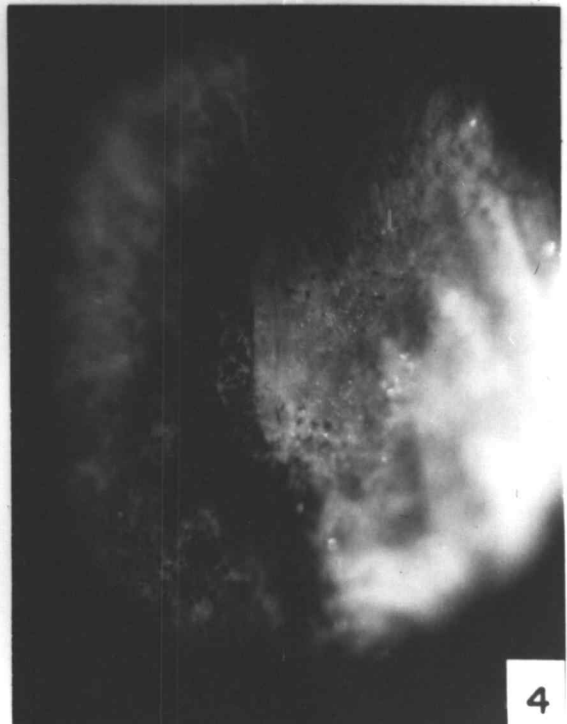
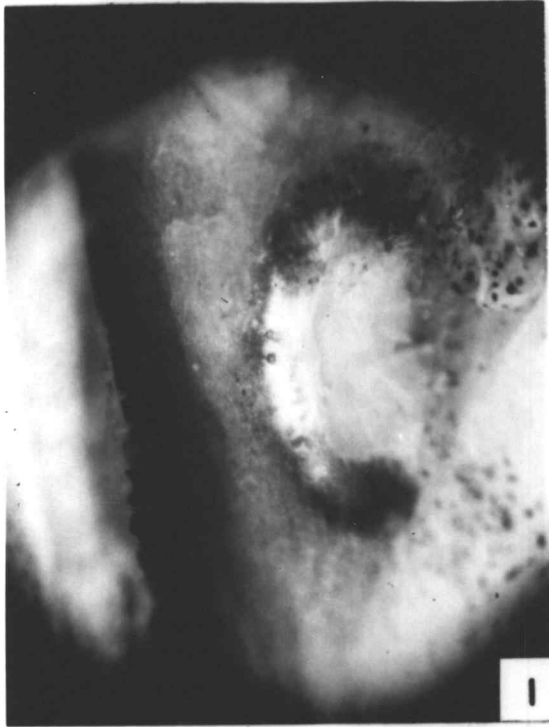


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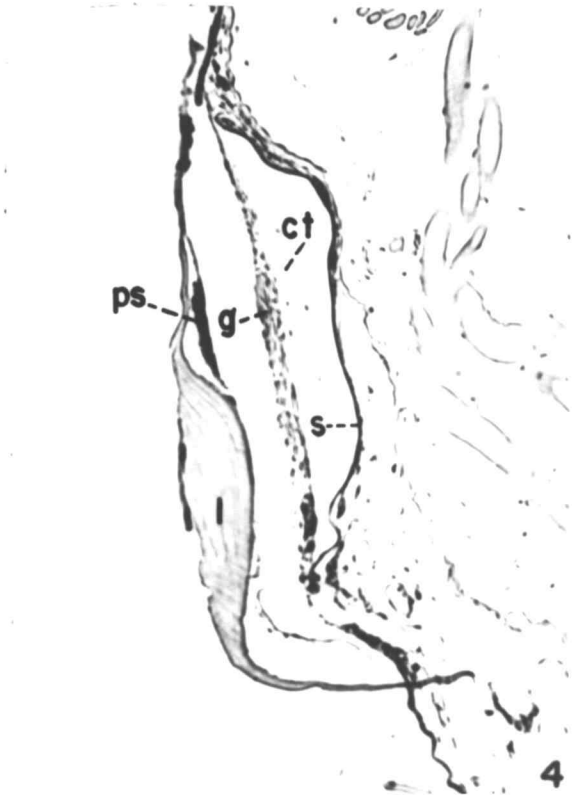
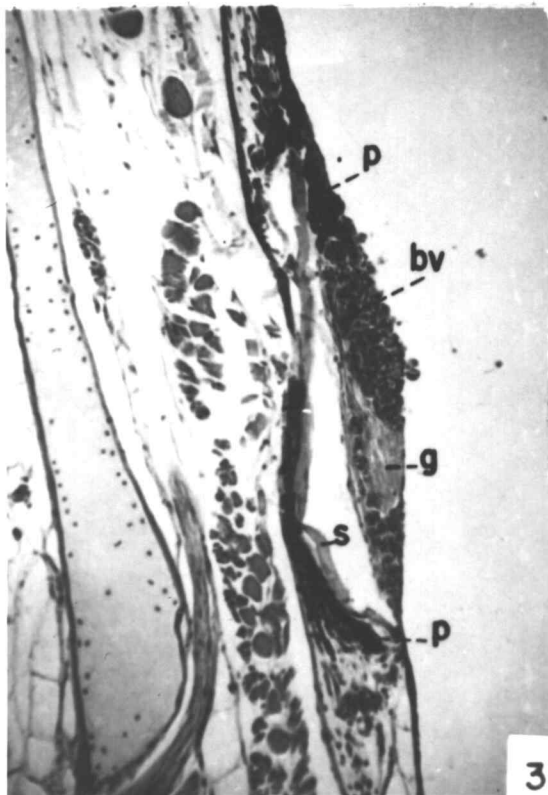
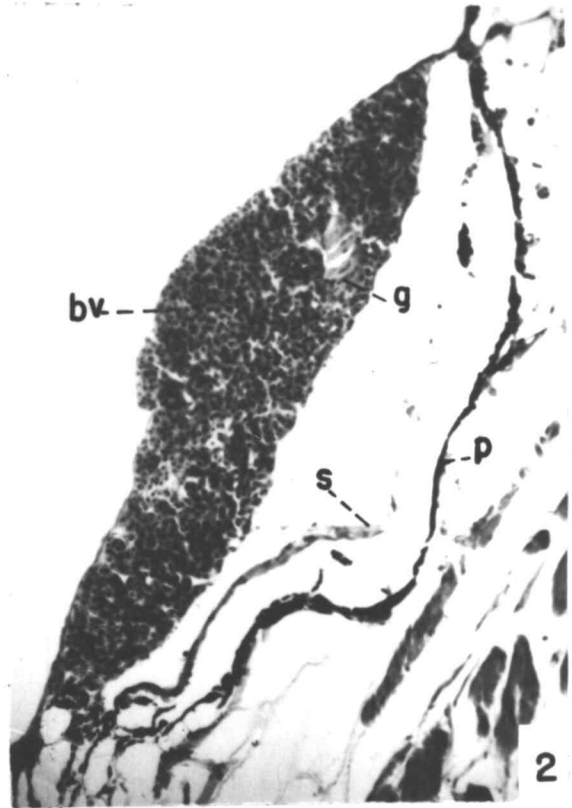
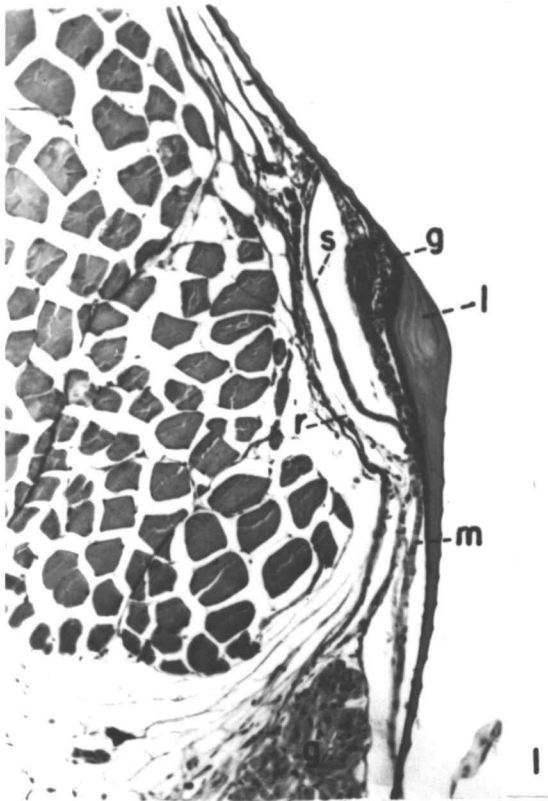


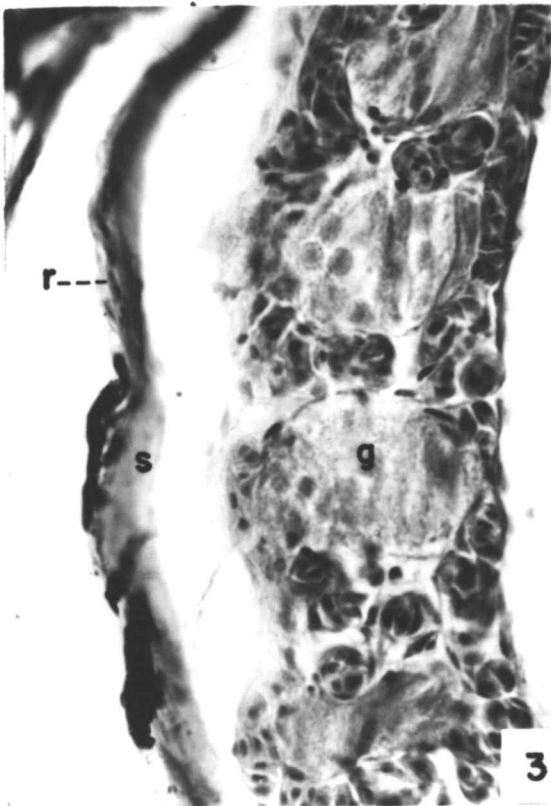
PLATE V



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PLATE VI

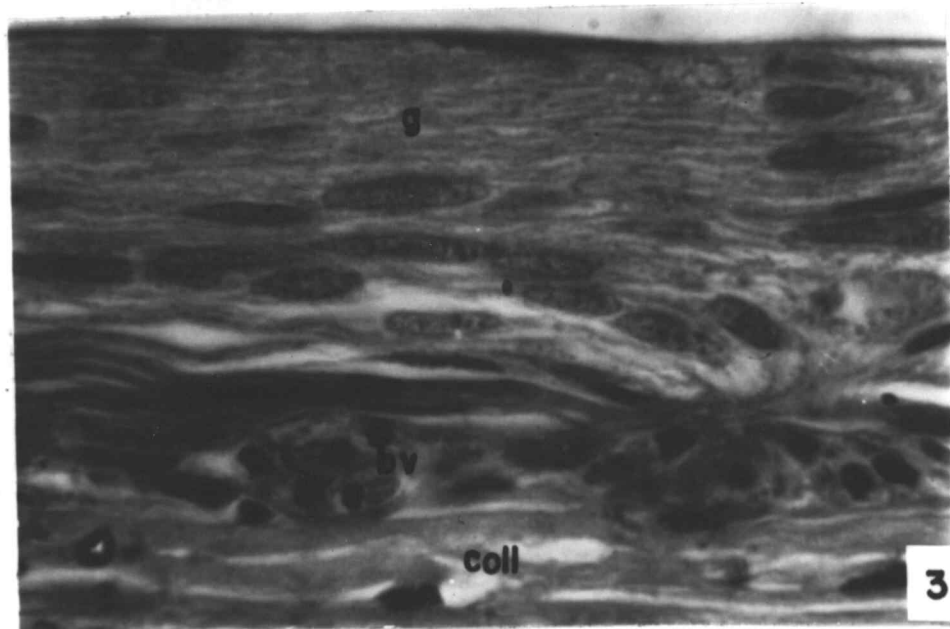
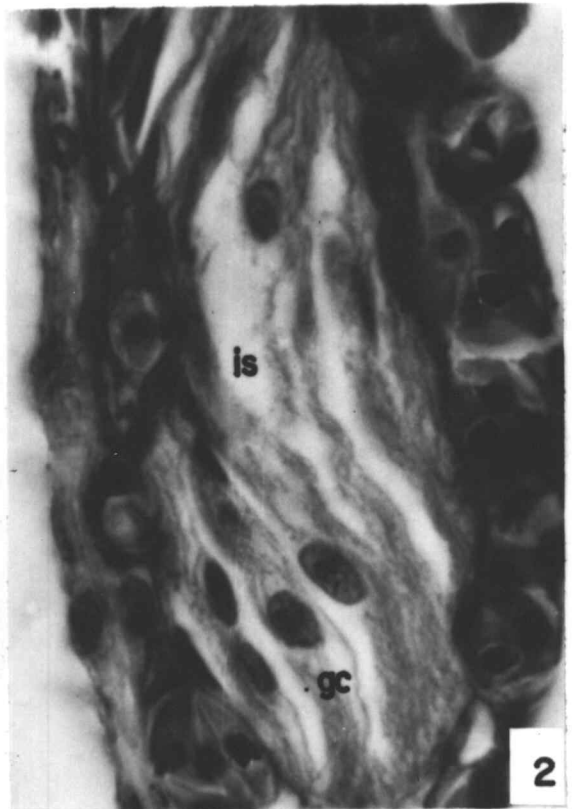
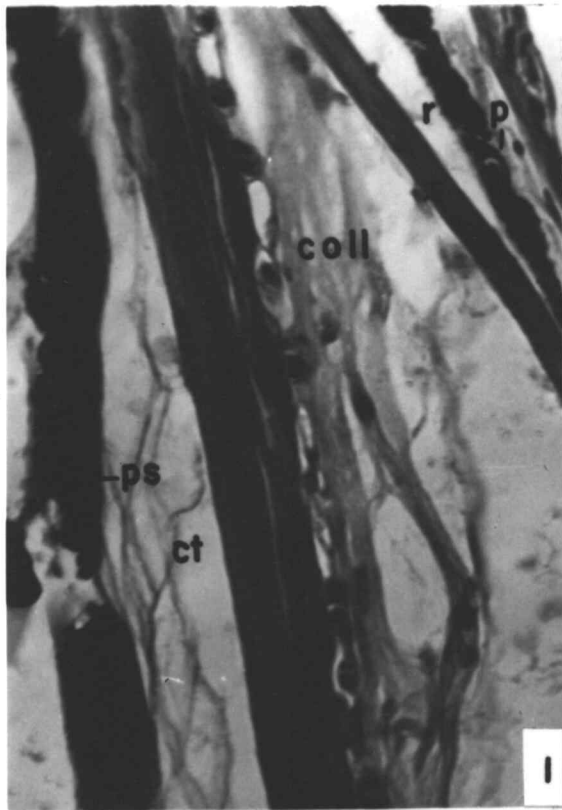


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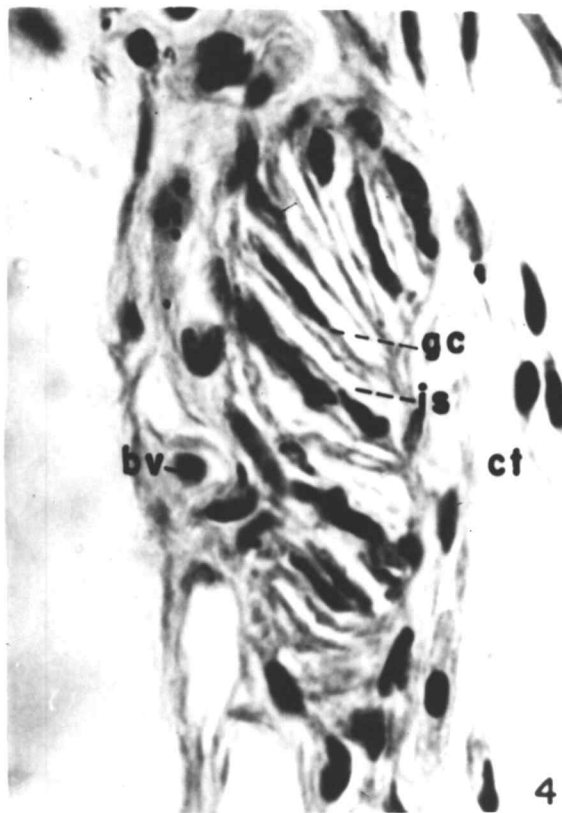
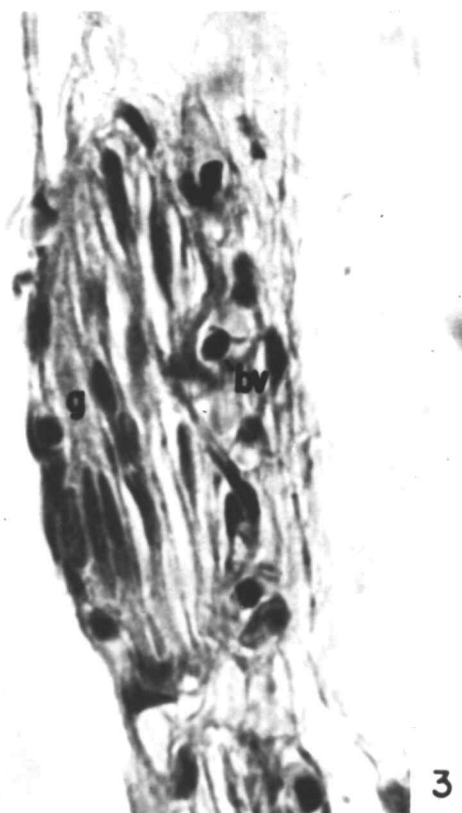
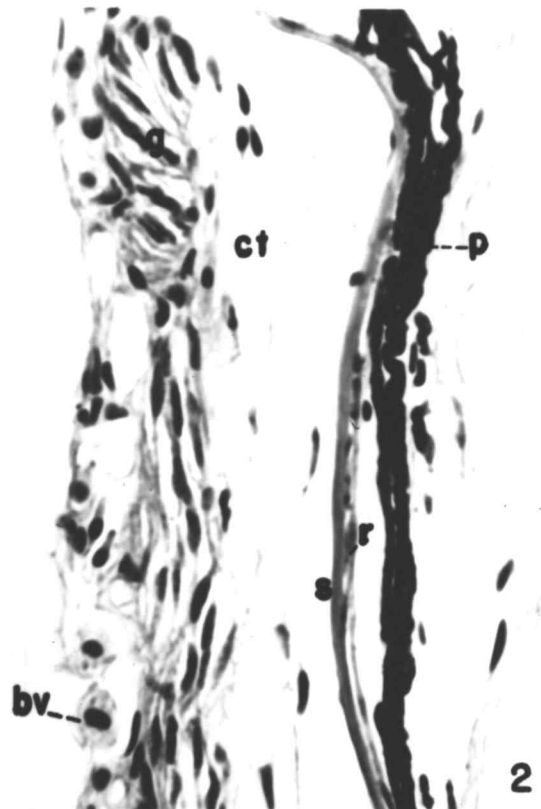
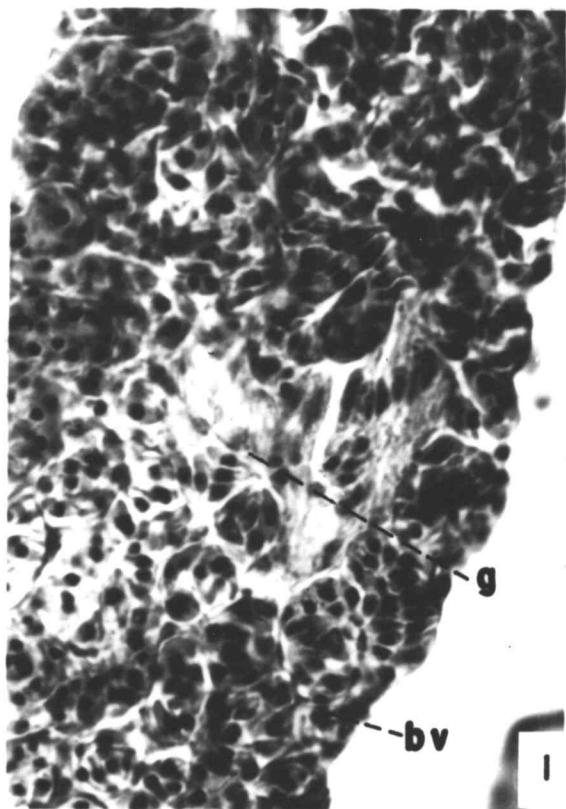


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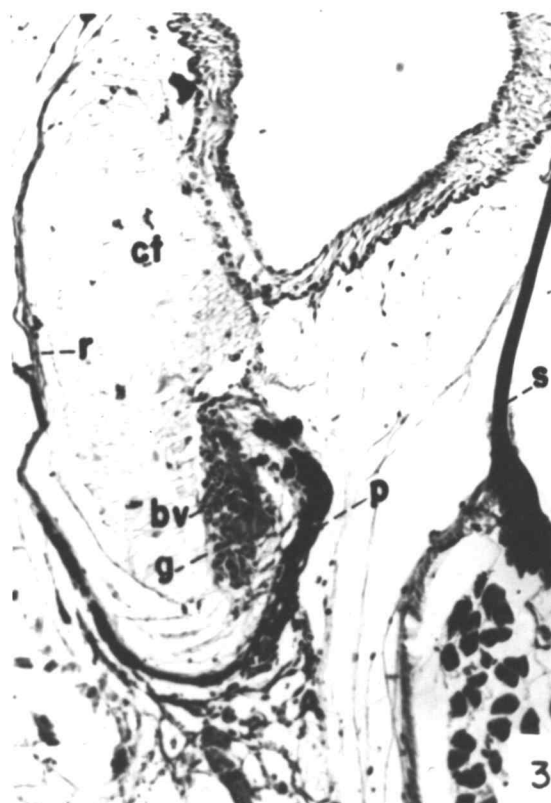
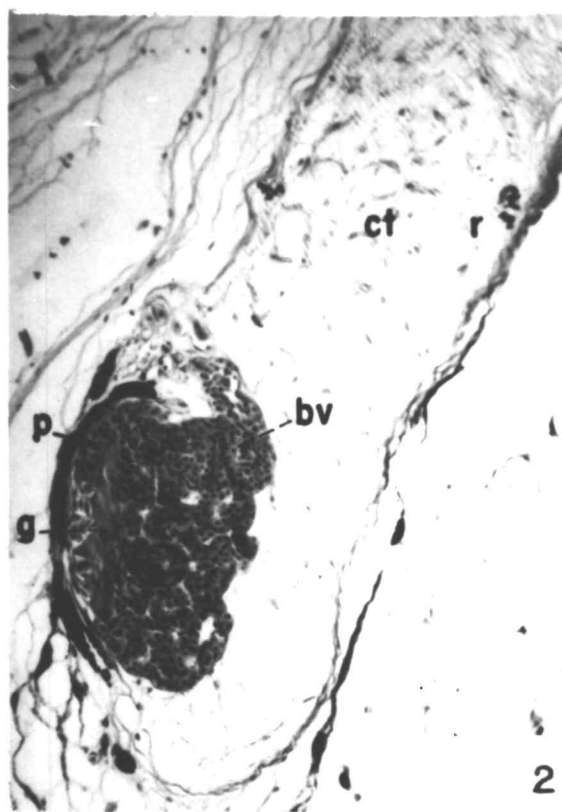
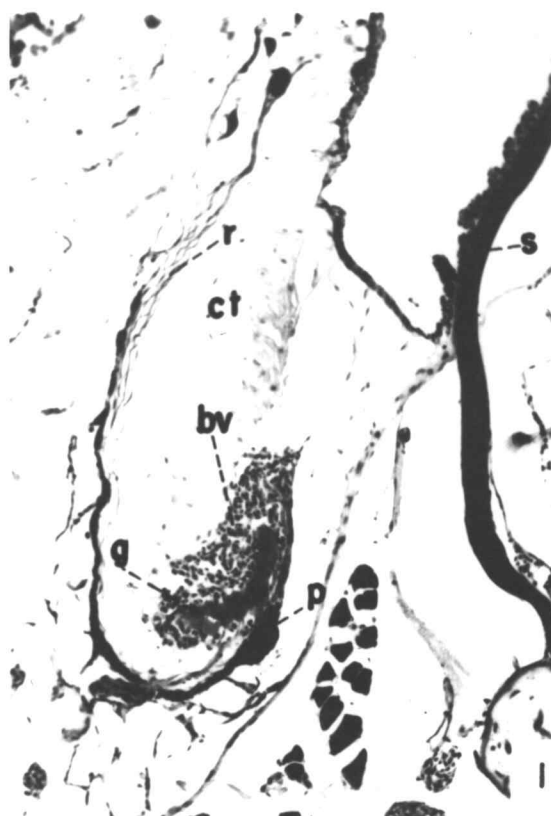
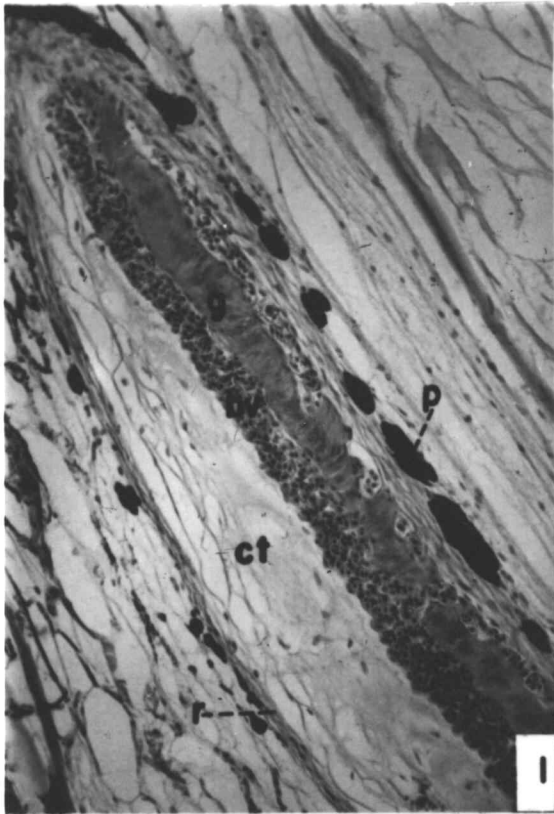
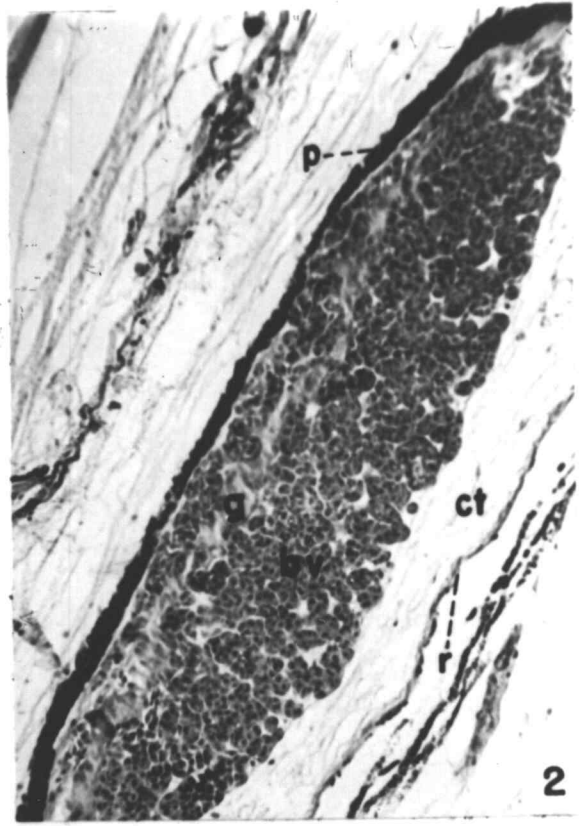


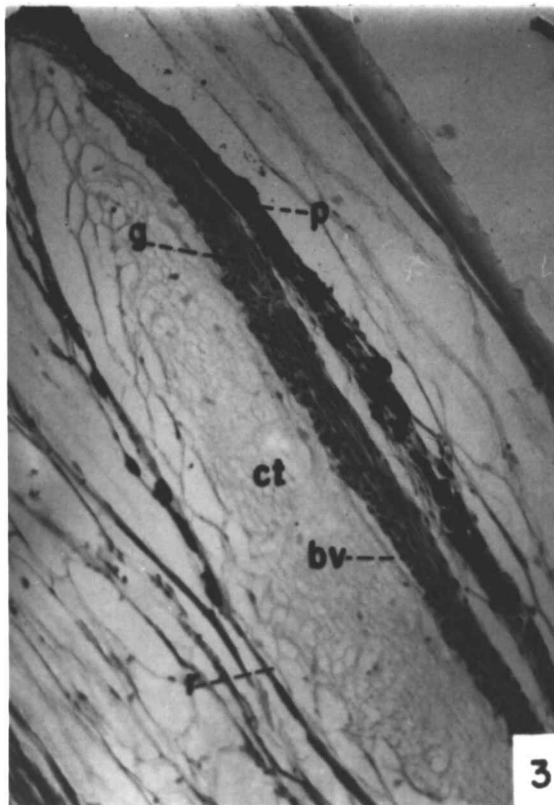
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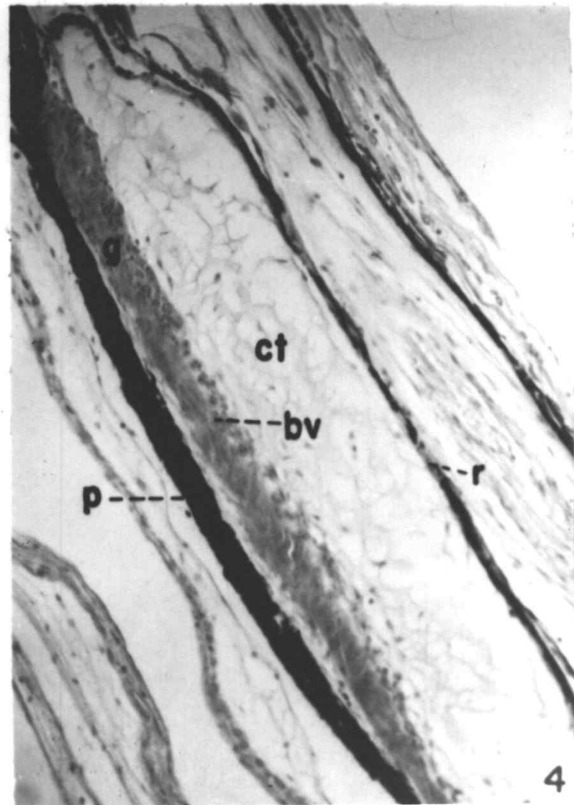
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PLATE X

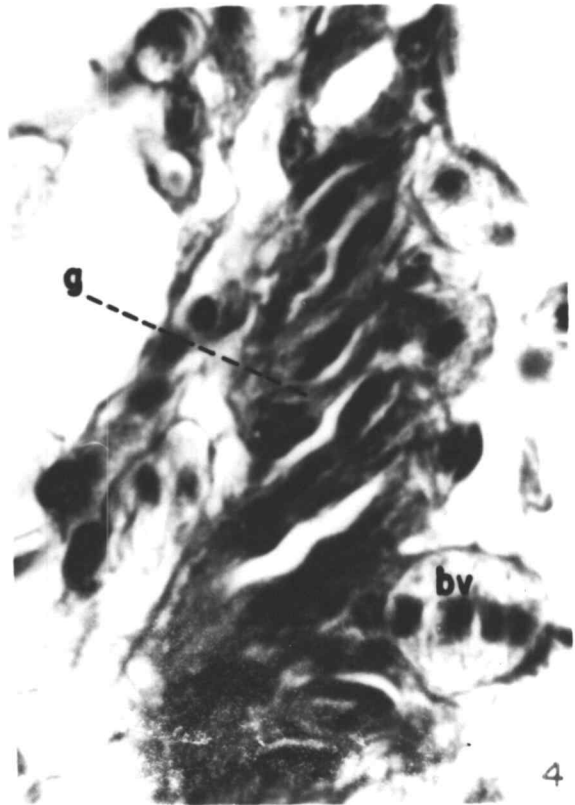
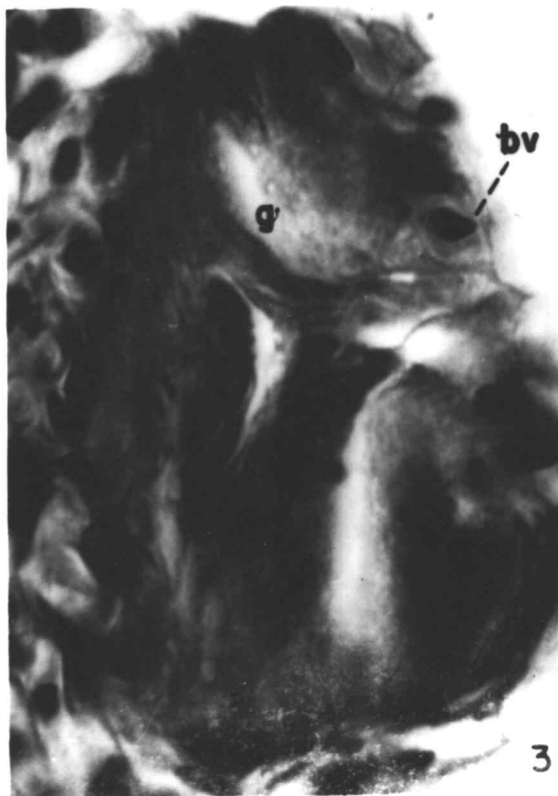
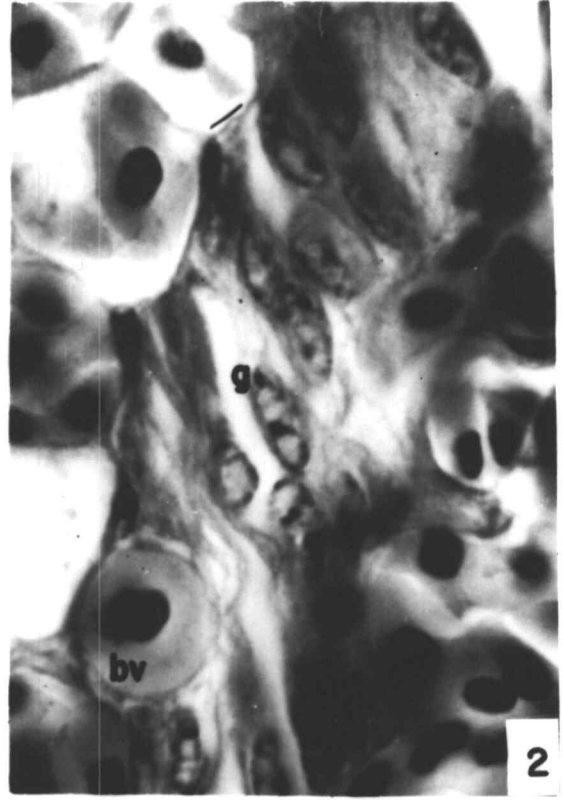
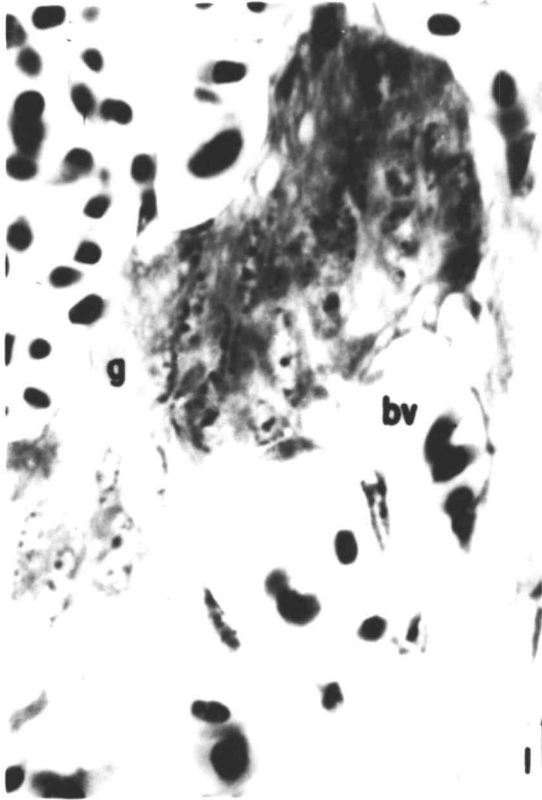


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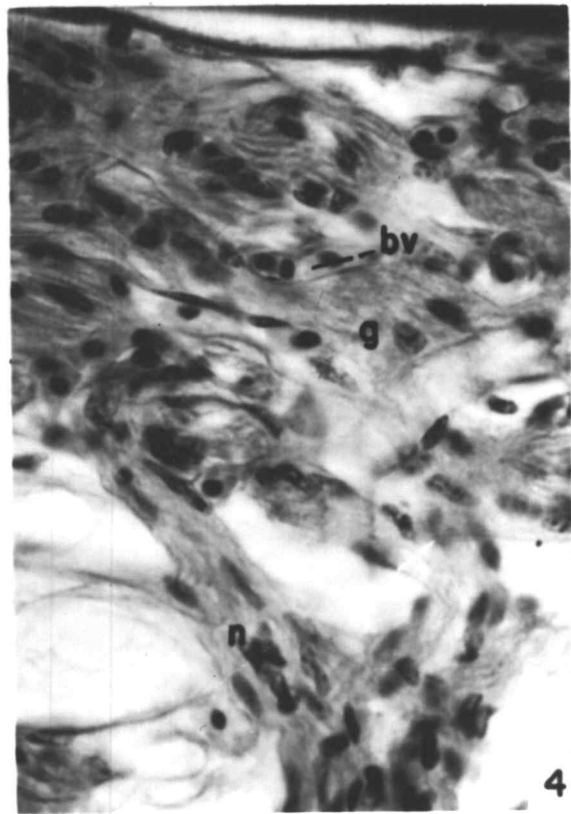
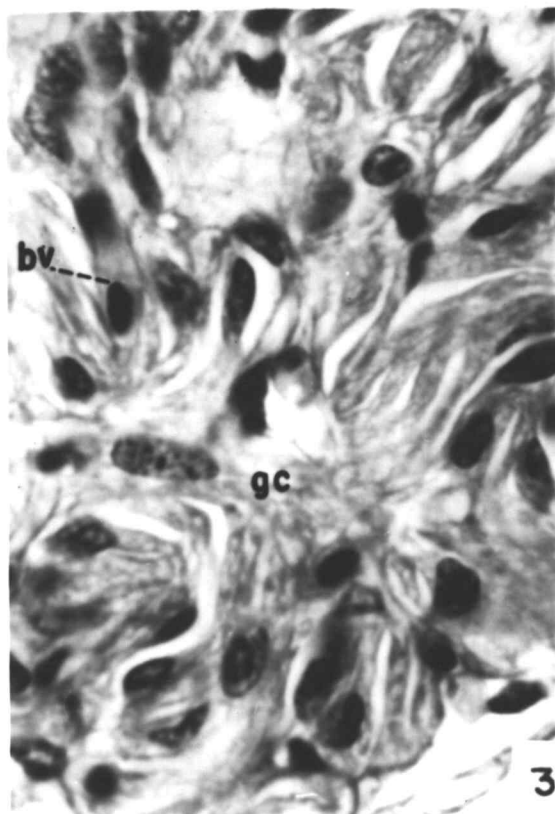


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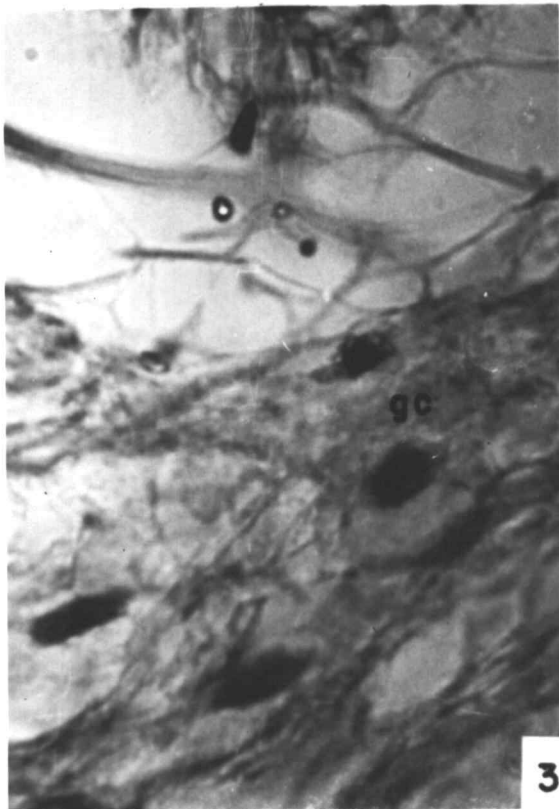
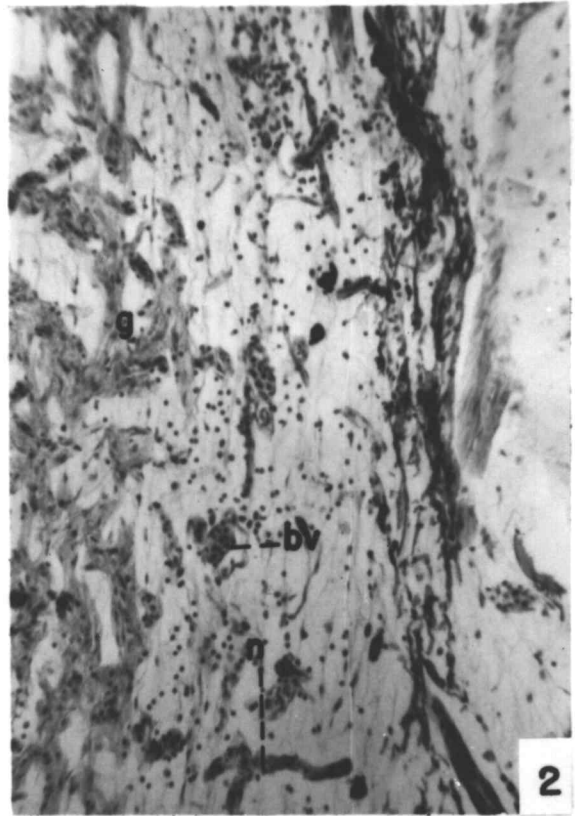
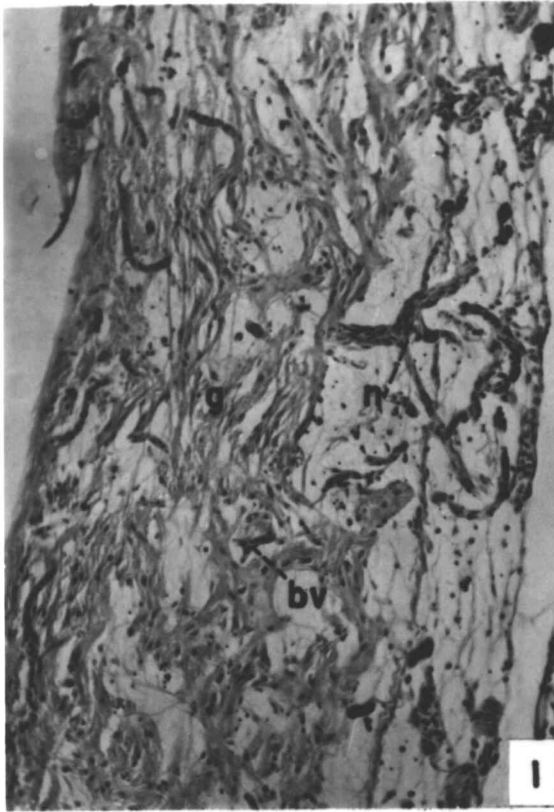


PLATE XIII

