FISHERIES AND MARINE SERVICE

Translation Series No. 3286

The fine structure of the swim bladder of Anguilla vulgaris L. Light and electron microscopic investigations

By E. Dorn

Original title: Ueber den Feinbau der Schwimmblase von Anguilla vulgaris L. Licht- und Elektronenmikroskopische Untersuchungen

From: Z. Zellforsch. 55 : 849-912, 1961

Translated by the Translation Bureau(JJ)
Multilingual Services Division
Department of the Secretary of State of Canada

Department of the Environment
Fisheries and Marine Service
Halifax Laboratory
Halifax, N.S.

1974

122 pages typescript

DEPARTMENT OF THE SECRETARY OF STATE
TRANSLATION BUREAU

MULTILINGUAL SERVICES DIVISION

CANADA

SECRÉTARIAT D'ÉTAT
BUREAU DES TRADUCTIONS

DIVISION DES SERVICES MULTILINGUES

FoM 3286

TRANSLATED FROM – TRADUCTION DE	INTO – EN
German	English

AUTHOR – AUTEUR

E. DORN

TITLE IN ENGLISH – TITRE ANGLAIS

The fine structure of the swim bladder of Anguilla vulgaris L. Light and electron microscopic investigations

TITLE IN FOREIGN LANGUAGE (TRANSLITERATE FOREIGN CHARACTERS)
TITRE EN LANGUE ÉTRANGÈRE (TRANSCRIRE EN CARACTÈRES ROMAINS)

Ueber den Feinbau der Schwimmblase von Anguilla vulgaris L. Licht- und Elektronenmikroskopische Untersuchungen

REFERENCE IN FOREIGN LANGUAGE (NAME OF BOOK OR PUBLICATION) IN FULL. TRANSLITERATE FOREIGN CHARACTERS.
RÉFÉRENCE EN LANGUE ÉTRANGÈRE (NOM DU LIVRE OU PUBLICATION), AU COMPLET, TRANSCRIRE EN CARACTÈRES ROMAINS.

Zeitschrift fuer Zellforschung

REFERENCE IN ENGLISH – RÉFÉRENCE EN ANGLAIS

Journal of Cell Research

PUBLISHER – ÉDITEUR	DATE OF PUBLICATION / DATE DE PUBLICATION			PAGE NUMBERS IN ORIGINAL / NUMÉROS DES PAGES DANS L'ORIGINAL
not shown	YEAR / ANNÉE	VOLUME	ISSUE NO. / NUMÉRO	849-912
PLACE OF PUBLICATION / LIEU DE PUBLICATION				NUMBER OF TYPED PAGES / NOMBRE DE PAGES DACTYLOGRAPHIÉES
not shown	1961	55	not shown	122

REQUESTING DEPARTMENT / MINISTÈRE-CLIENT: Environment

TRANSLATION BUREAU NO. / NOTRE DOSSIER N°: 676722

BRANCH OR DIVISION / DIRECTION OU DIVISION: Fisheries Service, Office of the Editor

TRANSLATOR (INITIALS) / TRADUCTEUR (INITIALES): JJJ

PERSON REQUESTING / DEMANDÉ PAR: Jutta Dale, Halifax Laboratory

JAN - 2 1975

YOUR NUMBER / VOTRE DOSSIER N°:

DATE OF REQUEST / DATE DE LA DEMANDE: 16/9/74

UNEDITED TRANSLATION
For Information only
TRADUCTION NON REVISEE
Information seulement

SOS-200-10-6 (REV. 2/68)
7530-21-029-5333

DEPARTMENT OF THE SECRETARY OF STATE
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MULTILINGUAL SERVICES
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CLIENT'S NO. / Nº DU CLIENT	DEPARTMENT / MINISTÈRE	DIVISION/BRANCH / DIVISION/DIRECTION	CITY / VILLE
	Environment	Fisheries Service Office of the Editor	
BUREAU NO. / Nº DU BUREAU.	LANGUAGE / LANGUE	TRANSLATOR (INITIALS) / TRADUCTEUR (INITIALES)	
676722	German	JJ	JAN - 2 1975

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The fine structure of the swim bladder of Anguilla vulgaris L.
Light and Electron microscopic investigations

by

E. DORN, Institute of Anatomy, Kiel University (Prof. W. BARGMANN, M.D., Director) and the Institute of Zoology, Mainz University (Prof. H. MISLIN, Director)

with 44 illustrations in the text

(MS. received on July 13, 1961)

This project was carried out with the support of the Deutsche Forschungsgemeinschaft ("German Research Association"). I am indebted to Dr. W. BARGMANN for providing research facilities and for promoting the project.

CONTENTS

A. Introduction

The swim bladder of teleosts is a hollow, gas-filled, retroperitoneal organ beneath the vertebral column, originating as a dorsal evagination of the stomodeum. In the physostomes, the connection between the swim bladder and the digestive tract remains intact throughout the life of the animal; in the physoclists, it disappears more or less early in life, leaving the swim bladder completely closed.

Although the swim bladder may serve a variety of functions, —as a hydrostatic, respiratory, sensory, or sound-producing organ,—its structure is that of a hollow cavity filled with gas. The gas consists mostly of a mixture of oxygen, carbon dioxide and nitrogen, varying greatly in its percentual composition according to the species and biotope of the fish. This mixture must be regulated constantly, for two reasons: (1) to replace the gas, small quantities of which continuously diffuse into the neighboring tissues, where the partial pressure is considerably lower than in the cavity of the swim bladder; and (2) to facilitate rapid major changes in the amount of gas. In physostomes, this occurs essentially 850
by means of swallowing air at the water surface and releasing it through the mouth. In the physoclistous swim bladder, the process seems to be much more complex. Many juvenile fishes (e.g., Syngnathidae, sticklebacks, Lebistes) still have an open connection between the swim bladder and the esophagus during the first days of life, and must swallow air through their mouths to expand the bladder for the first time and to maintain the pressure; but this air passage soon undergoes involution, and the gas must then be regulated in another manner.

The following differentiations are thought to provide the substrate for the functions of the swim bladder:

1. Glandular modifications of the cavity lining in the anterior part of the swim bladder, known as the "gas glands"

(called "cellular fringes" ["zellige Saeume"] by JOH. MUELLER 1839), with which the highly complex retia mirabilia of the "red bodies" (DELAROCHE 1809) are connected; and

2. the "oval", a highly vascular area covered by a particularly thin membrane, which can be closed off from the lumen of the swim bladder by a sphincter. The oval is located well removed from the gas glands, in the posterior dorsal region of the swim bladder, and it is often separated from the latter by a muscular diaphragm.

The thinly covered area of the oval, abundantly supplied with blood, is believed to be the site at which gas is "resorbed" from the swim bladder cavity into the bloodstream; this absorption may be readily explained as a diffusion process, since the partial pressure of the gas in the swim bladder is considerably higher than in the blood. The gas enters the lumen of the swim bladder by way of the "gas glands", in a process known as "gas secretion". But it is not yet entirely clear whether the cells of the gas glands actually release a gaseous secretion (or a predecessor which subsequently breaks down into gaseous components) or the gas originates from other sources and merely diffuses through these cells.

The controversy regarding this question dates back to the turn of the century. HUEFNER (1892), one of the first to refer to the secretion of gas in the swim bladder, advocated the diffusion hypothesis. He viewed this gas secretion as the simplest type of "secretory" process, since the substances to

be released did not have to be produced in the cell, but were already prepared in the blood, and were merely transported by way of the cell.

The first workers to study the morphology of gas secretion were JAEGER (1903), REIS (1906), and REIS & NUSBAUM (1905-1907). JAEGER found fragmented blood cells in the gas gland of Sciaena. On the basis of this finding, he constructed the hypothesis that the gas glands secrete a toxic substance which decomposes the blood cells. As a result of this decomposition, he thought, all of the oxygen in the oxyhemoglobin was liberated, creating a high partial pressure. But this hypothesis is no longer tenable. On the one hand, it was found to be based on an artefact of fixation, insofar as the blood cells had become dissolved in the preparation, which had been fixed for years. On the other hand, BOHR (1905) removed the foundation of the theory with the following calculation: A cod fish weighing one kilogram can easily secrete ten cubic centimeters of oxygen within six hours. During this time, all of the blood cells 851 and the entire supply of hemoglobin would have to be decomposed and built up again. But this process never takes place.

REIS (1906) and REIS & NUSBAUM (1905-1907) assumed that breakdown processes take place in the cells of the gas gland epithelium, giving rise first to granular and flocculent substances, and from these, to gas, which is released into the swim bladder

cavity in the form of bubbles. However, these supposed bubbles and their predecessors were also later found to be artefacts.

Even today, it remains undecided whether the swim bladder is filled with gas by secretion or by diffusion; therefore, we shall outline the current opinions regarding the physiology of this process. According to JACOBS (1930-1938, 1940), v. LEDEBUR (1928-1937), FAENGE (1945-1958), COPELAND (1951-1952), HARDEN JONES (1951-1957), HOGBEN (1958), SCHOLANDER (1951-1956), BALL, STRITTMATER, COOPER (1955, 1958), and others, gas secretion takes place in the following manner: In the cells of the gas gland, which are rich in glycogen (COPELAND, 1952), glycolytic processes take place, probably in response to nervous stimuli (COPELAND, 1952; FAENGE, 1953). These processes give rise to lactic acid and carbon dioxide (FAENGE 1953; STRITTMATER, BALL & COOPER 1952; BALL, STRITTMATER & COOPER 1955), which lower the pH-value (HALL 1924; HOGBEN 1958) of the blood in the capillaries of the gas glands.

An important role in this process is apparently played by the enzyme carbonic anhydrase (LEINER & LEINER 1938; LEINER 1940; SOBOTTKA & KANN 1941; BLACK 1946; FAENGE 1953). Regarding the swim bladder of Cyprinidae, FAENGE & MATTISON (1956) stated: "It would be of interest to examine the distribution ... of the enzyme carbonic anhydrase in the different layers of the ...swimbladder because the gas gland epithelium of euphysoclists is characterized by high amount of these substances" (i.e., glycogen and carbonic anhydrase). As FAENGE (1953) observed,

injection of an inhibitor specific for this enzyme brings gas secretion to a stop. By the action of carbonic anhydrase, increased quantities of carbon dioxide are liberated in the blood. The carbon dioxide, in turn, leads to increased dissociation of oxygen from the hemoglobin in the blood (ROOT 1931; SCHOLANDER & VAN DAM 1954). Since the pressure of the gas inside the swim bladder is considerably higher than that of gas in the blood and the neighboring tissues, a still higher pressure must be attained locally to permit the gas to pass into the lumen of the swim bladder; this is achieved by the adjacent retia mirabilia of the red bodies. The parallel rows of capillaries are thought to represent a hairpin counterflow exchange system (HALDANE & PRIESTLEY 1935; SCHOLANDER 1954; KUHN & KUHN 1961), in which the venous blood leaving the gas gland releases its gas to the blood flowing into the swim bladder in the arterial capillaries. In this way, the gas pressure is built up within the area of the red bodies until it exceeds the pressure of the gas inside the swim bladder (HALDANE & PRIESTLEY 1935; KUHN & KUHN 1961), thus causing gas to pass into the swim bladder by way of the gas gland cells.

According to this view, the gas glands are active secretors, but rather in the fashion of an endosecretory gland (JACOBS 1930, 1954); for they release substances into the blood, and only these substances bring about the actual

process of gas secretion. The gas then passes on into the swim bladder by a process of diffusion. According to FAENGE (1953), the inner surface of the gas gland epithelium is coated with a fluid in which gas bubbles first form like soap bubbles before passing into the cavity of the swim bladder. SCHOLANDER (1954), on the other hand, expressed the view that the retia mirabilia are not adequate to build up sufficient gas pressure, and —at least in the case of deep sea fishes— we must assume active secretion of oxygen by the cells of the gas glands. 852

It is the purpose of the present study to reveal structural characteristics of the tissues of the swim bladder which may be connected with the functions discussed above. In particular, a study of the submicroscopic structure of the swim bladder is necessary; for with the exception of a brief communication concerning the fine structure of the rete mirabile in the swim bladder of Opsanus tau (FAWCETT & WITTENBERG 1959) and the preliminary report on the present study (DORN 1960), to the best of my knowledge, only light microscopic studies are available so far. Consequently, important structural components found in every cell, such as mitochondria and Golgi apparatus, have not yet been identified in the tissues of the swim bladder. A knowledge of these organelles may itself provide an adequate basis for drawing conclusions with respect to such questions as whether, and to

what extent, a cell shows secretory action.

We must also look for special structures in those places where an exchange of materials would be most likely to take place; viz., in particular, the walls of the blood vessels, and especially of the capillaries, the permeability of which is crucial for the exchange of materials between the blood and the environment. This refers, first of all, to the walls of capillaries in the red body, where the exchange of gas between the blood in the venous and in the arterial capillaries is supposed to take place; secondly, to the walls of the blood vessels in the barrier between the blood gas and the swim-bladder gas, which is located in the gas gland and in the absorptive area; and finally, to the cells of other tissues involved in the formation of this barrier.

The subject chosen for this study was the swim bladder of the Eel, which is peculiar in many respects (Figure 1).

It is a physostomous swim bladder; i.e., the body of the swim bladder is connected with the digestive tract by a sizeable ductus pneumaticus. But the opening of the ductus pneumaticus into the esophagus is very small —it is, indeed, hardly suitable for the active uptake and elimination of air—and hidden deep in the folds of the mucous membrane of the esophagus. In addition, however, the swim bladder of 853
the Eel is equipped with all the modifications of a physoclistous swim bladder. The gas-secreting area, of "gas gland", is present, albeit in a peculiar form. It is not limited to a

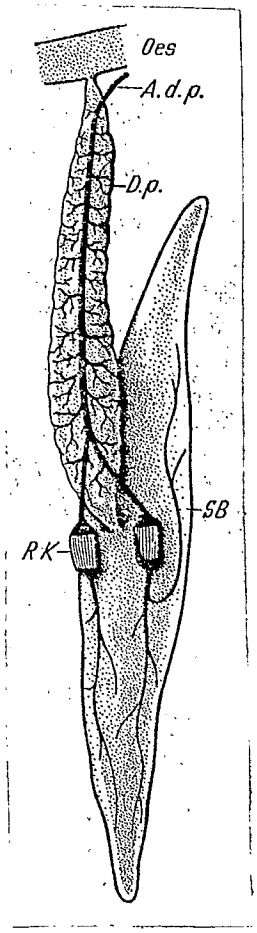

Figure 1. Schematic representation of the swim bladder of the Eel, viewed from the left. Swim bladder and ductus pneumaticus are slightly expanded. SB- swim bladder D.p.-ductus pneumaticus A.d.p.- arteria ductus pneumatici Rk- red body Oes- esophagus

particular area in the wall of the swim bladder; rather, the entire epithelial lining of the swim bladder cavity represents the gas-secreting area. We therefore have a gas gland which is very extensive, but unusually simple from a morphological point of view. Precisely because of its "schematic" simplicity, this organ represents a promising source of information concerning the process known as "gas secretion".

Moreover, in the swim bladder of the Eel, the capillary formations of the retia mirabilia —the "red bodies", which are connected with the gas gland— are present, once again in a special form. In many physoclistous swim bladders, retia mirabilia and gas glands are inseparable; but in the Eel, they lie far apart. So far as we know, the two "red bodies" of the Eel swim bladder are the most highly complex retia mirabilia in any swim bladder. These paired, bipolar retia mirabilia (J. MUELLER 1840) originate in a bifurcation of the swim bladder artery. Over a very short distance, each of the two branches divides into a large number of very fine parallel capillaries grouped in bundles measuring about one centimeter in length. At the opposite end of the red bodies, these capillaries reunite into two large vessels. The latter run into the wall of the swim bladder, and directly beneath the epithelium, they divide to form a second network of capillaries. These capillaries unite to form veins, which, like the arteries, again branch out into capillaries in the area of the red bodies. The venous capillaries intermingle with the arterial capillaries and run parallel with them, but do not anastomose with them. At the rostral pole of the red bodies, the venous capillaries converge into two large veins which unite to form the swim bladder vein, emptying into the portal vein (PAULY 1882; WOODLAND 1911). Hence, in the Eel, the capillaries of the red bodies are separate from those supplying the gas gland epithelium, so that each portion of the paired, bipolar rete mirabile may be studied separately.

Finally, the area of absorption is represented not by the wall of the swim bladder, but by the ductus pneumaticus. The fact that the ductus does not have the same circulatory network as the rest of the swimbladder is particularly interesting in this connection. The arterial source is the same; both the swim bladder and the ductus pneumaticus draw their arterial blood from the arteria coeliaca. But the ductus pneumaticus has its own venous vascular network; the vena ductus pneumatici runs directly into the ductus cuvieri, creating a separate minor circuit (PAULY 1882).

Hence, the swim bladder of the Eel is an especially good subject for studying in isolation those areas which are important in the exchange of materials, viz., (1) the swim bladder epithelium, (2) the capillaries passing through this epithelium, (3) the ductus pneumaticus, and (4) the capillaries of the red body.

B. Material and Method 854

We studied the swim bladders of 28 adult specimens of Anguilla vulgaris L. The animals were killed by decapitation, and the swim bladders were removed and fixed directly after killing. A portion on the swim bladders was injected with fixative fluid and then placed in the fluid. Only after fixation were the swim bladders divided and subjected to further treatment. From other specimens, we removed and fixed individual

pieces of the swim bladder wall, the ductus pneumaticus, and the red body.

The fixation fluids used were Susa fixative, Bouin fixative, formalin 1:4, formalin 1:9, Carnoy fixative, alcohol-picric acid-formalin according to GENDRE, and acetone.

The fixed specimens were embedded in paraffin from methyl benzoate. Sections measuring 4-8 μ in thickness were prepared as follows: From the wall of the swim bladder, cross sections and horizontal sections; from the ductus pneumaticus, cross sections and longitudinal sections; and from the red body, cross sections and longitudinal sections.[1]

The following staining processes and reactions were carried out on the sections embedded in paraffin: Hematoxylin-eosin, iron hematoxylin (HEIDENHAIN), azan (HEIDENHAIN), GOLDNER'S trichrome stain, GOMORI'S modification of GOLDNER's stain, GOMORI's chrome alum hematoxylin-phloxin, the panoptic method of PAPPENHEIM and PAPPENHEIM-CARDOS, Elastica stain with resorcinol-fuchsin, PAP's lattice fiber preparation, KORSON's orange G-methyl green-toluidine blue, methylene blue, and PAS.*

Frozen sections were prepared from the fresh material using a cryostat, for use in the following reactions and staining

[1] I am indebted to Miss K. JACOB for microtechnical and microphotographic assistance.

*TRANSLATOR'S NOTE: Periotic acid Schiff reagent

processes: HAEUSLER's test for carbonic anhydrase, succinic acid dehydrogenase demonstration, lipid demonstration with Nile blue sulphate, Sudan black B, scarlet, and staining with methyl green-pyronin.

In addition, preparations of whole swim bladders were made. For this purpose, the swim bladders were cut in longitudinal sections and fixed in formalin while stretched on a frame. Afterwards, the following staining methods were used: Resorcinol-fuchsin-chromotrope 2R (PETRY) for demonstration of the elastic fibers, and hematoxylin for the demonstration of the muscles.

Moreover, the blood vessels of the swim bladder were injected. The animal was narcotized in urethane-containing water, and the vessels of the swim bladder were injected with undiluted Scribtol* in situ; the ink was injected into the aorta descendens. After the injection, the swim bladder was removed, fixed in toto in formalin, dehydrated, and cleared in wintergreen oil.

Electron microscopic examination[2]: Pieces of the swim bladder wall, the ductus pneumaticus, and the red body were fixed in buffered 1% or 2% solutions of osmic acid (according

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*TRANSLATOR'S NOTE: A type of India ink

[2]I am indebted to Dr. A. KNOOP for her assistance in the laboratory of the Department of Electron Microscopy of the Institute of Anatomy of Kiel University.

to SJÖSTRAND's method) for 2 and 4 hours, respectively. After dehydration in alcohol, the specimens were embedded in butyl- and methylmethacrylate (10:1 and 11:1, respectively, with 2.5% Perkadox as activator). Thin sections were prepared with a PORTER-BLUM ultramicrotome, and examined using a Siemens Elmiscope I (beam voltage, 80 kV). The micrographs were prepared by Dr. A. KNOOP.

C. Findings

I. Light microscopic findings

1. Swim bladder. The wall of the eel swim bladder is described in the early literature (e.g., OPPEL 1905) as consisting of a lamina interna, a lamina externa, and a serosa. However, it seems advisable to follow the terminology suggested by FAENGE (1953), which conforms with the terms applied to the walls of the intestinal tract.

A cross section through the wall of the swim bladder (Figure 2) shows the sequence of layers characteristic of all parts of the swim bladder. These layers are treated in the following paragraphs in the order of their appearance from the outside in, i.e., starting from the "serosa".

(a) The submucosa. The submucosa is a loose connective 855
tissue traversed by a fine tomentum of argyrophil filaments. The lamelliform structure already mentioned by previous authors

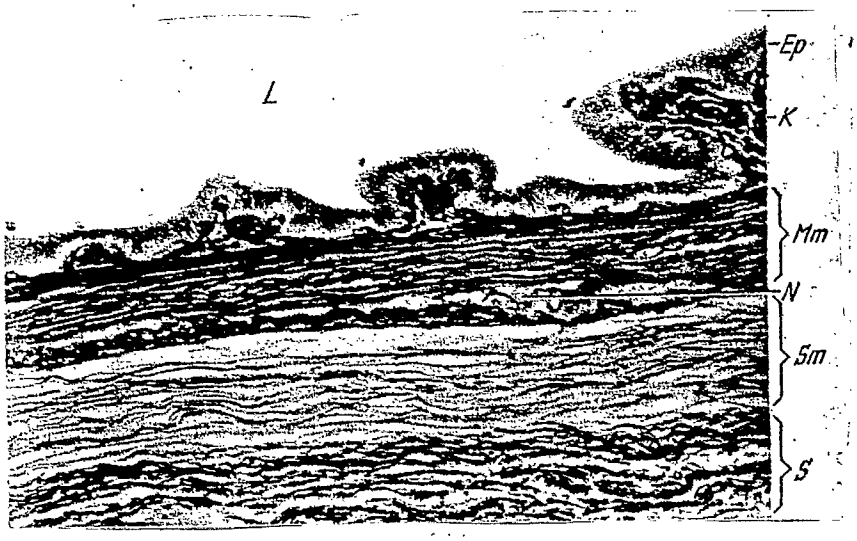

Figure 2. Sequence of layers in the wall of a swim bladder. Paraffin section, 6 μ, azan stain. L-lumen Ep-epithelium K-capillaries Mm- muscularis mucosae N-nerves in the muscularis mucosae Sm-submucosa S-serosa. x170.

is most distinctly seen in untreated cryostat sections. These sections show that, in a relatively relaxed swim bladder, the lamellae of the submucosa are arranged in "zigzagging" folds. The reaction of this layer to lipid staining methods is worthy of note: With scarlet, it stained bright red; with Nile blue sulphate, blue; and with Sudan black B, extremely dark blue.

(b) The muscularis mucosae. The muscularis mucosae consists of several strata of smooth muscle cells running in different directions; but these layers are not distinctly separated (Figure 3). In the innermost layers, most of the muscle fibers are arranged in a circular pattern, while the adjoining outer layers show a more longitudinal orientation.

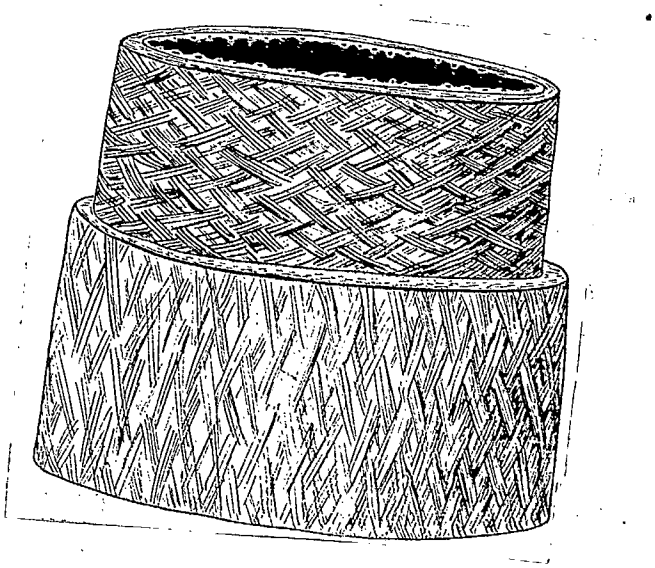

Figure 3. Schematic representation of the arrangement of muscular fibers in the muscularis mucosae of the swim bladder

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The cells of the inner muscle layers wind smoothly around the body of the swim bladder in such a way that the different strata intersect and probably even intertwine. The resulting 856
pattern resembles a scissorlike lattice with an adjustable mesh. The cells in the outer muscle layers intersect in a similar fashion, but they turn in much steeper spirals, so that in this outer lattice, the shears tend to point in a longitudinal direction. The muscle layers are surrounded by a fine network of very delicate elastic fibers (Figure 4), most of which seem to expand longitudinally. Usually, there is a particularly distinct layer of elastic fibers between the thin, outermost muscular stratum and the rest of the muscularis mucosae. Numerous nerve fibers pass throught the muscularis mucosae (see Figure 2).

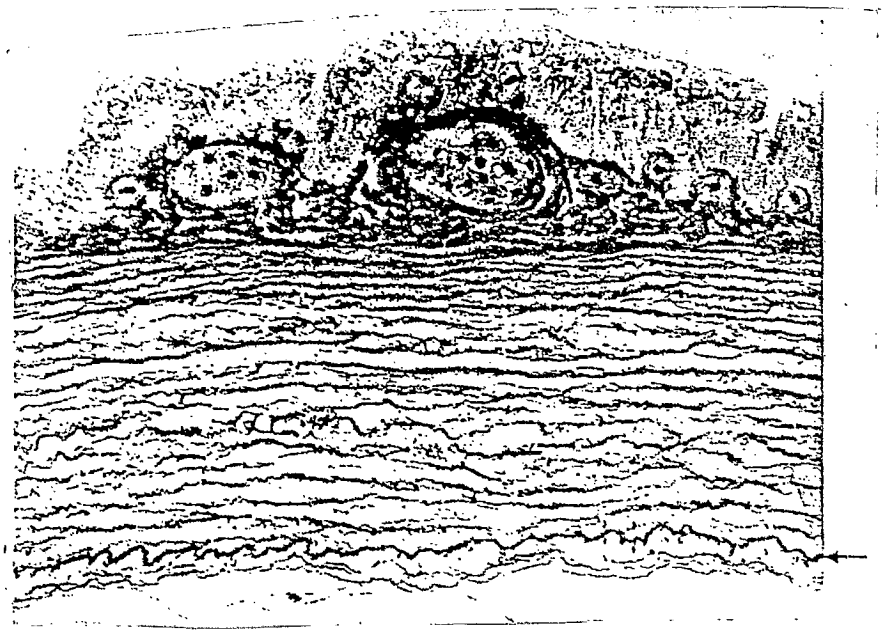

Figure 4. Section through the wall of a swim bladder; elastic fibers stained with resorcinol-fuchsin. The outermost layer of fibers (←—) is particularly distinct. Paraffin section, 6 μ, x480.

(c) The lamina propria. The lamina propria, called an "inner layer of vascular connective tissue" by previous authors, is adjacent to the muscular layer, towards the inside. It contains the very dense vascular network of the swim bladder (Figure 5). In a fresh subject, the lamina propria, with its abundant supply of blood, shows a ruddy glow through the argentate outer covering of the swim bladder.

The vascular system of the swim bladder originates from the swim bladder artery, which approaches the swim bladder longitudinally, dividing into numerous vessels. These, in turn, pass into a dense network of fine capillaries (Figure 5). The arrangement of the capillaries varies from one area to another. In the rostral portion of the swim bladder, the capillaries

Figure 5. Capillaries of a swim bladder, injected with Scribtol; the whole bladder has been fixed and cleared in wintergreen oil. Magnification ca. x4.

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tend to spread over the surface (Figure 6). In the middle portion of the swim bladder, we find parallel blood vessels, usually oriented along the longitudinal axis of the swim bladder (Figure 7). In the caudal section, the capillaries subdivide in an arborescent pattern (Figure 8). Arterial and venous vessels generally run parallel, either alongside of one another or —apparently more often—in different planes. They are interconnected by loops

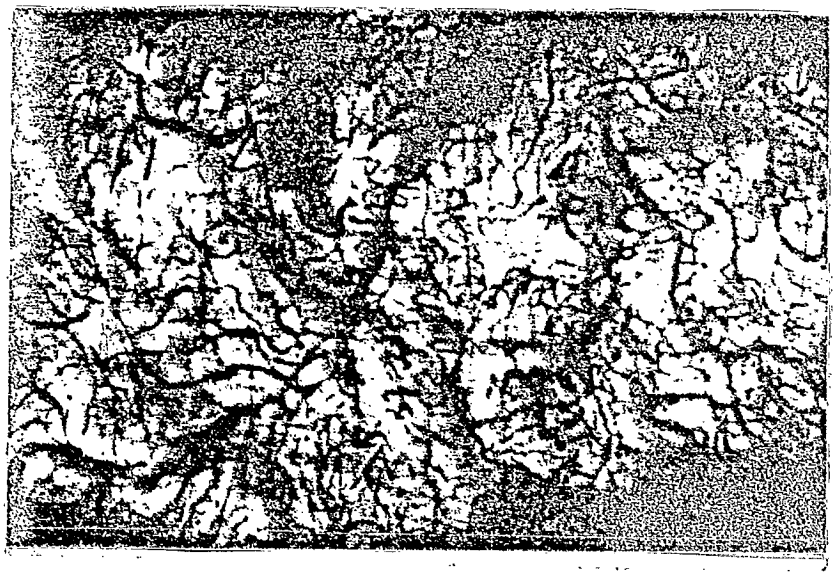

Figure 6. Superficial distribution of capillaries in the rostral portion of the swim bladder; the treatment used was the same as in Figure 5; x120.

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of capillaries branching out in the form of arcades (Figure 9). 857
The vascular network in this area is not flat, but three-dimensional.

(d) The epithelium of the mucosa. The single-layered epithelium of the mucous membrane rests directly on the blood vessels. A true model of the course of the vascular network can be seen outlined in relief on the surface of the mucous membrane (Figure 10). A horizontal section through the mucosa shows the folds formed by the mucous membrane above the blood vessels in a particularly distinct manner. The cells of the swim bladder epithelium are cuboidal to prismatic (Figure 11), with their surface slightly vaulted on the side facing the

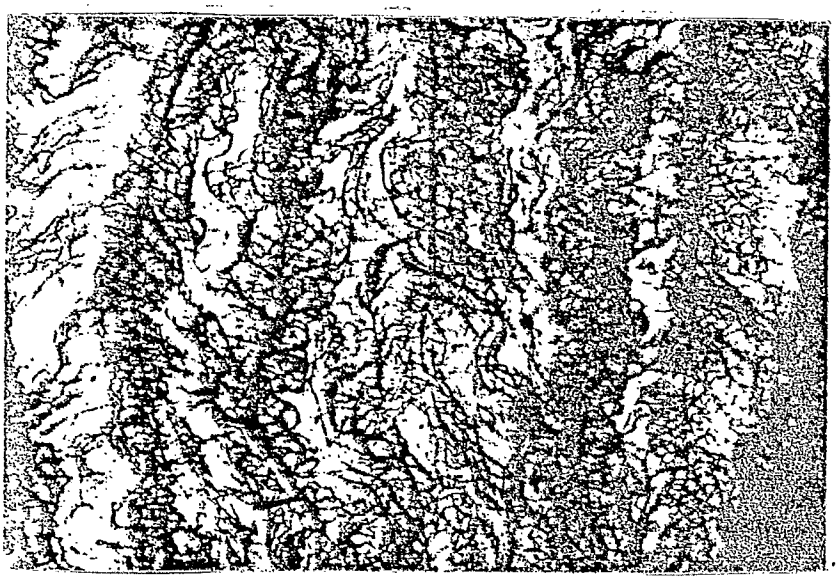

Figure 7. Capillaries in the middle portion of the swim bladder; same treatment as in Figure 5; x35.

lumen. The round nuclei, located in the apical third of each cell, contain a readily discernible central nucleolus.

The cytoplasm in the epithelial cells varies in density. In some cells, the cytoplasm appears light and loosely packed, while in others, it has a much deeper color. On the whole, however, the cell body has a light appearance, particularly in the basal portion, in many parts of which there are even vacuoles. In hematoxylin-eosin preparations, this basal portion of the cells stains with a somewhat more bluish hue than the rest of the cytoplasm. Occasionally it also shows indications of a fine longitudinal striation. Throughout the cytoplasm, there is a fine, powdery granulation, which shows

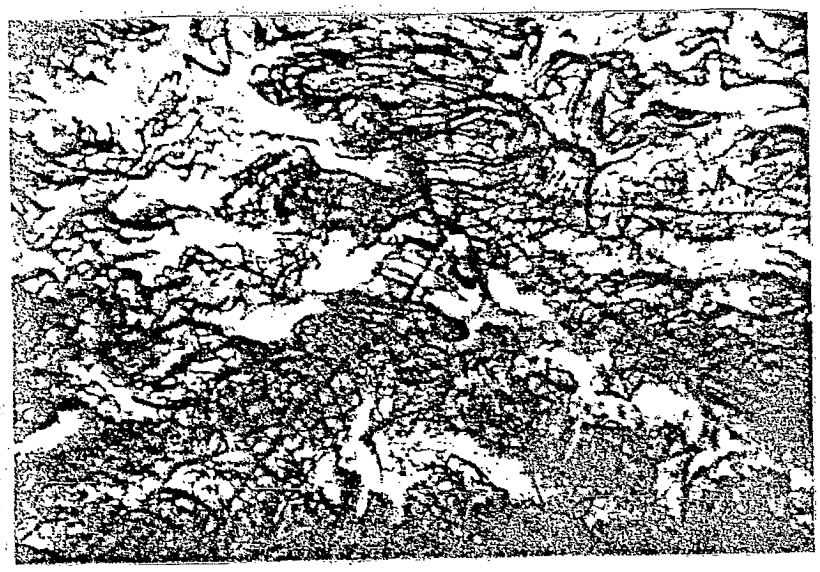

Figure 8. Capillaries in the caudal portion of the swim bladder; same treatment as in Figure 5; x35.

a markedly light shade of blue in hematoxylin-eosin preparations, and a more cobalt blue in sections stained using PAPPENHEIM's method. These granules are distinctly differentiated from the very abundant, much larger granules (Figure 12) occurring chiefly in the upper part of cells in which the basal region appears particularly light, and sometimes even "empty". These large granules stain red-violet with hematoxylin-eosin, yellowish red with azan, phloxin red with chrome alum-hematoxylin-phloxin (GOMORI), and from cobalt blue to ultramarine with PAPPENHEIM's method. In untreated cryostat sections, numerous red granules, especially in the basal portion of the epithelial cells, can be revealed with scarlet staining fluid. 858

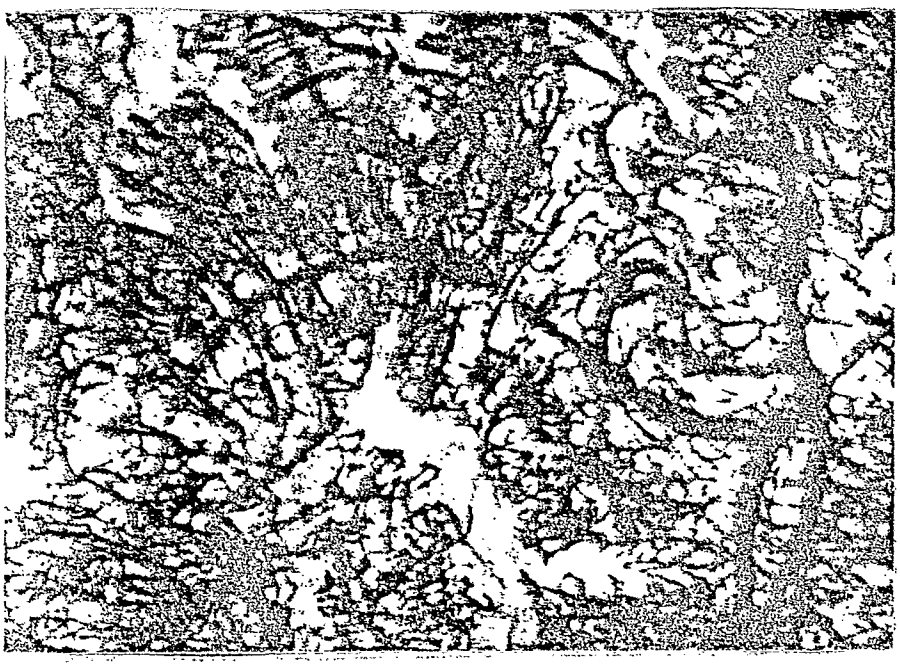

Figure 9. Arcading capillaries in the middle part of the swim bladder; same treatment as in Figure 5; xEIO.

The test for carbonic anhydrase indicated a high level of enzyme activity in the epithelial cells. Already after a brief incubation period (from three to five minutes), the reaction product was visible as a black precipitate in the basal portion of the cells (Figure 13).

2. The ductus pneumaticus. The ductus pneumaticus runs towards the rostrum from about the middle of the swim bladder along its left side, into the esophagus. Its point of origin is on the left side of the swim bladder, between the dorsal and ventral red bodies. A striking feature is its great elasticity. 859

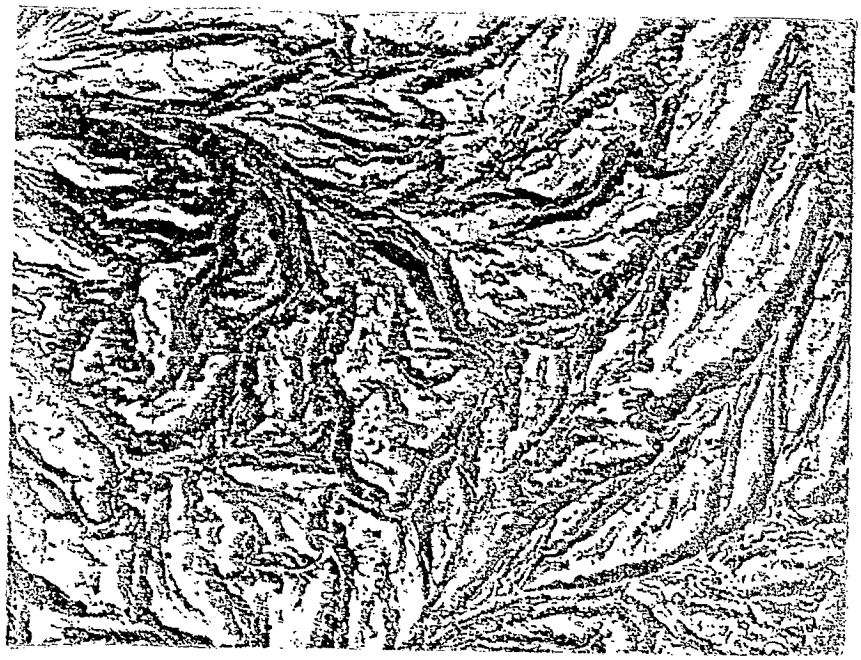

Figure 10. Relief pattern in the mucous membrane of a swim bladder. The whole swim bladder has been treated with resorcin-ol-fuchsin-chromotrope 2R; x35.

Hence, it is found in a quite different degree of expansion in different animals. When fully expanded, the ductus pneumaticus may attain nearly the size of the swim bladder. In this condition, it becomes quite transparent, and it is surrounded by a very dense network of shiny, red blood vessels, also extremely dilated.

Two large blood vessels run along the side of the ductus pneumaticus. First, the arteria vesicae, originating from the arteria coeliaca, runs along the side of the ductus, sending into it the numerous vessels mentioned above; this artery then bifurcates and subdivides to form the capillary systems of the red bodies. The second vessel along the wall

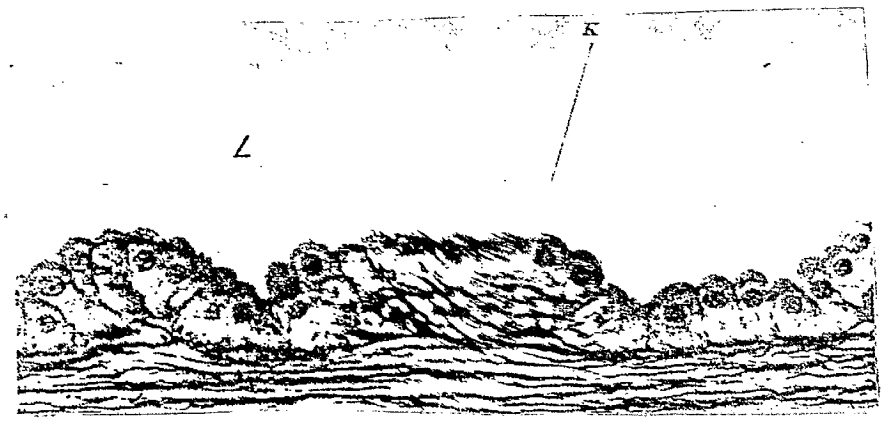

Figure 11. Swim bladder epithelium. Paraffin section, 6 μ, azan stain. L-lumen of swim bladder K-capillary x520

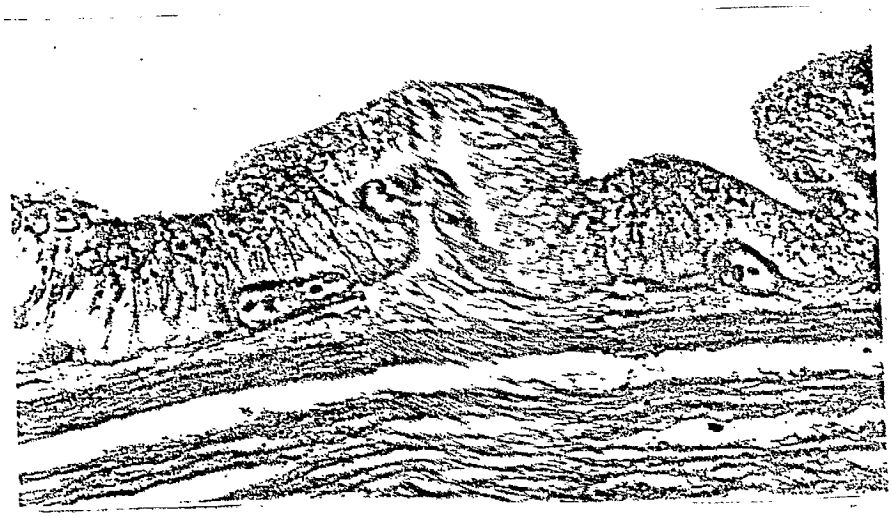

Figure 12. Granules in the swim bladder epithelium. Paraffin section, 6 μ , PAPPENHEIM's panoptic stain; x170.

Figure 13. Identification of carbonic anhydrase in the swim bladder epithelium. Cryostat section, 10 μ. Test for carbonic anhydrase according to HAEUSLER's method. The product of the reaction appears in the basal portion of the epithelial cells. x1240.

of the ductus is the vena ductus pneumaticis which is fed only by the numerous veins of the ductus pneumaticus, and leads to the right ductus Cuvieri, thus completing a minor separate circuit.

The walls of the ductus pneumaticus also show a stratified structure, as shown in cross section in Figure 14. Our discussion will follow the sequence of layers from the outside in.

(a) The epithelium of the mucosa. The lumen of the ductus is lined with an extremely delicate, smooth epithelial covering, which can just barely be discerned with a light microscope (Figure 15). This epithelium covers numerous very high folds in the propria, which show smaller secondary folds. A large number of blood vessels with very wide lumina lie under the epithelium; these vessels resemble sinusoidal capillaries.

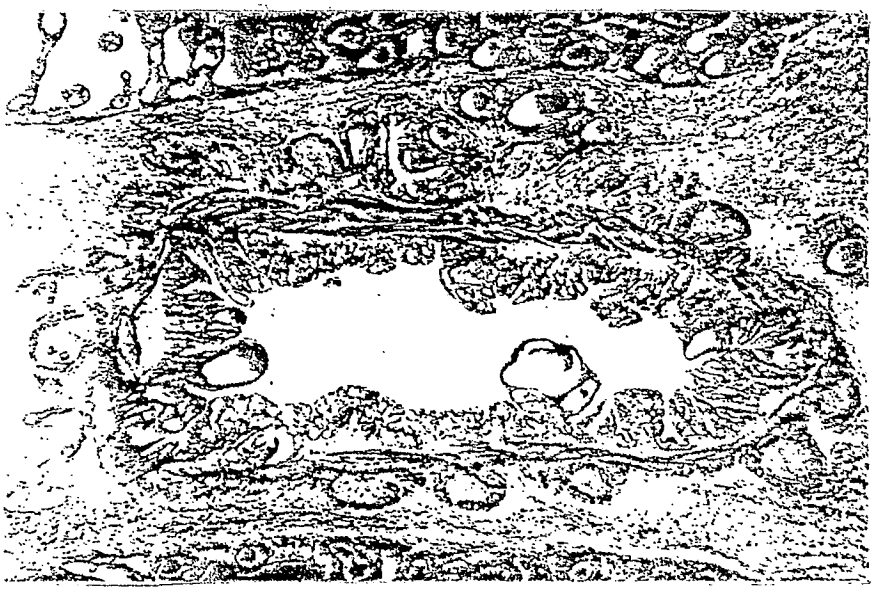

Figure 14. Cross section through the ductus pneumaticus near the point of communication with the lumen of the swim bladder (in the center of the picture). Paraffin section, 6 μ, azan stain; x42.

They are superposed on one another in several layers, in close proximity to one another. They are embedded in the loose connective tissue of the lamina propria.

(b) The lamina propria is penetrated only by a few elastic fibers.

(c) The muscularis mucosae. The innermost layer of the 861
muscularis mucosae is a stratum of smooth annular muscles, but these do not form a continuous circle around the ductus on all sides. There are, for example, deep evaginations of the mucous membrane, near which the muscle layer exhibits a gap (Figure 16). The fibers of the annular muscles wind around the ductus in smooth spiral turns, as shown in the longitudinal section presented as Figure 17. Two systems running in opposite directions

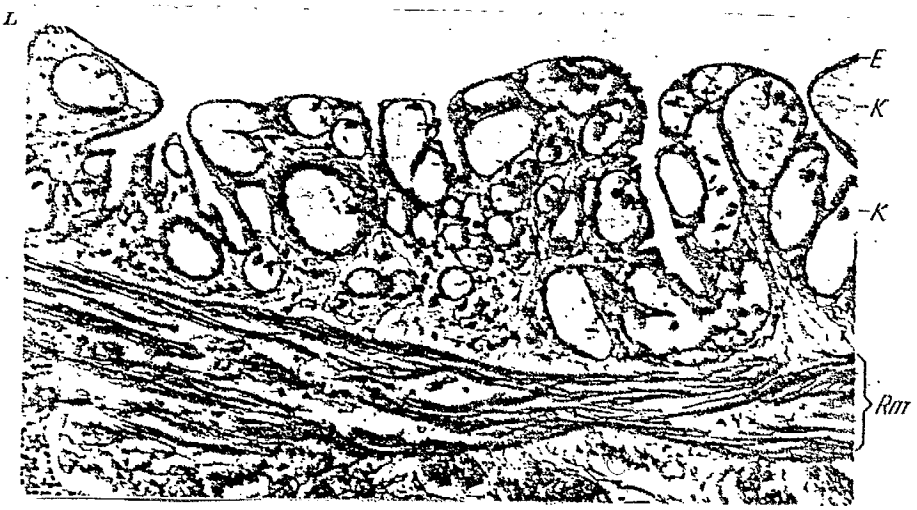

Figure 15. Cross section through the wall of the ductus pneumaticus; plicate epithelium (E) with underlying capillaries (K). Rm-annular muscles, L-lumen. Paraffin section, 6 μ, azan stain, x170.

interweave to form another scissorlike lattice. Next to the annular muscles, towards the outside, are the longitudinal muscles; but these do not form a continuous layer.

The annular muscle layer is encircled on the outside 862
by a series of longitudinal, nonmedullated nerves spaced at quite regular intervals. Each of these nerves is surrounded by a semicircular to circular sheath of longitudinal muscle bundles (Figure 18). These longitudinal muscular bundles evidently originate from the annular muscles, by branching out from one of the smooth spiral coils, doubling back, and

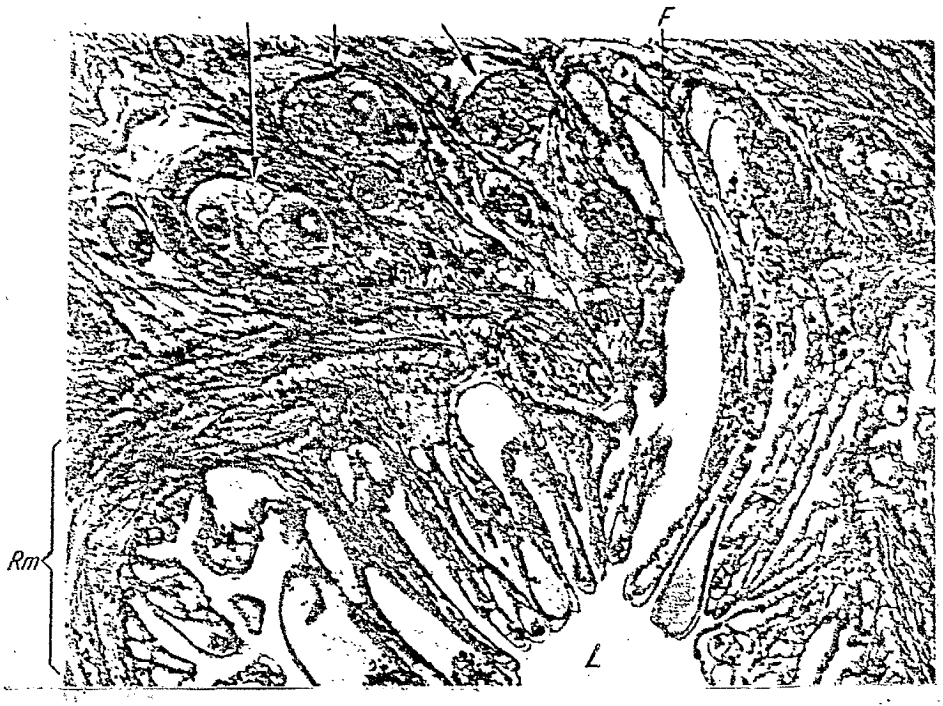

Figure 16. Cross section through the wall of the ductus pneumaticus. Chrome-hematoxylin-phloxin stain (GOMORI). A fold in the epithelium (F) interrupts the annular muscle layer (Rm). L-lumen of the ductus. ⟶ -nerves with ganglionic cells. x120

running parallel to the nerves along the longitudinal axis of the ductus (Figure 19). Clearly, at another location, the longitudinal bundles re-enter the annular muscles and resume their spiral course. The purpose of the muscular sheaths around the nerves may be to protect them from being stretched and displaced during sudden changes in the volume of the organ. The nerves originate from numerous large ganglia attached to the wall of the ductus. Occasionally, cells occurred with serrated nuclei which could be misinterpreted as amitoses.

863

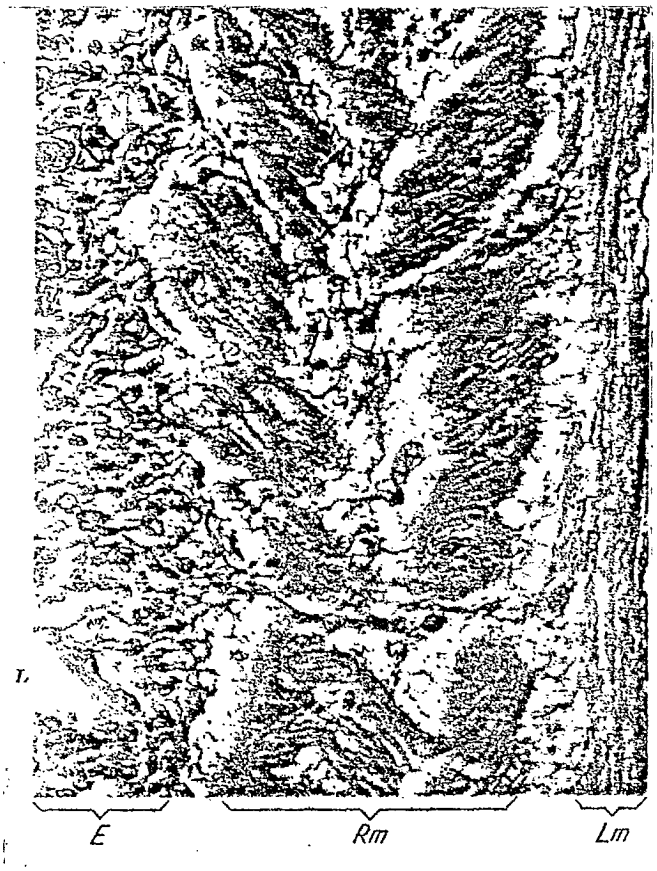

Figure 17. Longitudinal section through the wall of the ductus pneumaticus. Left- lumen (L), bounded by epithelium (E). Center- two portions of annular muscles (Rm), running in opposite directions. Right- longitudinal muscles. Paraffin section, 6 μ, GOLDNER's trichrome stain, x480.

Although the sequence of layers remains the same throughout the ductus pneumaticus, cross sections show somewhat different patterns in the different regions. Near the point of communication with the cavity of the swim bladder, between the red bodies, the mucosa of the ductus pneumaticus is more densely plicate; the number and the caliber of the blood vessels are particularly high (see Figure 15). In the rest of the exposed area (Figure 20), on the other hand, the folds are less voluminous, and more often found over small blood vessels.

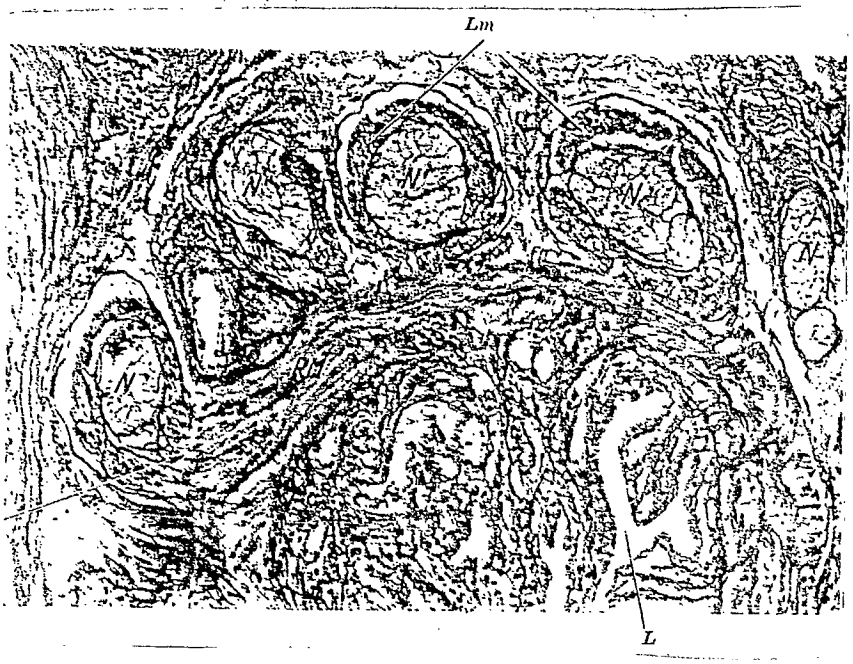

Figure 18. Cross section through the wall of the ductus pneumaticus; same area and treatment as in Figure 14. L-lumen, surrounded by plicate epithelium Rm-annular muscle layer → -point of transition from annular muscle fibers into longitudinal muscles (Lm) forming sheaths around the nerves (N) 120x

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3. The red bodies. The red bodies are located dorsally and ventrally at the beginning of the ductus pneumaticus, on the left side of the swim bladder. Their characteristic shape results from the fact that the swim bladder artery divides into two parts, which split within a very short distance into a large number of arterioles, and subdivide again immediately afterwards to form a very large number of parallel capillaries. The latter reunite just as quickly at the

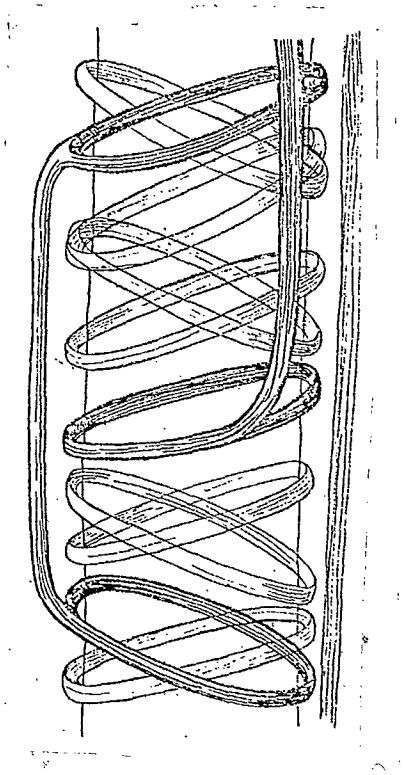

Figure 19. Schematic illustration of the arrangement of muscles in the ductus pneumaticus. Details are explained in the text.

opposite poles of the red bodies to form a few vessels and then again one artery, which runs in a caudal direction inside the swim bladder wall, supplying the capillary network of the swim bladder epithelium, which we have already discussed. The vein originating from these capillaries divides into capillaries in the red bodies, just as the artery does, and these red body 864
capillaries finally unite to form the swim bladder vein. This arrangement of blood vessels was designated as a "rete mirabile bipolare geminum" by JOH. MUELLER (1840). WOODLAND's (1911)

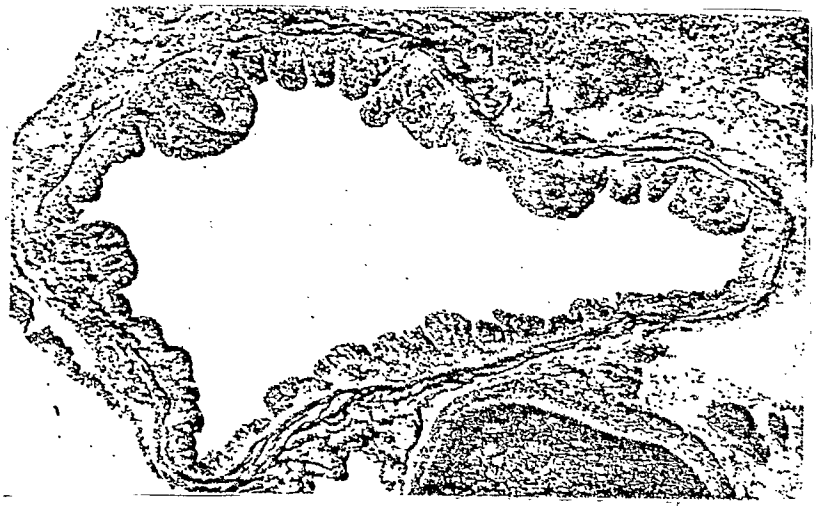

Figure 20. Cross section through the exposed portion of the ductus pneumaticus. Paraffin section, 6 μ, azan stain, x43.

schematic illustration of the rete mirabile has continued to appear in all textbooks and relevant publications up to the present day.

A longitudinal section through a red body (Figure 21) shows, first, how short a distance is required for the arteries and veins to subdivide into parallel capillaries, and secondly, that melanophores are deposited in large numbers along the walls of the blood vessels in the conical, rostral section of the red bodies. The dark pigmentation of this section is conspicuous even macroscopically. It is limited to this area, and marked off from the capillary section by a sharp, straight line.

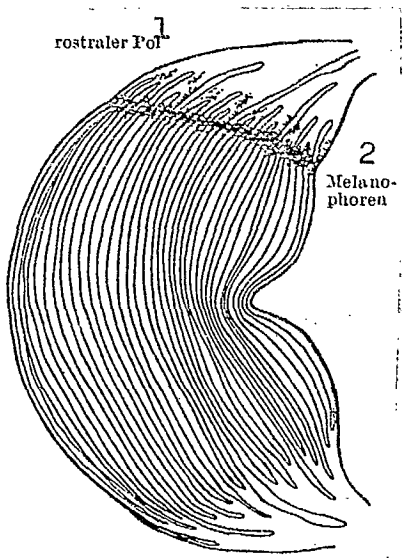

Figure 21. Longitudinal section through the red bodies, represented somewhat schematically
Key: 1-rostral pole 2-melanophores

The connective tissue between the dividing blood vessels in the conical portions of the red bodies exhibits numerous elastic fibers. A longitudinal section (Figure 22) shows, in addition to the subdivision of the blood vessels, the extremely dense arrangement of the capillaries, which occupy the greater part of the red body (Figure 23). The walls of the capillaries are surrounded by a thick reticulum of argyrophil fibrils. The parallel capillaries show a slight curvature; the red body is approximately reniform in shape. This structure explains the distribution of vessels usually seen in cross sections, in which vessels with large lumina are always found on the side facing the ductus pneumaticus, while those with narrow lumina

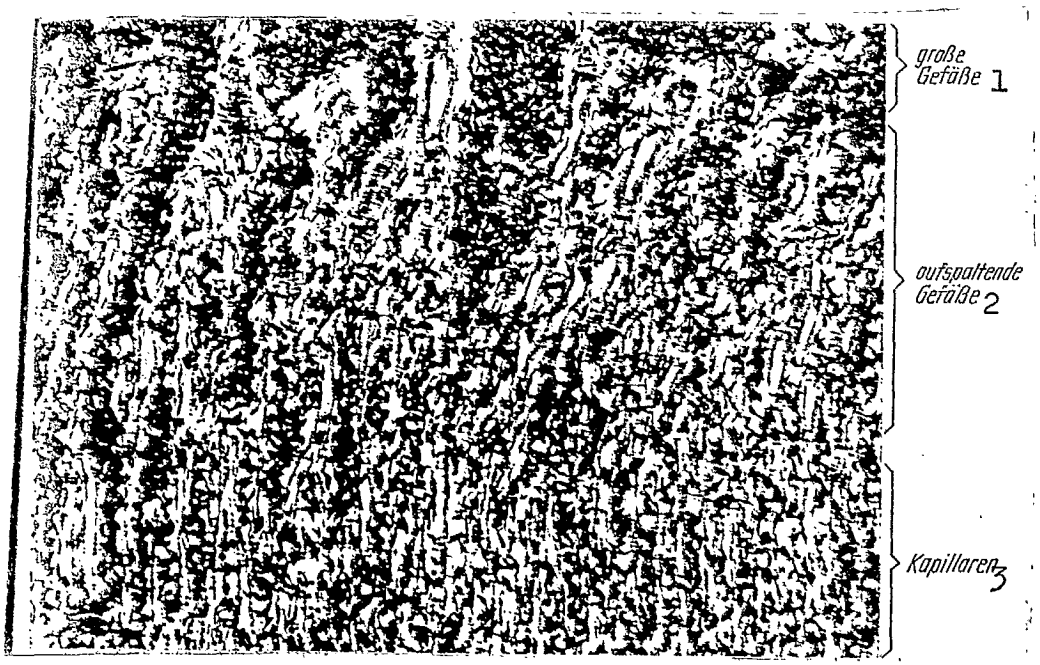

Figure 22. Red body; longitudinal section through the region of subdividing vessels. Upper edge- large vessels; center- dividing vessels; lower edge- parallel capillaries. Blood cells appear dark. Paraffin section, 6 μ, GOLDNER's trichrome stain, x170. Key: 1-large vessels 2-dividing vessels 3-capillaries

are on the outer edge. Cross sections through the conical portion of the red bodies (Figure 24) show both arteries and veins with strikingly wide lumina. A section somewhat closer to the capillary area (Figure 25) shows the large vessels on the side towards the ductus, but already capillaries on the outer sides. 865

Different patterns in cross sections appear also within the capillary region (Figure 26). On the side facing the ductus pneumaticus, capillaries with narrow lumina and those with wide lumina are arranged in such a manner that in cross section, a high-caliber vessel is always surrounded by a circle of lower-caliber capillaries. On the outer side of the

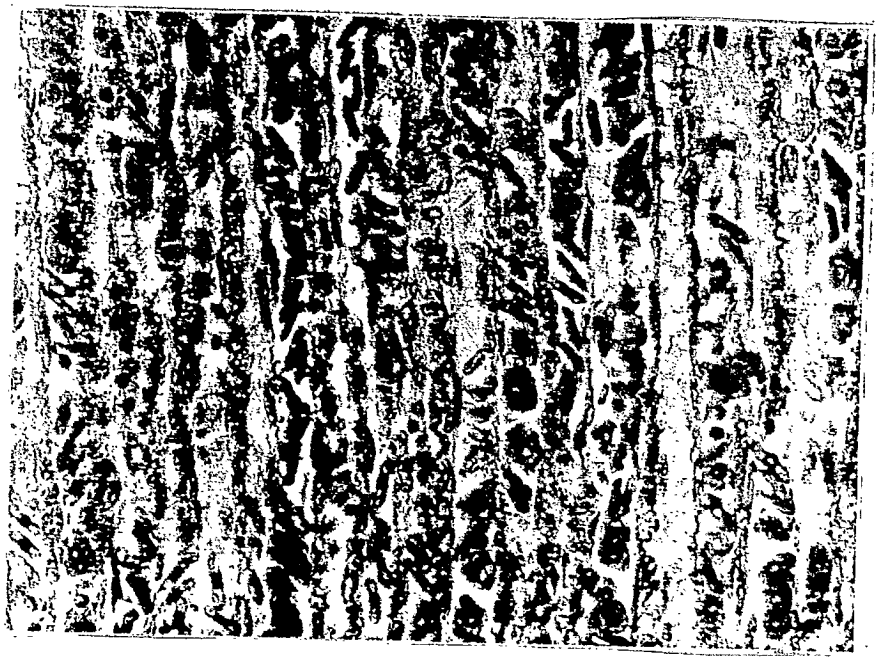

Figure 23. Longitudinal section through the central region of the red body; parallel capillaries. Paraffin section, 6 μ, azan stain, x520.

red body, however, there is a dense, narrow-mesh network of capillaries of equal width.

II. Electron microscopic findings

1. Swim bladder epithelium. At a first view, it is already possible to distinguish two types of epithelial cells on the basis of their different electron optical density: Some cells are only slightly dense; these have a light appearance, and are therefore referred to, for the sake of brevity, as "light epithelial cells" in what follows. The second type appears much darker

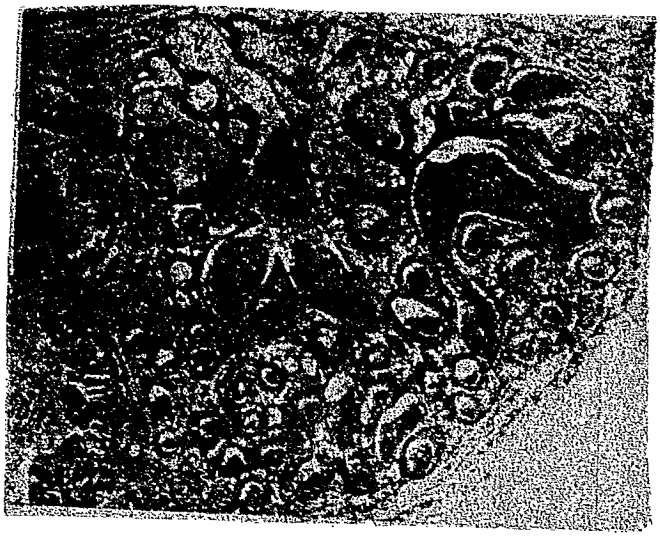

Figure 24. Cross section through the red body in the vicinity of the rostral pole. Left- section of the ductus pneumaticus (D.p.). A-arteries, V-veins. Paraffin section, 6 μ, hematoxylin-eosin, x31.

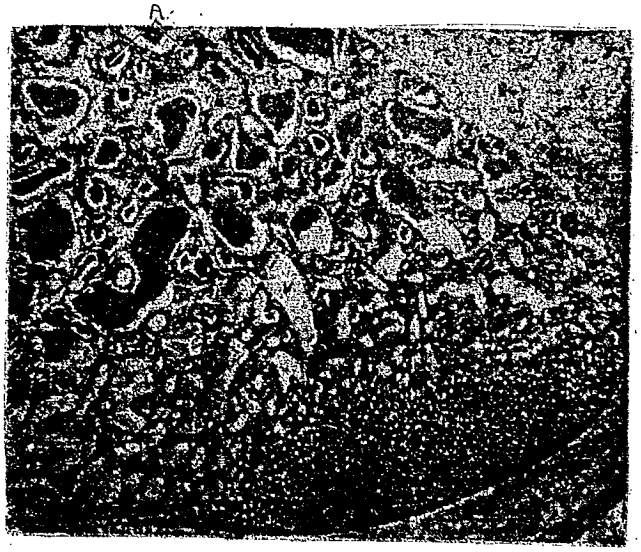

Figure 25. Cross section through the red body in a region slightly removed in a caudal direction from that shown in Figure 24. Upper left corner- large vessels; A-arteries, V-veins. Lower right edge- capillaries (K). Paraffin section, 6 μ, azan stain, x31.

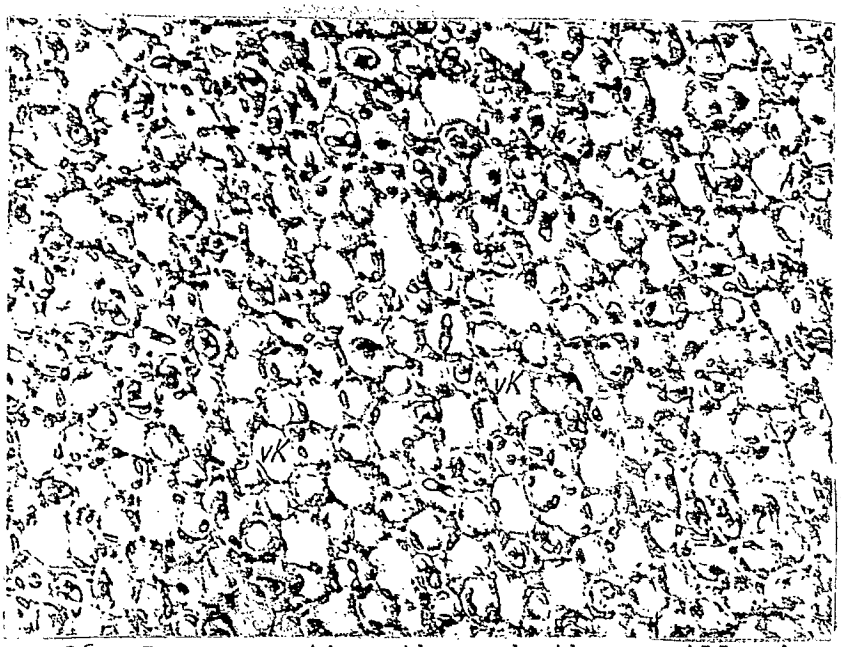

Figure 26. Cross section through the capillaries of the red body. A venous capillary (vK) is surrounded by arterial capillaries. Paraffin section, 6 μ, hematoxylin-eosin, x520.

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and very dense; we shall call these cells "dark" or "dense epithelial cells". There are, in addition to the first, striking difference, other differences between the two types of epithelial cells, which are described in the following 866
paragraphs (cf. the diagram in Figure 37).

(a) "Light" epithelial cells. The light epithelial cells are cuboid to highly cuboid. The surface of each cell is slightly vaulted on the side of the lumen (Figure 27). The exposed surface of the cell bears inconspicuous, fine, low microvilli. The intercellular boundaries exhibit a very wide variety of shapes:

1. There are fine denticulations of the cell membrane, especially in the vicinity of the exposed surface of the epithelium. Directly beneath the epithelial surface, cytodesmata were found (Figure 27).

2. In only a very small number of cases, neighboring cells diverged, leaving narrow openings between them (Figure 28).

3. In some places,—especially among the central cells,— the intercellular membranes appeared to be discontinuous, interrupted by cytoplasmic bridges (Figure 27). It is difficult to judge whether the illusion of an interruption was created in these cases because plicate sections of the cell membrane were viewed at an oblique angle, or whether cytoplasmic bridges actually occurred.

4. Near the base of the epithelium, the denticulations of the cells are particularly sharp and dense. The cell boundaries follow a tightly maeandering course (Figure 27). In this area, there are frequent intercellular cavities, as may be seen in Figure 29. The basal surface of the epithelium also has a turbulent appearance due to major inflexions and protrusions. Some areas along this surface showed indications of a membranous vesiculation.

869

As we have mentioned already above, the cytoplasm of the epithelial cells is not very dense; it has a light gray coloration and shows very delicate, pale granulation. Free ribosomes

Figure 27. "Light" swim bladder epithelium with denticulations along the cell boundaries, accompanied by cytodesmata (C.D.). S.B.L.-swim bladder lumen K-capillary E.R.-endoplasmic reticulum N.F.-nerve fiber The arrows indicate interruptions in the cell membrane. x3900

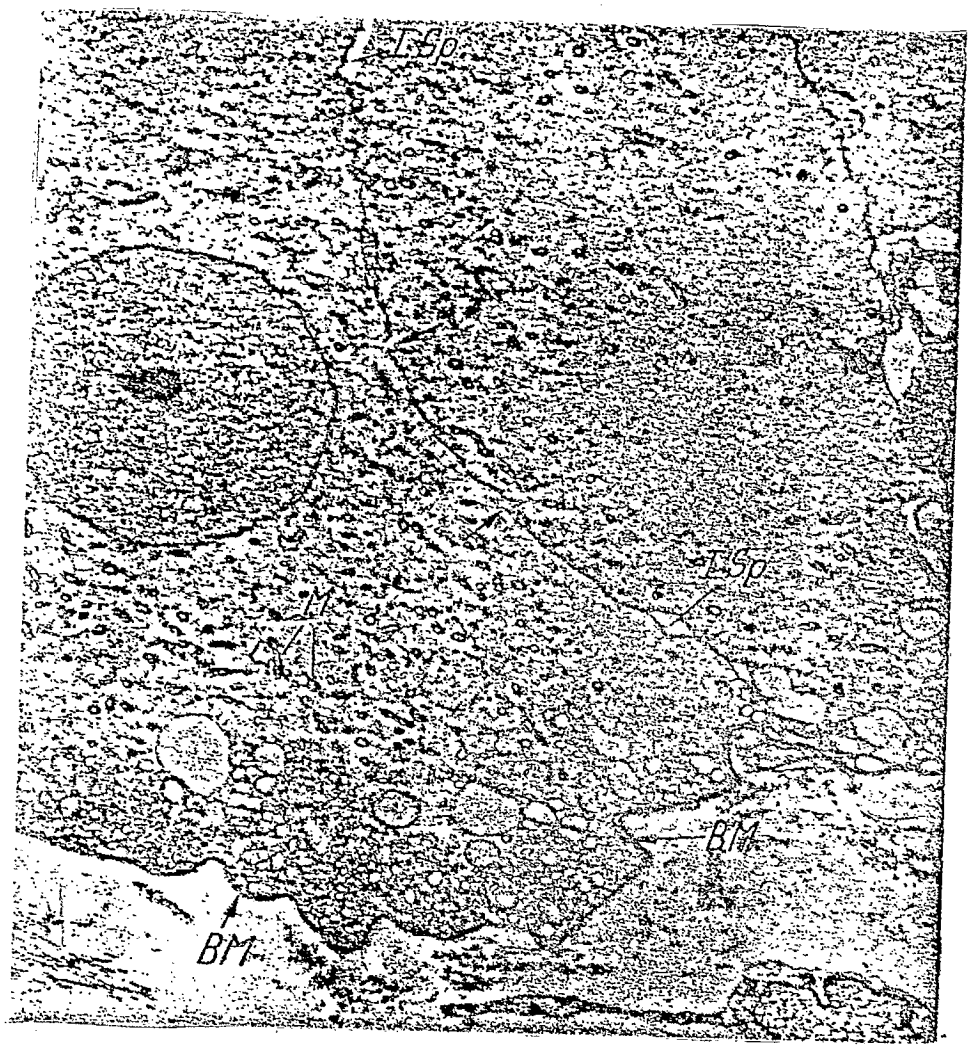

Figure 28. Cells of the swim bladder epithelium; vesicles are visible in the basal region of the cell, and a cell nucleus appears on the left. → -interruptions in the cell membrane BM-basement membrane M-mitochondria I.Sp.-intercellular interstices x5100

(Palade's granules) are distributed throughout the cytoplasm. The endoplasmic reticulum is not very conspicuous. Only occasional channels cut at an oblique angle showed accumulations of ribosomes (Figure 27). Whether the apparently vesicular formations frequently observed along the base of the cell, which were

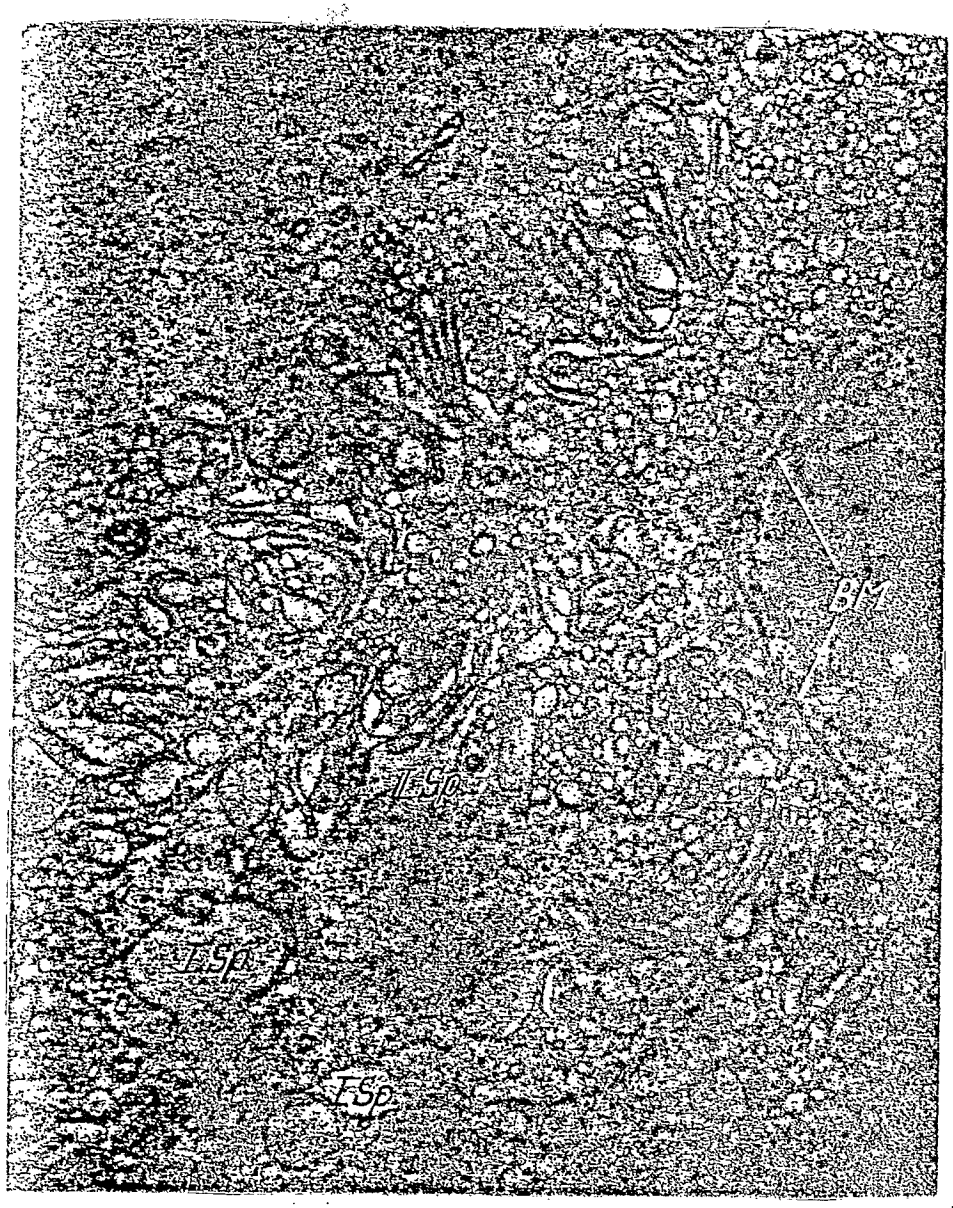

Figure 29. Basal region of light swim bladder epithelium, with denticulations of the cell membrane, enlarged intercellular spaces (I. Sp.), and vesicles in the cytoplasm; BM-basement membrane; x 12,700.

circular in cross sections, represented agranular portions of the endoplasmic reticulum is not clear.

The mitochondria are not very numerous; usually, they are distributed in an irregular fashion throughout the cell. Only in one case were they arranged somewhat more densely in the vicinity of the nucleus. The mitochondria (tubular type) evidently form long, thin, tortuous filaments (measuring 150 mμ in diameter).

Numerous inclusions showing a wide variety of structures occurred in the cytoplasm. There were dark, round particles with plain outlines and a homogeneous appearance, possibly representing fat droplets (Figures 27, 28), and also inclusions with internal structures in the form of concentric, stratified lamellae.

A striking phenomenon was the abundance of "vesicular" or vacuolar formations appearing in cross sections, particularly in the basal region of the epithelial cells. These were predominantly vesicles with an empty appearance and smooth, plain outlines (Figure 30). They were nearly circular in cross section, but varied greatly in size; the diameter of 870
the smallest such vesicle observed —about 100 mμ —was slightly less than the transverse diameter of the mitochondria. These small vesicles comprised the great majority of these structures (Figures 29 and 30). Large vesicles were less numerous. It is not clear whether these large vesicles arise

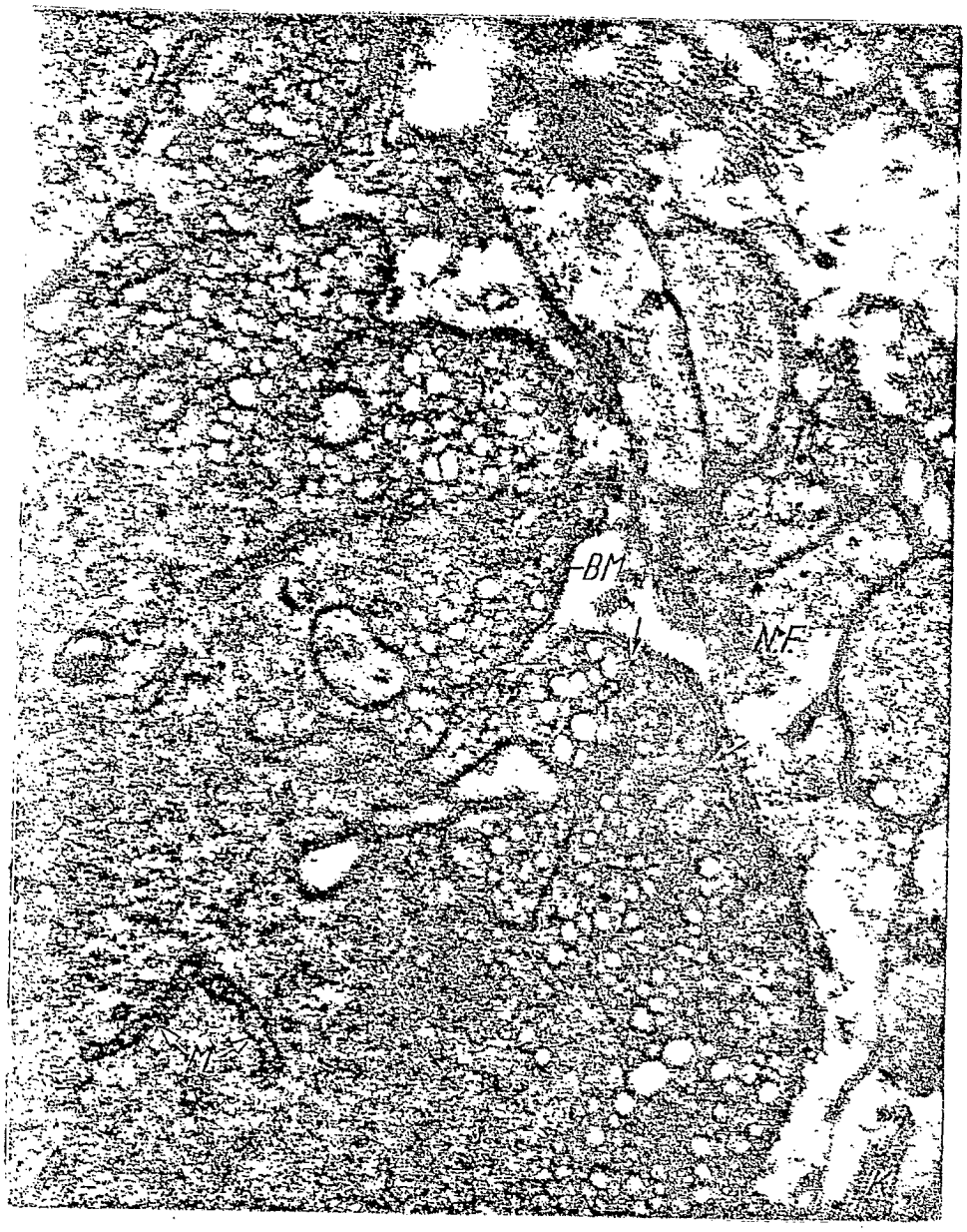

Figure 30. Swim bladder epithelium; the base of a cell, with vesicles in the cytoplasm and infolds in the cell membrane (→).
M-mitochondria BM-basement membrane N.F.-nerve fiber
K-collagen fibers x24,000

from a combination of small vesicles, or whether the large
871
vesicles become constricted to turn into small vesicles. The vesicles were usually found quite close together along the base of the cell. Less often, the small vesicles appeared in a coronal or moniliform arrangement (Figure 29). Only in isolated cases were they found in other parts of the epithelial cells, e.g., near the exposed surface of the cell. In some places in the basal region of the epithelial cells, we observed groups of large, irregularly shaped, vesicular sacs with plain outlines, separated from one another by narrow cytoplasmic septae. The areas between these sacs were differentiated from the rest of the cytoplasm by numerous small vesicles, which gave them a rather spumous appearance (Figure 31). In the large sacs, we could discern contents, which sometimes appeared indistinctly granular,
872
but at other times rather filamentous. The cell boundaries in this part of the epithelium frequently diverge, leaving intercellular interstices similar in size and shape to the vesicles in the cytoplasm. In one case, along the upper edge of a very large, irregularly shaped vesicle, we observed several paired rows of fine, oblate vesicles, possibly representing the Golgi apparatus.

The cell nucleus has a round shape and a smooth
873
surface, without folds or invaginations. The nuclear membrane

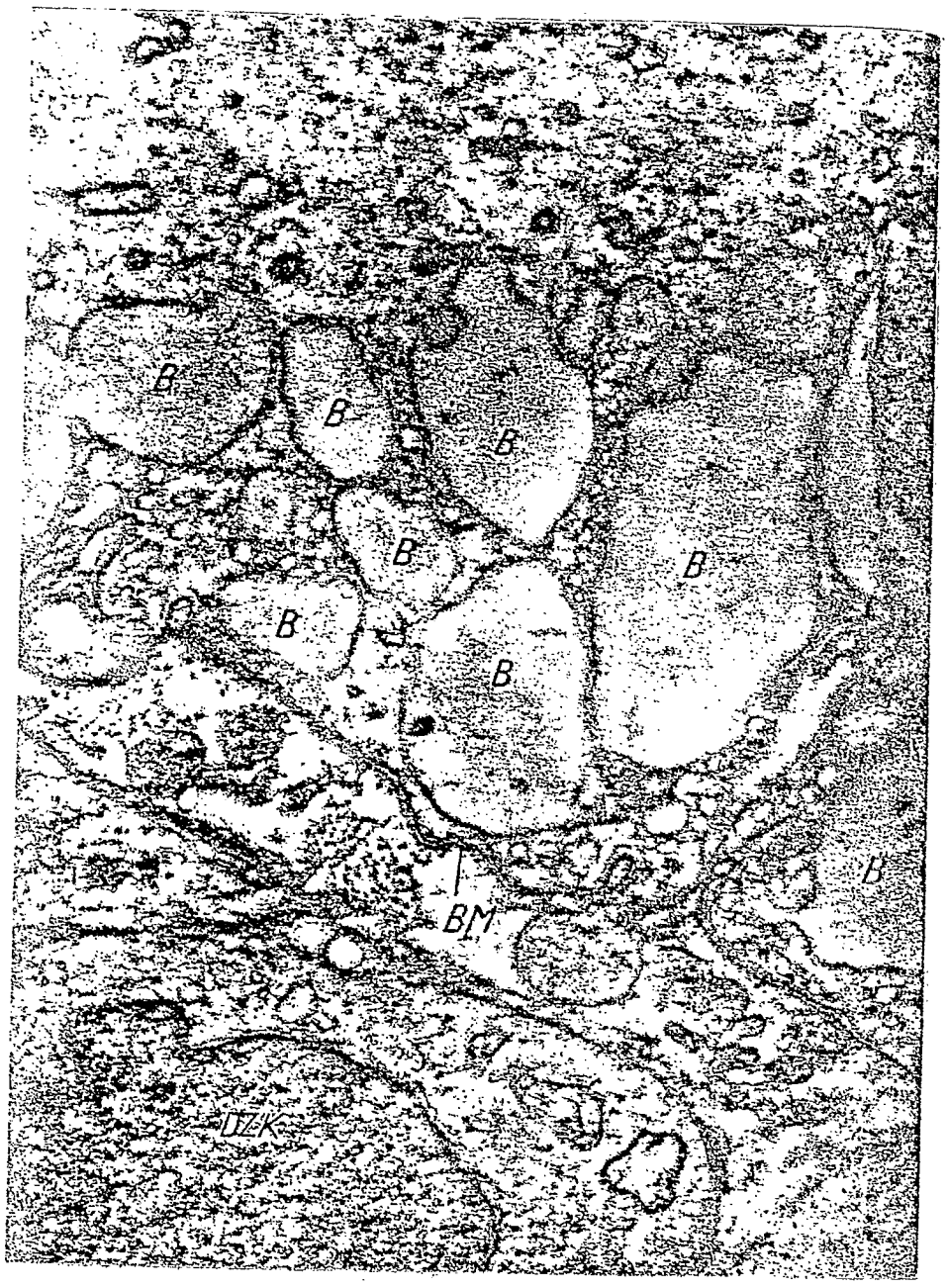

Figure 31. Basal region of a cell in the swim bladder epithelium. B-large vesicles BM-basement membrane Lower left— capillary wall DZK— nucleus of a capillary adventitial cell x13,800

appears as a double outline with distinctly visible nuclear pores; the circumnuclear cisterna was discerned only in a few places. The karyoplasm shows a uniform, fine granulation; the nucleus as a whole is barely darker than the cytoplasm. The nucleolus is a striking central area with a round to oval shape and dense granulation.

The base of the epithelium borders on a thin basement membrane, which will be discussed below (see p. 879). 874

(b) "Dark" epithelial cells. In addition to the very light epithelial cells, we found considerably more densely structured elements which appeared darker in electron micrographs. These did not differ from the light epithelial cells in shape and size; they, too, were cuboid to highly cuboid (Figure 32). Among them, once again, elements with very finely granulated cytoplasm of a nearly homogeneous appearance were differentiated from those with a much rougher granulation. 875

The exposed surfaces of the "dark cells" show short microvilli projecting into the lumen of the swim bladder; between these are cryptal depressions, so that in appropriate sections, the regions near the surface of the cell appear to be permeated by many vacuoles. Neighboring epithelial cells are interconnected by denticulations, especially in the 876

Figure 32. Swim bladder epithelium with dense cytoplasm; the nucleus of a cell is visible in the right half of the picture. Numerous sectors of mitochondria, inclusions (⟶), and thick infoldings of the cell membrane along the base of the epithelium are visible. Next to the latter, in the center of the picture, is a tangential sector of a capillary loop (K). SBL-swim bladder lumen x8000

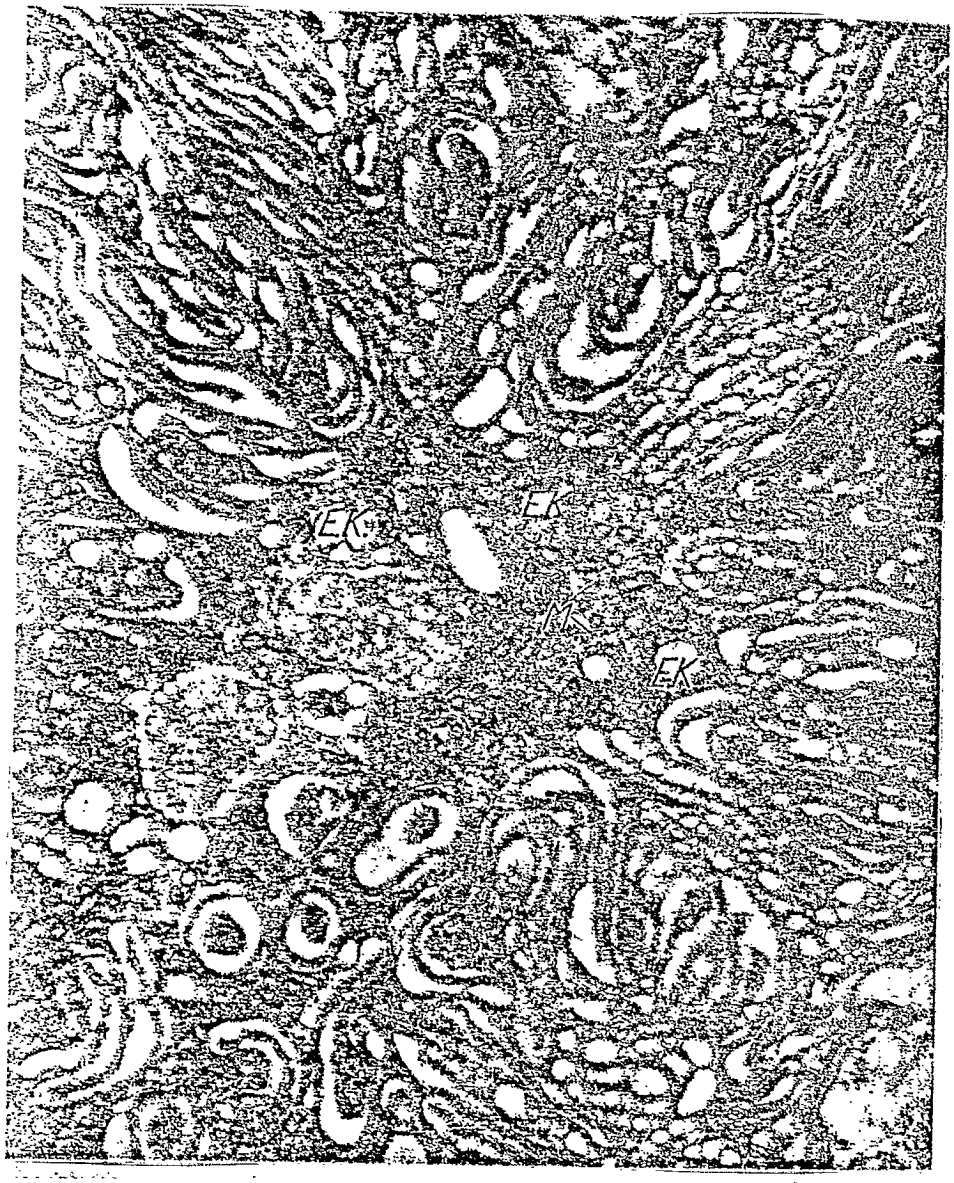

Figure 33. Base of a cell in the swim bladder epithelium, with infoldings of the cell membrane. M-mitochondria E.K.-inclusions x14,500

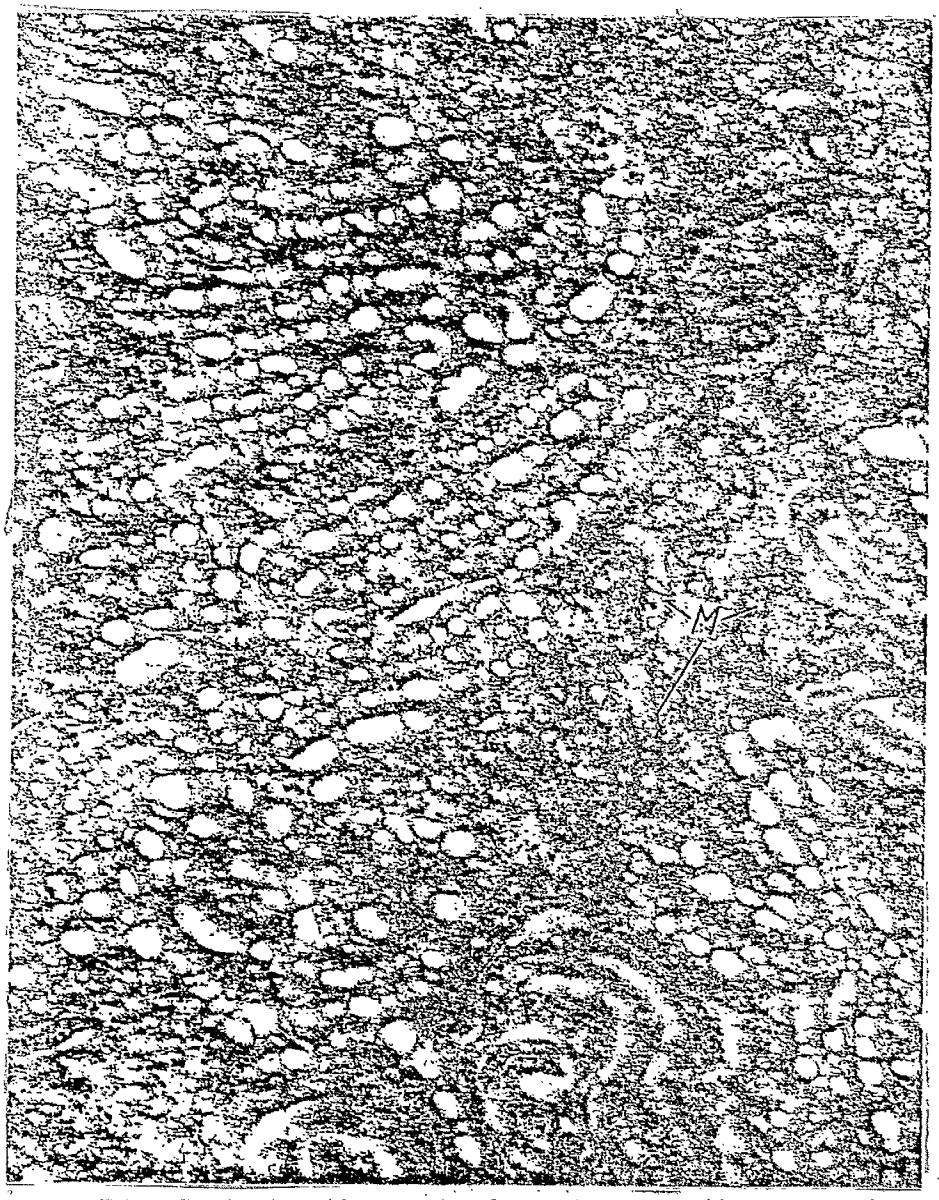

Figure 34. Cell in the swim bladder epithelium showing rows of vacuoles. M-mitochondria x21,000

vicinity of the epithelial surface. Directly beneath that surface, cytodesmata are found. The cells are so close together that their boundaries are often difficult to differentiate; there is only a slight contrast between the plasmalemma and 877
the dense cytoplasm. Occasionally a narrow, slightly widened intercellular interstice occurs over a limited distance.

At the base of the epithelium, the cells exhibit very numerous, densely juxtaposed inflexions cutting deep into the cytoplasm (Figures 32, 37). These infoldings, forming a basal labyrinth, enclose lightly colored interstices 878
showing a wide variety of shapes. Whole bundles of parallel interstices with approximately equal lumina may extend into the interior of the cell perpendicular to the surface of the epithelium. These bundles of inflexions are often also coiled in a wide variety of directions, so that a section through the base of the cell may show manifold structural patterns (Figure 33). In addition, helical or arcuate rows of round dilations 879
are often observed, giving rise to moniliform formations. Sections through the cell regions penetrated by such dilations look like sieves perforated with parallel or concentric holes. Again, in other places (Figure 33), the dilations are arranged in the form of a closed corona. In isolated cases,

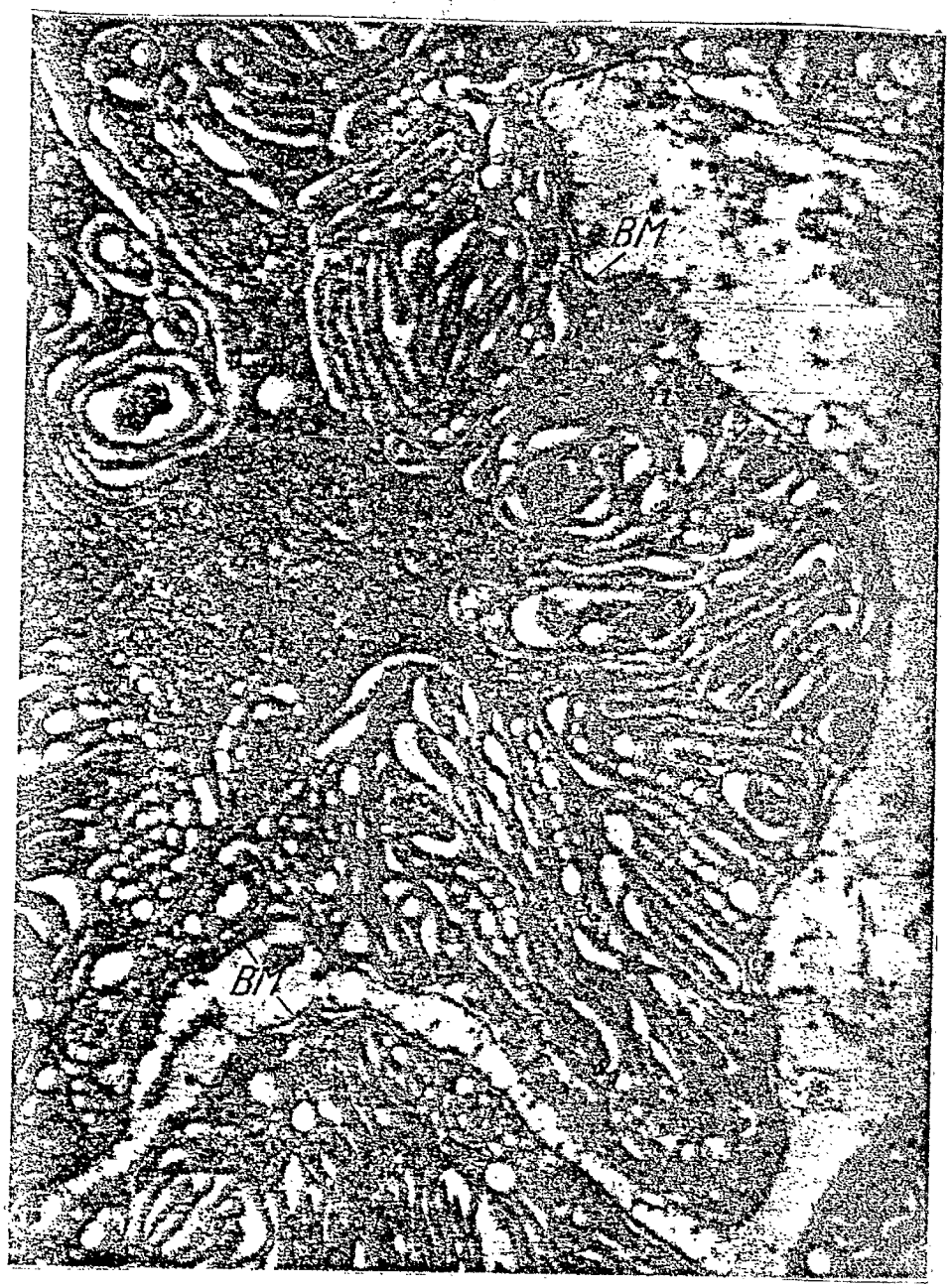

Figure 35. Basal region of the swim bladder epithelium with infoldings of the cell membrane. BM-basement membrane x15,600

these moniliform rows of vesicles were found also in higher cell sections. The size of these cavities is by no means uniform; frequently, the interstices are enlarged to many times their original breadth. In some cases, the inflexions of the cell surface must be thought of as tubular cavities, arranged in bundles; these are coiled in many different directions, so that they appear sometimes as parallel rows of interstices, when cut longitudinally, and at other times, when cut obliquely, as parallel rows of round vesicles, helical rows of apertures, or even concentric, circular rows of apertures. In addition, rimiform inflexions also occur. In such cases, the sections show patterns such as those in Figures 33 and 35. In these patterns, dilated cavities, cut longitudinally, lie adjacent to cavities cut obliquely near the domes of invaginations and seen as concentric circular interstices alternating with annular strips of cytoplasm. only seldom were mitochondria found in the compartments of cytoplasm bounded by the infoldings of the base of the cell.

The hyaloplasm of the epithelial cells is finely granulated throughout; its appearance is nearly homogeneous. Ribosomes were not observed. Long, narrow, coiled mitochondria (tubular type) are distributed throughout the cell body (Figure 32); their matrix exhibits the same density as the

Figure 36. Body enclosed in the cytoplasm of the "dark" swim bladder epithelium, with granulated, stratified, lamelliform contents. The nucleus of the cell is visible on the right. x23,000

hyaloplasm. No endoplasmic reticula were found in any part of the dense dark epithelial cells. We were also unable to identify any Golgi apparatus.

The nature of the vesicular structures of varying size distributed through the cytoplasm remains uncertain. These vesicles are small, round (measuring about 100-130 mμ in diameter), have an empty appearance in electron micrographs, and are distributed throughout the cell; they are somewhat more numerous in the vicinity of the exposed surface (Figure 32).

More extensive vesicular formations, with contents consisting of granulose structures with indistinct outlines, were observed more frequently. Undoubtedly, many of these represented fatty or lipid inclusions, the partial solution of which gave rise to a wide variety of patterns in sections of the vesicular contents. Some of the large vesicles contained fragments of high-density, concentrically stratified, lamelliform structures (Figure 36).

The nucleus of the dense epithelial cells is ovoid or conical, and occasionally slightly sinuous. The karyoplasm exhibits rough granules with larger, less dense areas in between, so that the nucleus as a whole usually appears lighter than the cytoplasm in photographic reproductions. The nuclear substance can be discerned as a round area inside the nuclear space with somewhat undulate boundaries and very fine, dense granulation.

(c) The basement membrane. The basement membrane is a dark band measuring about 40 mμ in width accompanying the base of the epithelium over its entire length, and showing many contrasts in section preparations. It is separated from the epithelium by a light zone which may be narrower than the dark layer —and barely visible—or equal to the dark layer in width, depending on the angle of the section.

Adjacent to the basement membrane on the side 881
facing away from the epithelium, there is an area of extremely variable width separating the epithelium from the underlying capillaries. This space may be imperceptibly narrow, so that the capillary wall is directly adjacent to the basement membrane. In other places, it is filled either with an indistinctly granulated electron-dense substance or with bundles of collagen fibers, very distinctly identified by their transverse striation, and traversing the area in various directions, often parallel to the capillaries. Not infrequently, other tissue elements were also found in this crevice, such as nerve fibers, for example, which often press very closely against the base of the epithelium.

(d) The capillaries of the swim bladder epithelium. The capillaries underlying the swim bladder epithelium show the familiar structural components: endothelial tube, basement membrane, and adventitial cells.

(α) Endothelium. The endothelial cells, which are usually 882
very flat, are interconnected by single or multiple denticulations. They are especially flat at the sites of these denticulations, where aduncate cellular processes frequently protrude into the lumen of the capillary. The cell membranes often show cytodesmata at these points. Occasionally, not only two,

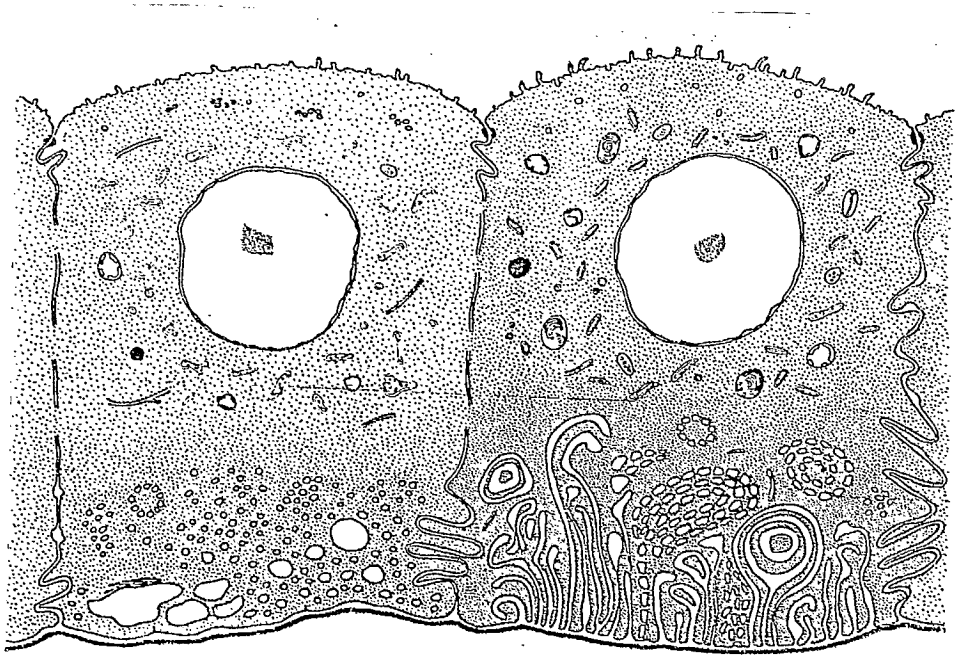

Figure 37. Schematic representation of the submicroscopic structure of the epithelial cells in the swim bladder of the Eel. Left: "light" epithelial cell. Right: "dark" epithelial cell. Details are explained in the text.

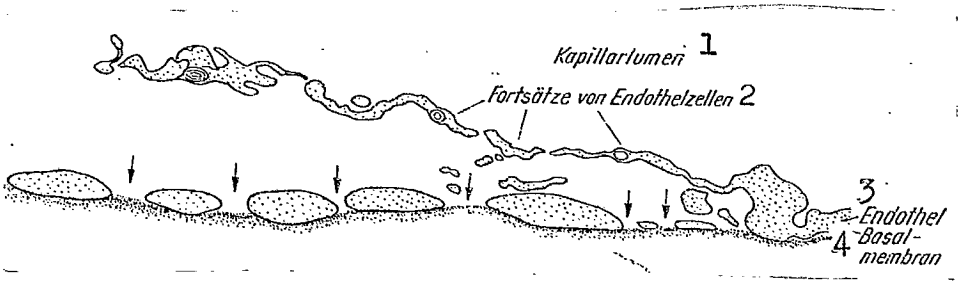

Figure 38. Section from the wall of a capiklary underlying the "light" swim bladder epithelium. Sectors of endothelial cell processes are visible in the lumen of the capillary.
⟶ -apertures in the endothelium. Illustration based on electron micrographs.
Key: 1-capillary lumen 2-processes of endothelial cells 3-endothelium 4-basement membrane

but several cells lie adjacent to one another, so that their processes then overlap. At other sites, the endothelial cells are fenestrate to such an extent that the only continuous boundary of the capillary tube is formed by the basement membrane (Figure 38). The apertures measure from 200 to 700 mμ in diameter. In some areas,—especially at the cell boundaries,— the exposed surface of the endothelial cells shows curved, digitaliform processes (see above), and also quite extensive lobular or villiform processes —evidently, also branched and coiled—which protrude into the lumen along a large distance and are then seen in sections as seemingly isolated formations (Figure 38).

Along the base of the endothelial cells, we often found round inflexions, and in some places even vesicles, which gave the appearance of being constricted,—a phenomenon which has been described as "membranous vesiculation".

Most of the cytoplasm in the endothelial cells is permeated by round vesicles with an average diameter of 100 mμ. No contents could be discerned in these vesicles. Relatively large mitochondria (measuring 180-200 mμ in diameter) of the tubular type were always found, but these were not very numerous. Portions of the endoplasmic reticulum, with a trimming of ribosomes, were always visible. The outline of

the endoplasmic reticulum is often arranged in a row, as it were, in the middle of the endothelial cells. The channels tend to run parallel to the longitudinal axis of the capillaries or of the endothelial cells. In some places, the channels of the endoplasmic reticulum appear extremely distended. In such areas, we found circular sections of channels with smoothly shaped walls bearing a dense trimming of ribosomes at regular intervals. The Golgi apparatus appears as a stack of oblate sacs.

The inclusions in the endothelial cells are numerous and show a variety of structures. In many cells, round particles (measuring 200-250 mμ in diameter) with smooth outlines and a homogeneous appearance are found in the vicinity of the nucleus; most likely, these represent fat droplets. In addition, vesicles occur which appear empty in electron micrographs. In other cases, large round vacuoles (measuring about 550 mμ in diameter) are observed containing loosely distributed, indistinctly shaped, gray granules (measuring about 35 mμ in diameter). Large vacuoles with slightly sinuous, plain outlines (measuring up to about 900 mμ in diameter) contain an indistinctly shaped cloudy gray substance. It may be assumed that the above cases represent patterns displayed by different phases of the dissolution of fatty substances. The most striking inclusions were extensive bodies (measuring 500-520 mμ in diameter) made up of concentric high-density strata.

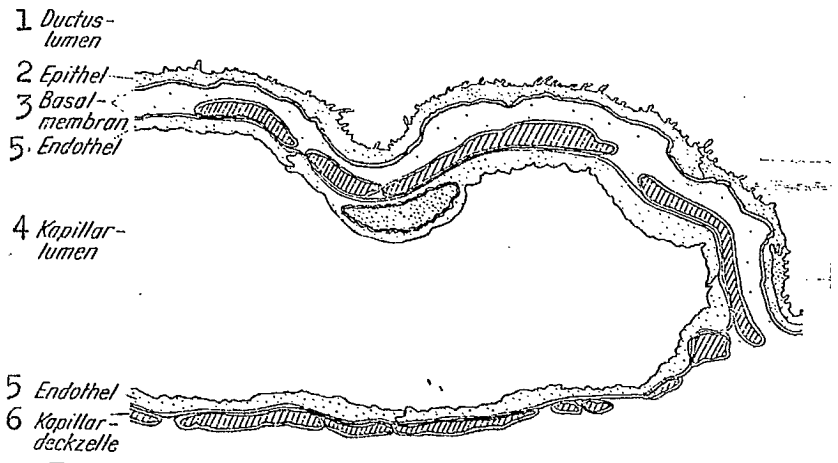

Figure 39. Epithelium of the ductus pneumaticus, with adjacent capillary. Schematic illustration based on electron micrographs. Dense dots- epithelium. Sparse dots- endothelium. Shaded area- adventitial cells.
Key: 1-lumen of the ductus 2-epithelium 3-basement membrane 4-lumen of the capillary 5-endothelium 6-capillary adventitial cell

(γ) Adventitial cells. The adventitial cells do not form a continuous covering around the capillaries; their processes leave large areas of the basement membrane exposed. Where they do cover the capillary, however, they press tightly against the surface of the basement membrane. Very low-caliber capillaries are enclosed more tightly and more completely than those with wide lumina. The mitochondria and endoplasmic reticulum of adventitial cells resemble those of the endothelial cells. The cytoplasm is of approximately the same density as that of the endothelial cells; vesicles occur in similar numbers and with a similar distribution. Membranous vesiculation was also observed.

The nucleate section of the endothelial cells protrudes distinctly into the lumen of the capillary. The nucleus always has a lobate shape (Figure 27). The nuclear membrane and nuclear pores are clearly discernible. In some places, the circumnuclear cisterna can be seen as a fine crevice. The nucleolus is distinctly visible as an area of dense, rough, dark granulation.

According to the observations of the present author, the endothelial cells of capillaries underlying "dark" epithelial cells are differentiated from those under the "light" epithelial elements by the fact that the endothelial cytoplasm in the former cells is more extensively permeated by vesicles. Also, as a rule, the endoplasmic reticulum in such cells, together with its ribosomes, can be traced over longer distances. 883

(β) The basement membrane. The outer surface of the endothelial tube is surrounded by a basement membrane measuring about 70-100 mμ in thickness, in some parts of which a three-layered structure is discernible: A dark, electron-dense, middle layer (measuring 30-35 mμ in width) is enclosed by two less dense, lighter layers (each measuring about 30 mμ in thickness). Usually, however, the basement membrane appears in section preparations as a gray strip with an indistinct structure. It can be identified most readily where the endothelium is fenestrate.

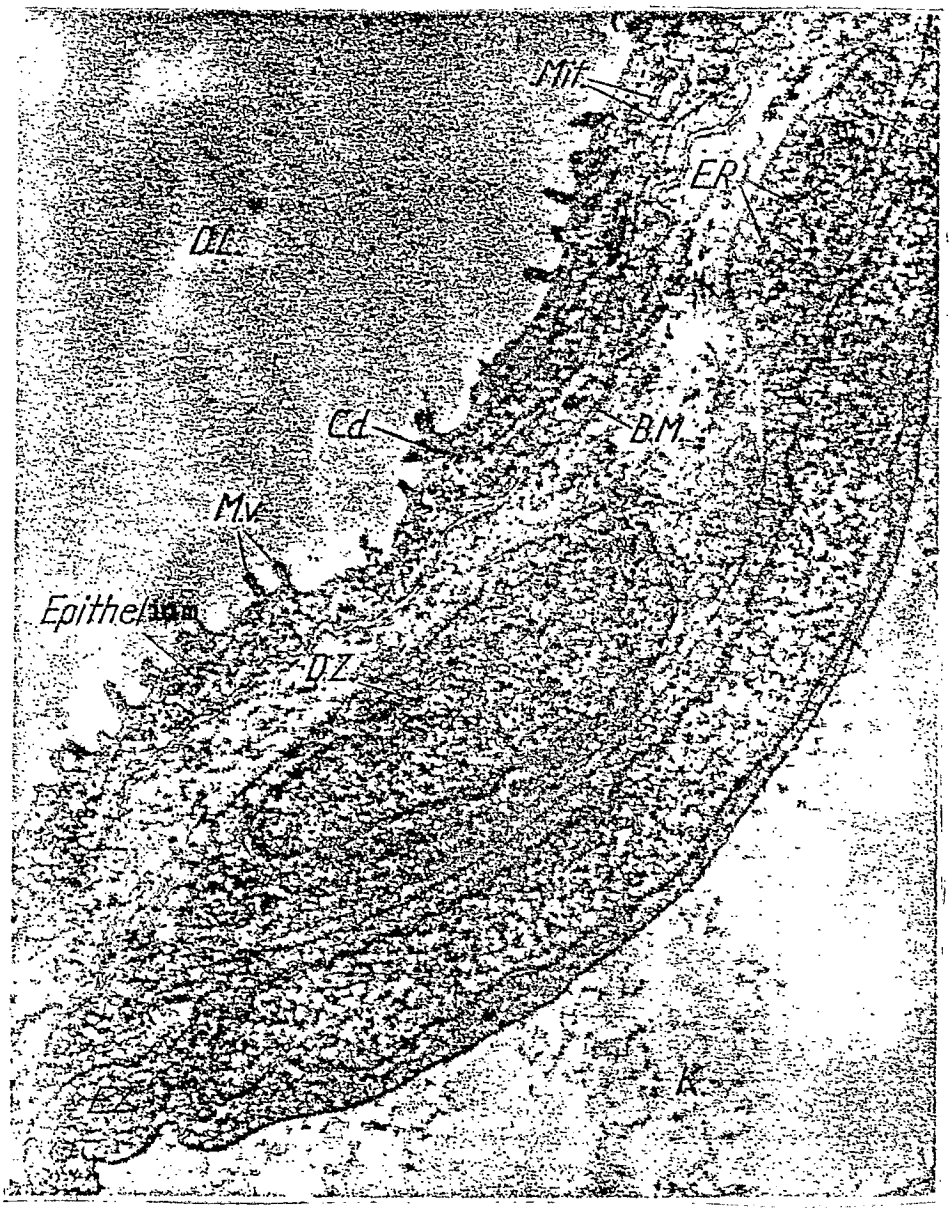

Figure 40. Epithelium of the ductus pneumaticus, with adjacent capillary. Upper left: lumen of the ductus (DL). Lower right: lumen of the capillary (K). M.v.-epithelium with microvilli C.d.-cytodesmata Mit.-mitochondria BM-basement membrane of the epithelium EZ-endothelial cell DZ-adventitial cell ER-endoplasmic reticulum of the adventitial cell x9300

2. Ductus pneumaticus. (a) Epithelium. The ductus pneumaticus is lined with a covering composed of very flat cells (Figures 39, 40) interconnected by sharp denticulations. Numerous digitate processes measuring about 250 mμ by 60 mμ protrude from the exposed surfaces of the cells (Figure 40). The majority of these processes seem to be unbranched; often they are slightly curved. Between these processes, the surface of the cell frequently shows a cryptal inflexion.

The basal surface of epithelial cells shows varying 884
degrees of sinuosity, depending on the extent to which the epithelium is stretched, which depends on how full the ductus is. In an extremely expanded epithelium, the surfaces of cells in the lower elements of the epithelium show smooth undulations (Figure 40). In places where the epithelium is less tightly stretched —and obviously also in the area of the perikaryon,— the cell is implanted in the underlying tissue by means of numerous processes. Occasionally the cells diverge to form intercellular interstices. In some places, the cytoplasm 885
of epithelial cells in the ductus showed a pale granulation. Only in isolated cases did we discern free ribosomes.

In most of the epithelial cells, we found round "vesicles" with smooth outlines; in individual cases, these were present in large quantities. The outlines of these vesicles were differentiated from the rather numerous cross sections of the endoplasmic reticulum by their size (approximately 100 mμ in

diameter) and their smooth boundaries. The endoplasmic reticulum (ribosomes) seems to run chiefly parallel to the longitudinal axis of the cell. The mitochondria are not very numerous; they seem to be of the tubular type.

The Golgi apparatus consists of parallel double membranes, appearing in both cross sections and transverse sections as vesicular outlines. Inclusions resembling vacuoles with pale boundaries exhibited low-density granules of indistinct shape.

The nucleate section of epithelial cells usually protrudes towards the base. The nucleus in epithelial cells is often elongated, and occasionally round, but most frequently lobate in shape. Its granulation is denser and more uniform than that of the cytoplasm. The area of the nucleolus is more finely and more densely granulated than the karyoplasm.

Throughout the ductus, the epithelial cells are separated from the subepithelial tissue by a continuous basement membrane. Directly below the plasmalemma, there is a light layer measuring 40-50 mμ in width, adjacent to a denser layer with a distinct boundary. The denser layer measures over 50 mμ in width, but its width can be given only approximately, since the distal edge was indistinct.

Below the basement membrane there is an area measuring about 1-2 mμ in width in which mumerous collagen fibers were found. In many parts of this area, we also found elastic substance.

Isolated sectors of cell processes traversed the area. In a few cases, sectors of nerve fibers and muscle cells were observed. Beneath this area lie the capillaries.

(b) Capillaries. The extremely thin wall of the capillaries shows the familiar structure consisting of endothelial tube, basement membrane, and adventitial cells.

(α) Endothelium. The endothelial cells form a continuous tube, with walls of fairly uniform thickness. This thickness varies from 0.5 to 1 μ, depending on the degree to which the capillary is expanded; the endothelial cells in extremely distended capillaries may be flattened out up to 150 mμ in height. Only their nucleate portions protrude. No apertures or pores were found in the endothelial tube. The smoothly undulate exposed surface of the endothelium does not show any processes. The endothelial cells are interconnected internally by denticulations; in some places, the edges of the cells also overlap. Frequently, a rather large process protrudes into the lumen of the capillary in the area of the cell boundary. At the denticulations, and normally directly beneath the surface of the endothelium, there are desmosomes.

The base of the endothelium is generally finely sinuous in moderately distended vessels, and almost flat in highly distended vessels. Occasionally, it protrudes

over a short distance in a slightly guttiform fashion along the basal side. Along the basal surface of the cell, there are numerous inflexions in the form of podicellate vesicles or invaginations. Vesicles of equal diameter are found in large numbers also in the cytoplasm of endothelial cells. Many 886
cells appeared to be completely permeated by smoothly outlined vesicles with approximately equal diameters (ca. 100 mμ); it may be assumed that these vesicles arose as a result of membranous vesiculation.

As a rule, the not very numerous mitochondria (tubular type) are found in the central area of the cell, usually with their longitudinal axis roughly parallel to the longitudinal axis of the capillary.

The endoplasmic reticulum is distinctly developed, especially in the center of the cell. Cross sections of its channels were often found arranged in a row in the middle of the cell body, parallel to the circumference of the capillary. The outlines of the Golgi apparatus appear as parallel rows of small, densely packed, smoothly shaped vesicles of approximately uniform size. Free ribosomes occurred only in isolated cases in the cytoplasm, which was almost entirely filled with vesicles.

Occasionally, we found smoothly shaped, round inclusions which appeared either very densely and finely granulated or homogeneous. These also probably represented fat droplets. Other sharply outlined inclusions, reminiscent of vesicles, were probably swollen mitochondria.

The shape of the nucleus in endothelial cells depends on the extent to which the endothelial tube is distended: in moderately distended capillaries, the nuclei are rather ovoid; in highly distended vessels, they are very flat (Figure 40). In narrowly contracted capillaries, endothelial nuclei occurred with many folds and deep invaginations. Nuclear pores are always visible; less often, the circumnuclear cisterna is discernible over a short distance. The nucleolus is distinctly differentiated. In some cases, its granules appeared as if they were arranged in a row along a twisted ribbon.

(β) The basement membrane. The basement membrane of the capillaries in the ductus pneumaticus (average thickness, 100 mμ) consists of three layers: two dense outer layers and a less dense, lighter, middle layer. Frequently, the area of the basement membrane also appears vaguely cloudy. Fine, fibrillar structures with their longitudinal axis oriented parallel to the circumference of the capillary were sometimes observed in the basement membrane. In places where adventitial cells are appressed to the capillary, the basement membrane divides, covering the adventitial cells with its outer lamella.

(γ) Adventitial cells. The adventitial cells are distinctly flattened elements, of about the same thickness as the endothelial cells, pressing closely against the capillary tube. They do not form a continuous covering, however, but leave many open gaps. They are enclosed by the basement membrane. In many cases, their cell membrane shows indications of vesiculation. The cytoplasm has the same density and structure as that of the endothelium, and equally abundant vesicles. The large mitochondria (measuring from 200 to 230 mμ in diameter) which are ovoid to round in shape, possess a fairly light matrix, permeated by tubuli. The endoplasmic reticulum is relatively highly developed. The Golgi apparatus was also discernible.

In addition to vacuoles obviously belonging to the Golgi apparatus, the adventitial cells also contain a few large, smoothly shaped vesicles which appeared empty in the photographic reproductions. There are also isolated round osmiophilic inclusions with smooth edges. In some adventitial cells, the portion of the cell facing the basement membrane —more often than other parts of the cell— contains a pale or cloudy substance, the nature of which we were unable to determine.

The cell nucleus, which is usually oblate, is always 887
indented or lobate, and sometimes even deeply cloven. In sections cut at an appropriate angle, these indentations in

the surface of the nucleus may assume the appearance of nuclear inclusions. The circumnuclear cisterna was readily discernible. The area of the nucleolus contrasts distinctly with the karyoplasm. Two different types of nucleolus could be differentiated: In some, the dark granules appeared as if they were arranged in a loose row along a twisted ribbon; in others, several areas filled with dark granules were discernible within the nucleus. In the latter case, it was not clear whether the nucleolus was very elongated and therefore cut several times in the same section, or several nucleoli were present.

3. Red body. The red body is made up of densely packed parallel capillaries. The arterial and venous capillary networks interpenetrate, but they do not interconnect by means of anastomoses. Rather,—as we know from experiments in which differently colored substances were injected, among other evidence,— the arterial and venous capillaries are arranged so that every venous capillary is encircled by a corona of arterial capillaries (KROGH 1919).

The difference between the two types of capillaries was readily discernible in our electron micrographs. Apart from the fact that —in the area under examination, at any rate (Figure 41)— the venous capillaries were of a somewhat

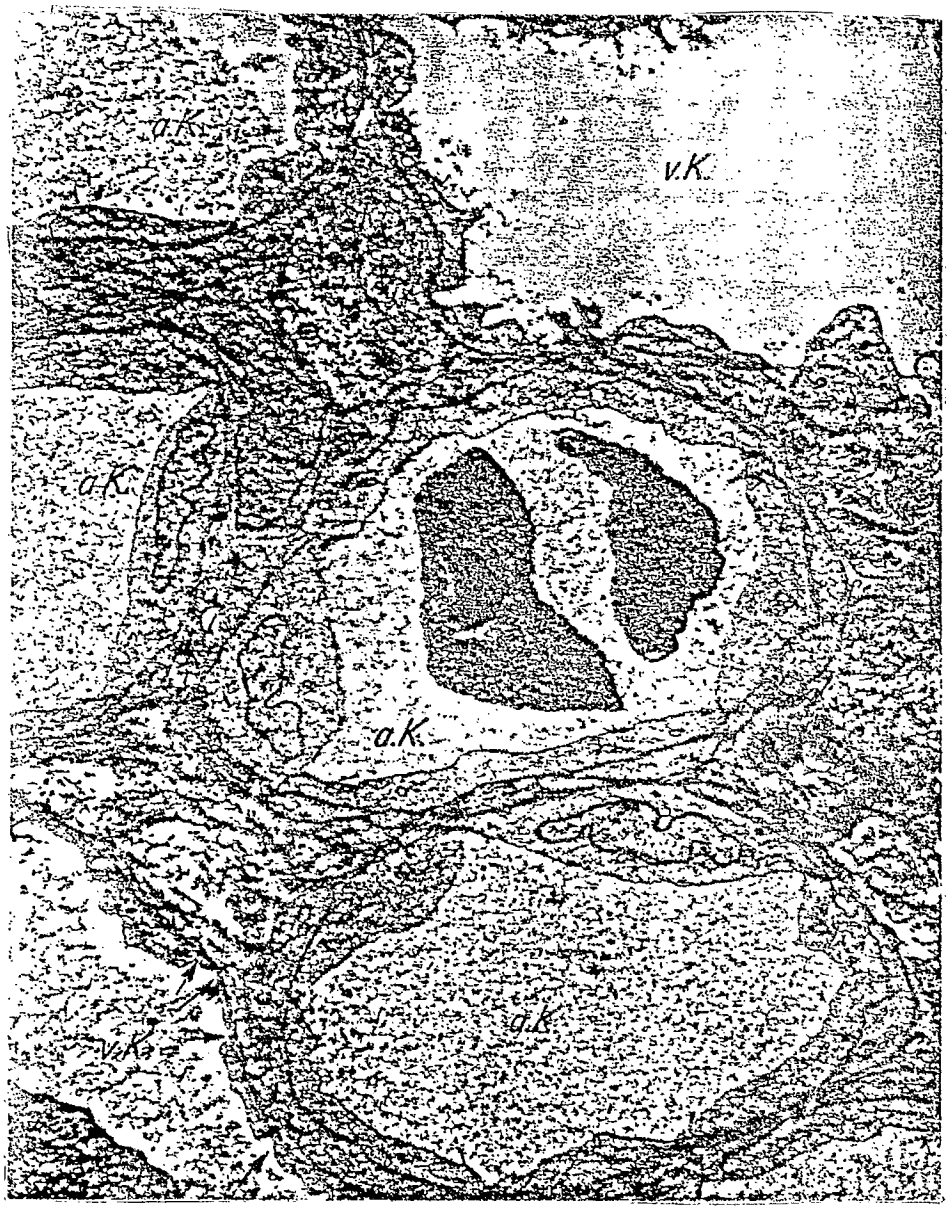

Figure 41. Cross section through the capillaries of the red body. a.K.-arterial capillary v.K.-venous capillary Sectors of erythrocytes are visible in the middle capillary. Pores are visible in the endothelium of the venous capillary (→). x14,800

higher caliber than the arterial capillaries, there was a distinct difference between the two types with respect to the morphological behavior of their endothelial cells.

(a) The arterial capillaries. The arterial capillaries are lined with endothelial cells of only slightly varying thickness. In cross sections, the capillary tube is lined with five or six cells with slightly protruding nucleate sections. Inflexions of the endothelial tube are always observed along the cell boundaries. The surface of these cells does not exhibit any microvilli. Denticulations are always present along the cell boundaries; they may be sigmoid or even more highly coiled, and they are always accompanied by desmosomes. No intercellular interstices were observed. Along the base of the endothelial cells, there are fine infoldings, sometimes resembling an extracellular labyrinth in appearance, and also vesiculations.

The cytoplasm is light, and permeated in a striking manner by dense, uniform vesicles. Consequently it appears, as a whole, to have a spumose or porous structure. The vesicles have plain outlines of approximately equal size (about 100 mμ in diameter) and appear empty in electron micrographs. Relatively large mitochondria of the tubular type are present in small numbers; the number of tubuli in these mitochondria is small.

The endoplasmic reticulum, with its distinctly prominent ribosomes, is readily discernible in the center of most of the cells; it seems to extend longitudinally, chiefly parallel to the circumference of the capillary. The Golgi apparatus is visible in most endothelial cells, showing parallel rows of small vesicles with dark outlines, and a few large vacuoles. Free ribosomes were observed in the cytoplasm only in small numbers. Highly dense, homogeneous inclusions occurred seldom.

The nucleus in endothelial cells is generally flat and highly lobate. Nuclear pores are visible in the nuclear membrane, which has a double outline, and the nucleolar substance appears as an area of dense, dark granulation (Figure 41).

The caliber of the arterial capillaries varies. Relatively high-caliber capillaries with flattened endothelial cells 888
are found alongside of others in which the lumina are narrowed by inward protrusions of the endothelial cells.

(b) The venous capillaries. The venous capillaries are sharply differentiated from the arterial vessels by the much more troubled pattern shown in relief by their endothelium. Moreover, on the whole, the endothelial cells are considerably smoother than those of the arterial capillaries. In the

smoothest areas, a coating of cytoplasm was still just barely visible at high magnification (Figure 42). In these places, 889
the endothelium measures about 100 mμ in thickness. In some areas, there are narrow pores, measuring 350-400 Å in width, in the endothelial coating (Figure 41). The nucleate area often arches out into the lumen of the capillary in a hemispherical fashion. The undulate surface of the cell does not exhibit any microvilli. On the other hand, there are tubular or infundibuliform indentations in the cell surface which, in sections cut at the appropriate angle, can create the 890
illusion that vacuoles are present (Figure 43). The denticulations along the cell boundaries are generally sigmoid, but they often also show a far more complex structure. At the sites of these denticulations, bordering cells each emit a long process into the lumen of the capillary. The base of the cell also shows very numerous infoldings and vesiculations. The mitochondria (tubular type) are not very numerous, but quite large. In most endothelial cells, the endoplasmic reticulum is very clearly visible. The Golgi apparatus is characterized by parallel layers of double membranes and fine vesicles, and large vesicles connected with these fine vesicles. (Figure 43). Moreover, the cytoplasm of the endothelial cells also exhibits a number of inclusions of various kinds, including rather frequent round formations with plain, smooth outlines and a uniform,

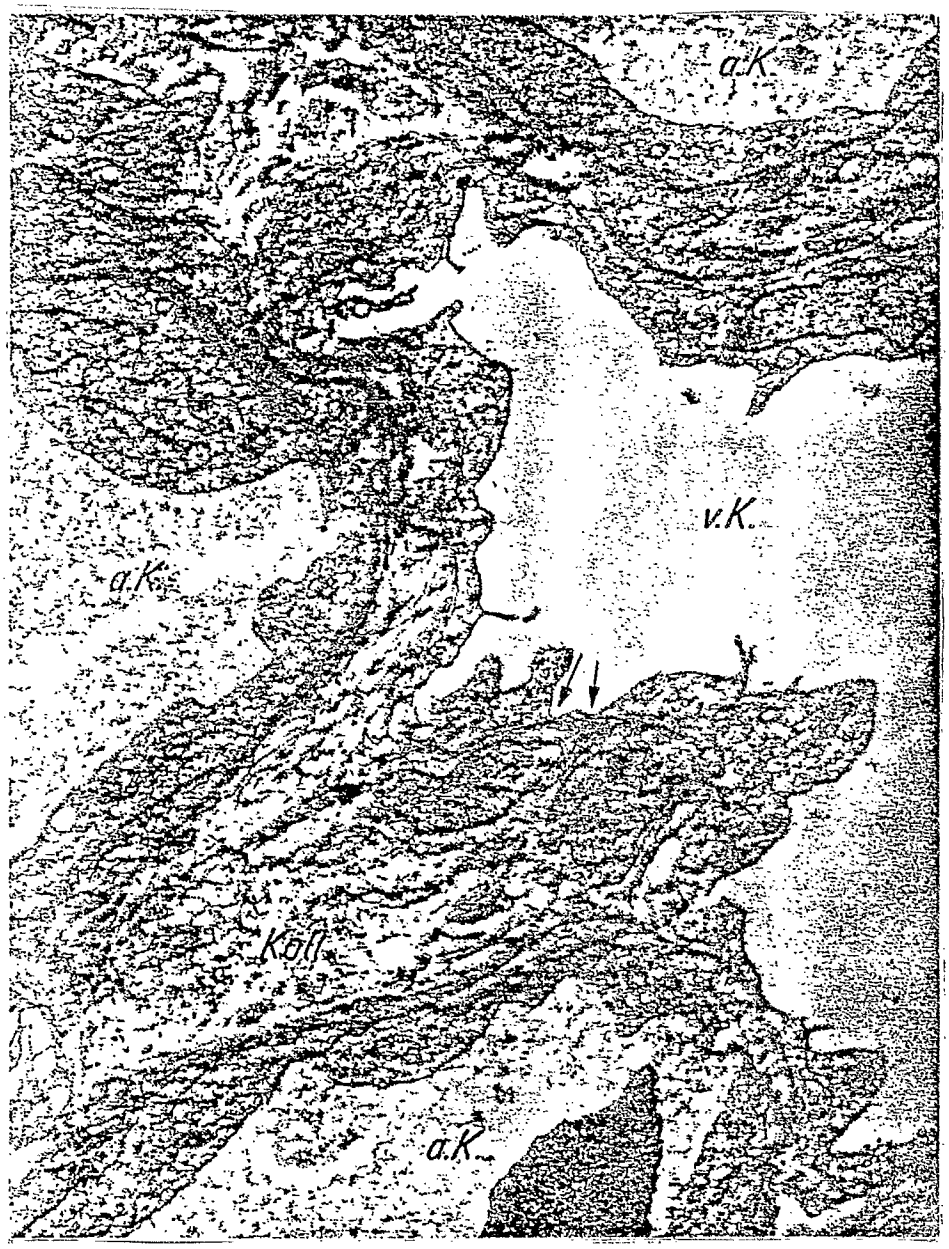

Figure 42. Cross section of the red body. aK-arterial capillaries vK-venous capillary, with distinctly flattened endothelium (⟶) Koll-collagen fibers x8000

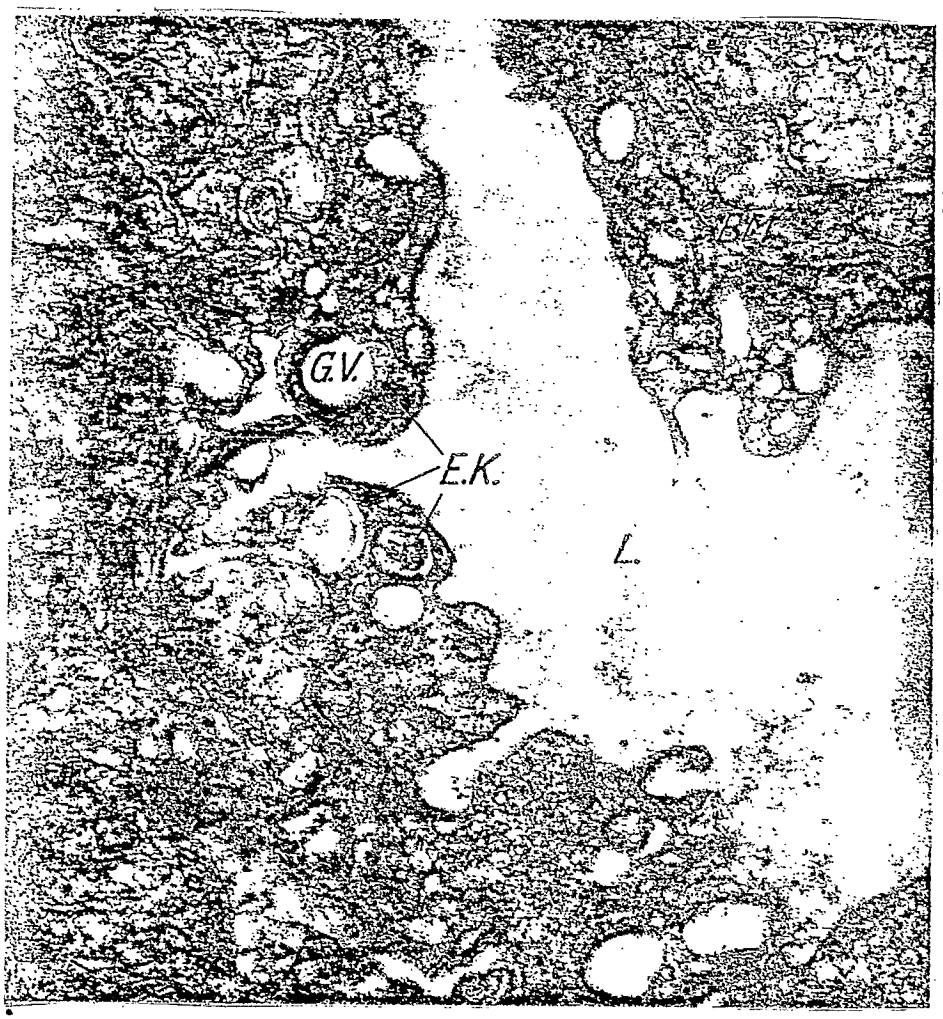

Figure 43. A venous capillary in the red body. In the cytoplasm of the endothelial cells, there are vacuoles, inclusions (EK), and Golgi apparatus with vacuoles (GV). BM-basement membrane L-lumen of the capillary x 24,000

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dark appearance, perhaps representing drops of fat or lipids. 891
Other inclusions consist of round corpuscles with sharp boundaries. In addition, large, more or less round vacuoles with dark outlines occur, containing isolated, pale gray, round particles. Finally, this cytoplasm, like that of

endothelial cells in the arterial capillaries, seems to be densely filled with light, smoothly outlined vesicles of nearly uniform size (about 100 mμ in diameter).

The nuclei of the endothelial cells in venous capillaries are less flattened than those in the endothelium of arterial capillaries. They are striking on account of their very distinct lobate and cloven character. The nucleolus was prominent in section preparations as a dark, densely granulated area.

(c) The adventitial cells. The capillaries of the red body are endowed with a covering of adventitial cells. These cells leave the basement membrane exposed in some areas. The generally very flat processes of these cells press against the capillary wall along their entire surface, while the nucleate sections are usually located in the intercapillary wedges (Figure 41).

In some areas, the cell membrane shows indications of membranous vesiculation. The cytoplasm of the adventitial cells is very similar to that of the endothelial cells with respect to density and granulation, but it does not exhibit as many vesicles as the latter. The large mitochondria are of the tubular type. The endoplasmic reticulum is always readily discernible. The Golgi apparatus is very striking; it is far more distinctly developed, and more frequently observed, than in the endothelial cells. It is characterized

by the familiar stacks of oblate sacs and vesicles, and by large vacuoles. Other large vacuoles, with plain boundaries, contain indistinctly shaped granules of varying density. Osmiophilic inclusions of a homogeneous appearance probably represented drops of fat or lipids.

The nuclei of the adventitial cells almost completely fill those sections of the cell located in the intercapillary wedges. They are large, with smooth edges, and an angular or oblate shape. Most of the nuclei of adventitial cells are distinctly differentiated from the nuclei of endothelial cells by their much denser, finer, and more massed granulation. Nuclear pores were always visible in the nuclei of the adventitial cells, and the nucleus was often observed in section preparations. The circumnuclear cisterna was frequently much more distinct than it was in simultaneously observed endothelial cell nuclei.

(d) The basement membrane. The basement membrane has the same structure in both arterial and venous capillaries; it always shows three layers. A dark middle layer measuring from 50 to 70 mμ in thickness is enclosed in two light outer layers measuring from 30 to 40 mμ in thickness. At many sites, the layers of the basement membrane diverge; in such areas, the middle zone seems to widen, and it shows a fine striation. Sometimes it also widens out into a broad, indistinctly structured stratum. In places where there are adventitial cells pressing against the capillary tube, the

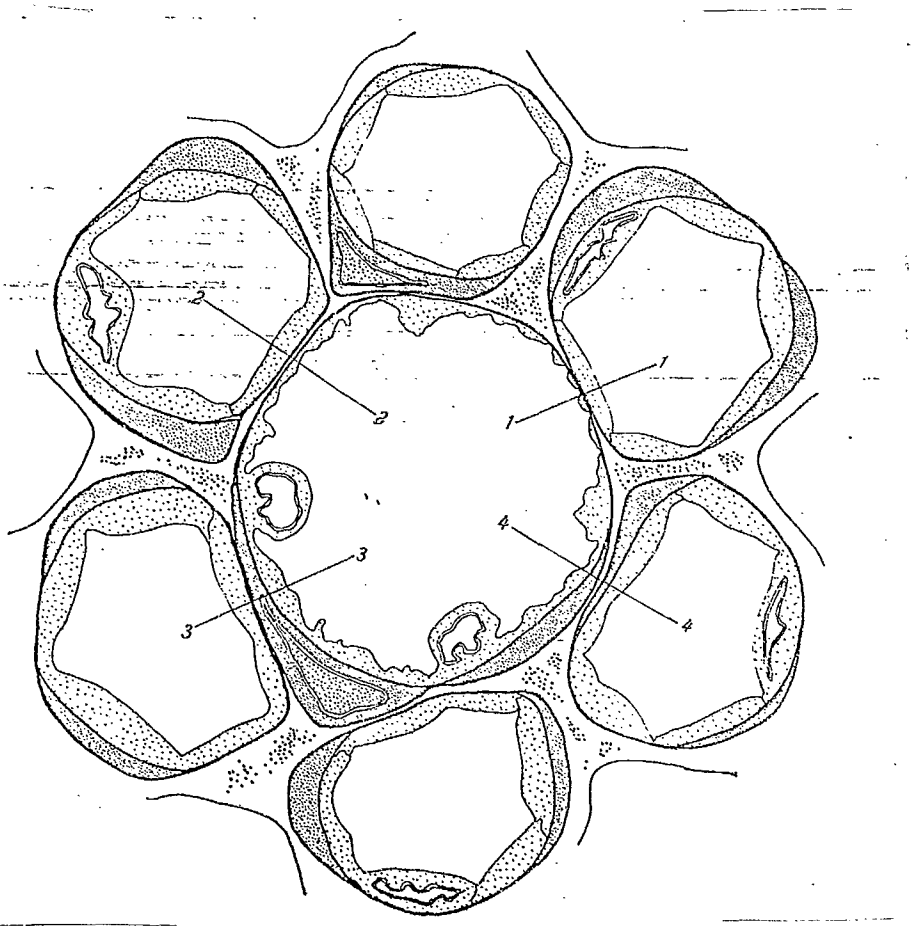

Figure 44. Illustration of the arrangement of the capillaries in the red body; a venous capillary is surrounded by arterial capillaries. Details are explained in the text. Sparse dots indicate endothelial cells; dense dots indicate adventitial cells.

middle layer divides in order to cover these cells (Figure 41). In these places, the portion of the basement membrane facing the capillary wall is always thinner than the part covering the opposite surface of the adventitial cell. Hence, the behavior of the basement membrane provides a basis for identifying the vessel to which an adventitial cell belongs.

Numerous collagen fibers were found among the 892
capillaries, especially in the wedges. These fibers generally run parallel to the longitudinal axis of the capillaries. In addition, there was an indistinctly structured substance believed to be elastic material. With the exception of isolated nonmedullated nerve fibers, no other tissue elements were found between the capillaries.

The capillaries touch one another with their walls, and often are slightly flattened against one another so that sections show an alveolar structure. The possible boundary structures between capillaries are as follows (Figure 44):

1. In areas where pores are present in the endothelium of the venous capillaries and where adventitial cell sections are absent, the venous blood borders upon the basement membrane of the capillary, and the latter borders on the basement membrane and endothelium of the arterial capillary (venous blood-basement membrane-basement membrane- endothelium).

2. In parts of the wall without adventitial cells or pores, the barrier is made up as follows: endothelium-basement membrane-basement membrane-endothelium.

3. When an adventitial cell is interposed, the following 893
pattern results: endothelium-basement membrane-adventitial cell-basement membrane-endothelium.

4. Finally, the following pattern may occur: endothelium-basement membrane-adventitial cell-basement membrane-basement membrane-adventitial cell-basement membrane-endothelium.

D. Discussion

Our light microscopic study of the swim bladder of the Eel has revealed a number of new structures not observed previously. First, let us discuss our findings concerning the vascular system of the swim bladder.

JACOBS (1898) first revealed the capillaries of the swim bladder by injecting the vessels. His illustration of the capillary network shows a "sheaflike or radial ramification" of the vessels, spreading out along the surface. This model corresponds to Figure 6 of the present study, which represents the capillaries in the rostral part of the swim bladder. The characteristic arrangement of the vessels in the other parts of the swim bladder, and in particular the arcading loops beneath the epithelium, were apparently not observed; at any rate, there is no mention of them, and no illustration of them, in JACOBS' study.

Reports regarding the organization of the muscles in the swim bladder have also been inconsistent. While PAULY (1882) describes an inner layer of annular muscles and an outer layer of longitudinal muscles, JACOBS (1898) reports that the swim bladder of the Eel exhibits only annular muscles, and no longitudinal muscles. OPPEL (1905), on the other hand, records that the muscles of the swim bladder consist of a layer of annular muscles and an outer layer of longitudinal muscles, and that

these two layers are not strictly separate. However, the fact that the muscular loops are arranged in the form of a scissorlike lattice has not been observed. The organization consisting of smooth inner muscular spirals with a rather circular course and outer longitudinal muscles winding in steeper spirals is explained by the origin of the swim bladder from the intestinal tract. It is most nearly comparable with the gall bladder in mammals and man.

In many other teleost swim bladders lined with smooth muscles, this organization is either much less distinctly developed than in the swim bladder of the Eel (SAUPE, 1939, Eurasian Perch) or limited to a certain area of the swim bladder wall. The dense net of elastic fibers is closely connected with the muscle fibers. The continuous muscularis consisting entirely of annular and longitudinal muscle layers must play an important role in the contractions which the eel swim bladder is capable of executing (FAENGE 1953). By means of these muscles, air is forced into the ductus pneumaticus, which is considered as a supplementary respiratory organ.

We have also obtained new findings regarding the muscles of the ductus pneumaticus. OPPEL (1905) reported the presence of a thick layer of annular muscles in the ductus pneumaticus under the layer of connective tissue. "In addition to this layer of annular muscles, however, cross sections

of the ductus pneumaticus show it surrounded at intervals by clearly differentiated bundles of longitudinal muscles lying in rather solid sheaths of connective tissue." We need not discuss whether OPPEL's "bundles of longitudinal muscles" refers to the nerves and his "solid sheaths of connective tissue" to the muscular sheaths covering the nerves. At any rate, the abundant supply of nerves running parallel to the lomgitudinal axis of the ductus pneumaticus and originating from vegetative ganglia (see also FAENGE & MATTISON 1956) is striking. The arrangement of the longitudinal muscles in the form of sheaths around the nerves is also remarkable. Nowhere else, so far as I know, has an arrangement of this kind been observed so far. The functional importance of this structural pattern may consist in protecting the nerves against stretching or displacement during the major variations in volume to which the ductus pneumaticus is subject. 894

Our electron microscopic study of the swim bladder of the Eel has revealed a characteristic fine structure for each part of the organ.

As late as 1952, COPELAND reported that neither mitochondria nor Golgi apparatus could be identified in the swim bladder of Fundulus. However, as was to be expected, mitochondria and Golgi apparatus do occur in the cells of the swim bladder epithelium. Our electron micrographs have

shown how it was possible for these structures to have remained unnoticed with previous light microscopic methods; they are very small, and not very striking. The long, filamentous mitochondria (tubular type) are exceedingly delicate (100-130 m μ). It was impossible to record their length, since they traverse the cytoplasm in multiple turns, without accumulating in any particular favored parts of the cell. The mitochondria are apparently subject to changes in their structure. Thus, mitochondria slender in shape were found alongside of others in the same cell with a highly swollen appearance. Even vacuolar transformation of mitochondria seems to occur, in which fragments of mitochondria may remain on the edge of the vacuoles; similar findings were obtained by BARGMANN & KNOOP (1960) on the pituitary of Cottus. Whether the vacuoles with granulated contents which were found quite frequently in the swim bladder epithelium originated from mitochondria cannot be decided at this time.

The extremely inconspicuous Golgi apparatus is only seldom visible in electron micrographs. In the electron-dense cytoplasm of the "dark" epithelial cells, we could not observe it at all. In the "light" epithelium, it was seen only twice: once in the familiar form of double lamellar stacks with a few vacuoles, and once in connection with very large, irregularly shaped cavities at the base of an epithelial cell. The endoplasmic reticulum also is not very striking.

Among the paraplasmic inclusions in the cells of the swim bladder epithelium, the smooth-edged osmiophilic inclusions, probably representing fat droplets, were most numerous. This finding is in agreement with the light microscopic identification of lipid inclusions which could be stained with scarlet. Inclusions with concentrically stratified, lamelliform, osmiophilic contents resemble the cytosomes known in the lung (SCHULTZ 1960, and others). It is not clear, however, whether these inclusions, like those in the lung, originate from mitochondria.

In the swim bladder epithelium, epithelial cells with very different types of structure occur alongside of one another within a small area. Apart from variations in the density of the cytoplasm ("light" and "dark" cells), there are also a number of other prominent characteristic traits, particularly with respect to the structure of the basal region of the cell. In "light" epithelial cells, this area exhibits a large number of vacuoles of approximately 895
the same size. In addition, there are small infoldings in the basal surface of the cell. More frequent formations are denticulations along the base of neighboring cells, as a result of which the intercellular spaces are widened into interstices or vacuoles. It is difficult to make any statement about the origin and contents of the vacuoles. It is not

clear whether they represent gas bubbles, or cavities originally filled with materials which have been dissolved and removed during fixation and embedding.

The base of the "dark" epithelial cells shows a much more varying pattern, due to extensive infoldings of the cell surface, referred to by RUSKA (1957) as an extracellular basal labyrinth. Infoldings of the base of the cell are known in epithelia of other organs: they occur in the kidney (epithelia of the principal limb-SJÖSTRAND & RHODIN 1953; RHODIN 1954; RUSKA, MOORE & WEINSTOCK 1954: junctional tubule- PEASE 1955: collecting tubules- PEASE 1955), in the ciliary epithelium (HOLMBERG 1955; PEASE 1956), in the glandula submaxillaris (PEASE 1956), and in the choroid plexus (MAXWELL & PEASE 1956; MILLEN & ROGERS 1956). But in none of the cases listed is the arrangement as extensive and complex as in the swim bladder epithelium. The greatest similarity exists between the structure of the epithelium in the choroid plexus and in the swim bladder. According to MAXWELL & PEASE (1956), thick infoldings of the basal surface of the cell occur in the plexus of the Rat; interestingly, the capillaries involved are equipped with a porose endothelium. MILLEN & ROGERS (1956) have presented similar pictures of plexus epithelium in the Rabbit. In this epithelium, just as in the swim bladder epithelium, there are vesicles of various sizes in the cytoplasm, and also infoldings —though these contain mitochondria—of the cell base, spiral turns of double membranes, and vesicles arranged in a catenulate or coronal pattern.

An extracellular basal labyrinth is generally observed in cells in which intensive secretory or absorptive fluid transport takes place. In all cases described so far, very voluminous mitochondria, thought to be producers of energy for the activities of this fluid transport, are found with great regularity in the compartments of cytoplasm separated by the cellular infoldings —as in the kidney, for example. In the swim bladder epithelium, in contrast, even one of the very delicate mitochondria is found in these compartments of cytoplasm only extremely seldom. The marked amplification of the surface indicates that extensive transport of fluids takes place on the swim bladder epithelium. Whether this fluid is moving towards the epithelium or towards the blood vessels cannot be determined using morphological methods.

In this connection, the following fact deserves attention: In the basal region of the cells of the swim bladder epithelium, carbonic anhydrase has been identified by histotopochemical methods. That the tissues of the swim bladder, and particularly those of the gas gland, contain large quantities of this enzyme was already ascertained by LEINER (1940). FAENGE (1953) demonstrated a high carbonic anhydrase content in tissue homogenates from the eel swim bladder. However, his results have to be corrected. FAENGE observed a particularly high level of enzyme activity in homogenates of the red body. But this

was probably connected with the erythrocytes, which cannot be eliminated during homogenation of the red body. In the present study, histotopochemical methods indicated no 896 carbonic anhydrase in the tissues of the red body. On the other hand, the high level of enzyme activity in the swim bladder epithelium corresponds well with FAENGE's chemical findings. A striking feature is the occurrence of the reaction product in the basal region of the swim bladder epithelial cells. It must remain an open question at this time whether it was located in the round vacuoles in the cytoplasm or in the interstices of the basal labyrinth.

It is uncertain whether the "light" and "dark" epithelial cells represent different types of cells or only different functional states of one and the same type of cell. It seems audacious to assume that the basal labyrinth serves as a substrate for secretion into the blood vessels and that the vacuoles in the basal region of the cell are gas bubbles. It is not even clear whether the extremely small, round cavities which appear empty in electron micrographs —which may occur also in the apical region of the cell—represent spaces containing gas.

Finally, it is remarkable that the cell membranes in the swim bladder epithelium were found to be interrupted in many places; with this obervation, we arrive at the problem of the syncytium. Most of the vertebrate syncytia known to

light microscopy have, when examined with an electron microscope, turned out to be unions of cells with cell boundaries. The cell boundaries are absent only in the syncytiotrophoblast of the placenta (BARGMANN & KNOOP 1959; SCHIEBLER & KNOOP 1959), in which perhaps a plasmodium is represented. In the present case, it is very difficult to decide whether folds in the membranes were cut at an oblique angle in our section preparations, causing them to disappear from view, or intercellular cytoplasmic bridges actually occurred.

The ductus pneumaticus of the Eel departs considerably from those of other physostomes in structure. The close resemblance between the ductus pneumaticus and the "cellular lungs" of reptiles and other primitively structured vertebrate lungs has been pointed out repeatedly (QUECKETT 1844; PAULY 1882; JACOBS 1898). A function similar to that of the lungs was already postulated for the ductus pneumaticus by K.E.v.BAER (1835) when he wrote that the ductus pneumaticus "serves as a respiratory organ when the animal leaves the water". This conception obtained important support from PAULY's (1882) discovery of the special pattern of venous circulation in the ductus pneumaticus, which corresponds to a pulmonary circuit. BERT (1870) had observed that an eel could survive up to 36 hours out of water, and JACOBS (1898) produced experimental proof that the Eel can live out of water as long as the supply

of gas in the swim bladder lasts. In fact, our electron microscopic findings have shown a close correspondence between the ductus pneumaticus and the lungs of lower vertebrates even in their submicroscopic structure. This is shown particularly clearly by comparison with the lung of Protopterus (DE GROODT, SEBRUYNS & LAGASSE 1958). The epithelial cells in the ductus pneumaticus of the Eel may be compared with the alveolar cells in the lung of Protopterus. Both emit numerous spiculiform cytoplasmic processes into the air-containing cavity. In both organs, there is an area filled with fibers and cells of connective tissue underneath the epithelium. The capillaries of the ductus pneumaticus resemble the pulmonary capillaries in virtue of the fact that their endothelium is completely continuous and of approximately equal thickness throughout. In contrast to the pulmonary capillaries, however, which exhibit a continuous covering 897
of adventitial cells, in the ductus pneumaticus there are exposed areas of the capillary surface in between the smooth processes of the adventitial cells.

A surprising feature is the large number of vesicles in the cytoplasm of all cells participating in the formation of the air-blood barrier, viz., the epithelial cells of the ductus pneumaticus, and the endothelial and adventitial cells

of the capillaries. In addition to this, there is the distinct vesiculation of the cell membrane. In many cases, we observed a connection between vesicles lying freely in the cytoplasm and the invaginations on the surface of the cell. The vesicles, therefore, evidently arise as a result of membranous vesiculation. They measure approximately 70-100 mμ in diameter. This findings is in agreement with other findings obtained for vertebrate lungs. BARGMANN & KNOOP (1956), for example, found round vacuoles in the pulmonary capillary endothelium of Xenopus and Rana esculenta; DE GROODT, LAGASSE & SEBRUYNS (1959) discovered vesicles measuring 500-750 Å in diameter in the endothelium of the pulmonary capillaries of mammals. These authors also found distinct vesiculation in the cellular lining of the pulmonary capillaries, on the side facing the air.

Therefore, the blood-air barrier in the ductus pneumaticus of the Eel shows resemblances to that in the lungs of lower vertebrates and mammals. Evidently, the cytopempsis which occurs in all of these cases in the tissues participating in the formation of the blood-air barrier is essentially for the transport of materials across this barrier (see also DE GROODT, LAGASSE, and SEBRUYNS). Thus, the findings reported in the present study are also consistent with the theory of a respiratory function of the ductus pneumaticus.

With regard to the importance of the rete mirabile in the swim bladder, J. MUELLER, as early as 1840, wrote the following remarks: "Since arterial and venous capillaries run together through the red bodies in large numbers, even though no blood can pass over directly from the arterial vessels into the venous vessels, a rather fine exchange probably can take place in the capillary bundles, such that materials pass over from the arterial to the venous vessels. If this is the case, the blood emerges from the arterial capillaries in an entirely different condition than it entered them; but the venous vessels, as they conduct the blood arriving from the swim bladder through the rete mirabile, simultaneously hold and conduct the admixture which passes over from the arterial portion of the capillaries in the rete mirabile. —In this way, the red bodies of the swim bladder may act on the composition of the blood to prepare it for the subsequent secretion of the gas." JACOBS (1930) advocated the view that the function of the red body in the swim bladder consists of an exchange of materials between blood in the arterial and in the venous capillaries. When HARGITAY & KUHN (1951) had demonstrated that the concentration of urine in Henle's loop in the kidney is based on the principle of a hairpin-counterflow exchange system, SCHOLANDER (1954) recognized that the capillaries of the red bodies in the swim bladder also represent such a counterflow exchange

system. KUHN & KUHN (1961; the publication appeared while the present report was at the press) have shown that high gas pressures can be built up by the rete mirabile of the swim bladder. The pressures are caused by the multiplication of small individual effects (variation of the pH and salinity of the blood by the gas gland) in the hairpin-counterflow exchange system of the rete mirabile.

The results of the only electron microscopic study 898
of the capillaries in the swim bladder so far have been reported in a brief preliminary communication by FAWCETT & WITTENBERG (1959) concerning the rete mirabile in the swim bladder of Opsanus tau. The rete mirabile in the swim bladder of Opsanus is a unipolar rete mirabile. In cross sections, two types of vessels can be differentiated: the first have a continuous endothelium measuring 2-4 μ in thickness; the second have an endothelium of greatly varying thickness, with alternating stretches measuring first 1-3 μ and then 10-70 mμ. Endothelial pores in the strict sense were not observed; even in the thinnest sections, a cytoplasmic membrane measuring about 10 mμ in thickness was always present. The endothelial cells of the thick-walled capillaries showed distinct vesiculation of the cytoplasm, interpreted as an indication of pinocytotic processes; in the

other vessels, however, this phenomenon was much more restricted.

Our findings obtained on the Eel correspond well with these findings. The endothelium of the arterial capillaries measured 1-4 μ in height; in the venous capillaries, it was subject to considerable variation. The thickest sections of the venous capillary walls measured 0.5-2 μ ; between these sections, there were stretches measuring 20-100 mμ in height. However, it appears that not only extremely flat endothelial sections, but also actual pores, measuring about 40 mμ in width, occur in the venous capillaries. In contrast to the findings on Opsanus tau, in the red body of the eel swim bladder, vesiculation occurs in both types of endothelial cells. Only occasionally were isolated vesicles, measuring up to more than 200 mμ in diameter, found in the endothelium of the arterial capillaries.

The findings obtained by LONGLEY, BANFIELD, & BRINDLEY (1960) on the rete mirabile of the renal medulla of the Rat offer an interesting parallel to our observations. In this subject also, it was possible to differentiate afferent from efferent capillaries on the basis of their endothelial structure. The former are endowed with a completely continuous endothelium measuring 0.2-4.7 μ in thickness;

the latter have a regularly fenestrate endothelium, in which the openings are bridged over by cell membranes and therefore do not represent true pores. In the rete mirabile of the kidney, the vessels are quite close together; but nevertheless, there are interstices, with numerous interstitial cells. In contrast, among the densely packed cells in the red body of the eel swim bladder, the interstices are chiefly limited to the wedges formed where the boundaries of several capillaries meet. They are traversed only by collagen fibers. Apart from the endothelial and adventitial cells, only isolated nerve fibers are found. In the rat kidney, vesiculation is found also in the cytoplasm of the endothelial cells of the rete mirabile, in both arterial and venous capillaries.

All of the retia mirabilia which we have discussed are substrates for counterflow exchange systems. The structural correspondence among the capillaries of these three vascular networks is remarkable. In every case, two types of endothelial cells occur: one forming a continuous layer of cells of approximately equal thickness, and the other consisting of a layer of cytoplasm of greatly varying thickness, equipped with pores. Of course, it is only in the case of the eel swim bladder and the rat kidney that the presence of a porose endothelium in the venous capillaries has been demonstrated; but a similar situation probably exists in the rete mirabile of Opsanus tau, even though this has not been noticed explicitly.

Evidently, two routes for the exchange of materials between blood vessels are embodied in these tissues: one through the pores of the endothelium; and the other through the entire layer of cytoplasm, by means of cytopempsis.

Perhaps the different materials are transported in different ways, dissolved gases being passed on by cytopempsis while larger molecules pass through the pores. It must be remembered in this connection that the actual barrier between the vessels is the basement membrane (BARGMANN 1950, POLICARD & COLLET 1961). It cannot be determined whether any transformation of materials takes place en route from a pore of the venous capillary through the endothelium of the arterial capillary; for, the latter contains only vesicles. The fact that, in the red body of the Eel, the Golgi apparatus is developed in an especially distinct manner in the endothelial and adventitial cells of the arterial capillaries perhaps indicates that these cells not only serve to pass through materials, but also play an active role in determining the composition of the capillary contents.

The structural differences observed in the walls of the capillaries in the retia mirabilia of certain swim bladders (e.g., Syngnathidae) by some investigators using a light microscope (WOODLAND 1911; RAUTHER 1922) are probably not comparable with the present findings. In Syngnathidae,

the arterial capillaries are equipped with prominences protruding far out into the lumen, the structure of which requires a separate study.

In conclusion, let us compare once again the types of capillaries occurring in the swim bladder. We may differentiate the following types of capillary:

1. Capillaries with a continuous endothelial tube, a basement membrane, and an incomplete covering of flat adventitial cells: (a) with a very flat endothelium (capillaries in the ductus pneumaticus); (b) with a high endothelium, flattened only along the cell boundaries (arterial capillaries in the red body, and some capillaries —or only portions of capillaries— under the swim bladder epithelium).

2. Capillaries with fenestration or pores in the endothelium, a basement membrane, and an incomplete covering of flat adventitial cells: (a) with very wide apertures, measuring 200 to 700 mμ in width, in the endothelium (capillaries under the swim bladder epithelium); (b) with narrow pores measuring 300-400 Å in width (venous capillaries of the red body).

Capillaries of the first type are known, e.g., in the brain and the interstitial connective tissue; those of the second type are found in numerous endocrine organs and in the renal corpuscles.

A striking common feature of the endothelial and adventitial cells of all swim bladder capillaries is the vesiculation of the cytoplasm. The vesicles have approximately the same size in all capillaries. Their diameter —about 100 mμ— is greater than that of the vesicles observed by RUSKA (1958) in the endothelial cytoplasm, which reportedly measured 50-70 mμ in diameter. The uniform occurrence of these vesicles in endothelial and adventitial cells of all swim bladder capillaries suggests the hypothesis that exchange processes by means of cytopempsis take place in all the vessels under consideration.

The pores in the endothelium of the venous capillaries of the red body measure 300-400 Å in width. This corresponds with the measurements known previously for endothelial pores. We know, for example, of pores measuring 600-1200 Å in width in the endothelium of the capillaries of Amphibia; in the endothelium of capillaries in endocrine organs, the size of the pores ranges from 300 to 700 Å. In contrast, the interstices in the endothelium of the swim bladder capillaries, which measure 200-700 mμ in width, are unusually large.

Summary 900

The swim bladder, ductus pneumaticus, and red body of the Eel were studied using light microscopic and electron microscopic methods. The findings obtained included the following:

1. Swim bladder. The smooth muscles of the swim bladder are arranged in the form of scissorlike lattices with adjustable meshes. An inner lattice of smoothly running spirals underlies an outer lattice with more longitudinally oriented turns. The two lattices intermingle in a middle zone. Elastic fibers accompany the muscles, forming an elastic lattice with a corresponding structure.

The capillaries of the swim bladder form a dense network structured differently in different parts of the swim bladder. The capillaries generally spread out superficially in the rostral area, run parallel to one another in the middle of the swim bladder, and branch out in an arborescent fashion in the caudal section.

The capillaries underlying the swim bladder epithelium possess a complete endothelial tube in some portions; in others, the endothelium is fenestrate, with apertures measuring 200 to 700 mμ in width. The adventitial cells do not form a continuous covering around the vessels.

Our electron microscopic study of the epithelium of the swim bladder led to the differentiation of dense ("dark")

and less dense ("light") epithelial cells. The base of the dark epithelial cells was characterized by very extensive and complex infoldings of the cell surface (basal labyrinth), to an extent nowhere previously observed. The basal region of light epithelial cells exhibited vesicles of varying size, which appeared to be empty. The Golgi apparatus, which escaped the notice of previous light microscopic investigators of the swim bladder epithelium, was observed only in the "light" cells, in the form of double lamellar stacks and vacuoles. The mitochondria, which also could not be identified in swim bladder tissues by light microscopic methods, are fine, coiled filaments measuring 150 mμ in diameter, with a tubular internal structure. Very fine droplets of fat were distributed throughout the epithelial cell.

In the basal sections of cells in the swim bladder epithelium, carbonic anhydrase was identified by histotopochemical methods.

2. Ductus pneumaticus. The muscles of the ductus pneumaticus also consist of smooth annular and longitudinal fibers. The annular muscles form a scissorlike lattice of smooth interwoven spirals. Individual bundles branch out from the annular muscles and form longitudinal muscles. These longitudinal muscles form semicircular to circular sheaths

around the nonmedullated nerves which run parallel to the longitudinal axis of the ductus pneumaticus. The nerves originate from vegetative ganglia in the wall of the ductus pneumaticus. The electron microscopic structure of the ductus pneumaticus shows remarkable similarities with the lungs of lower vertebrates (e.g., Protopterus, Amblystoma, and Xenopus). An extremely smooth epithelium with spiculiform processes lines the cavity of the ductus. Under this epithelium lie capillaries with very smooth, continuous endothelia and incomplete coverings of adventitial cells. All cells participating in the formation of the blood-air barrier — epithelial, endothelial, and adventitial cells— exhibit a distinct vesiculation of the cytoplasm, which may be 901 interpreted as an expression of cytopempsis in the process of the exchange of gases.

3. Red body. The red body contains two types of capillary, with differently structured walls. The arterial capillaries have a continuous endothelium, while the endothelium of the venous capillaries is perforated by pores (measuring 300-400 Å in width). The adventitial cells are chiefly restricted to the intercapillary interstices. The structure and arrangement of the capillaries in the red body, compared with the morphological behavior of capillaries in other organs, indicate the presence of a counterflow exchange system.

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27. History and anatomy of the (common) Eel and monograph on our species of this genus

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29. Natural history of fish

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