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DATA TO THE ELECTRON MICROSCOPIC STRUCTURE OF THE PINEAL ORGAN OF THE BIRDS

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Of late, the results of several electron microscopic investigations in respect of the pineal organ of the bird were published (BISCHOFF, 1967; 1969; BISCHOFF and RICHTER, 1966; COLLIN, 1966; 1967; 1968; FUJIE, 1968; MIKAMI, 1968; 1969; OKSCHE, 1965; 1968; OKSCHE–KIRSCHENSTEIN, 1969; OKSCHE and VAUPEL von HARNACK, 1965; 1966; RENSONI, EAKIN and QUAY, 1968; QUAY, 1965; 1968; UECK, 1969). The statements concerning the structure were completed and put in a new light by experimental, extirpation-, electrophysiological, bio- and histochemical investigations carried out similarly on different birds (AXELROD, WURTMAN, 1966; AXELROD, WURTMAN and WINGET, 1964; ARIENS KAPPERS, 1965; KELLY, 1962; KOBAYASHI, 1969; MORITA, 1966; MENAKER, 1965; 1968; 1969; MENAKER and KETT, 1967; OKSCHE, MORITA and VAUPEL von HARNACK, 1965; 1966; RALPH and DAWSON, 1968; QUAY, 1966; QUAY and RENZONI, 1963; WURTMAN, 1969; WURTMAN, AXELROD and FISCHER, 1964; WURTMAN, AXELROD and KELLY, 1968).

Comparing the different results obtained from the pineal organ of the various bird species to the large number of data found in sub- and superavian vertebrate groups respectively in the human (BARGMANN, 1943; DODT, UECK and OKSCHE, 1971; KAPPERS, 1971), we may establish that there isn't in the organism another organ as unknown as this peculiar protrusion of the thalamic tegmen.

In spite of the multilateral investigations and multisense illuminations, it can only be said even to-day that there is no certainty as to the origin and quality of its cells (neural, glial, ependymal, parenchymal), resp. the function of the whole organ (sense organ, receptor, photoreceptor, neurohumoral or exocrine, resp. endocrine gland or a rudimentary remain).

As not only the different classes of Vertebrate but even within these, in the various species, a strongly disparate structure may be found, it is highly justified getting on with studying the pineal organ.

Materials and Methods

We have investigated the ultrastructure of the pineal body of doves *(Columba livia domestica)*, turkeys *(Meleagris gallopavo)* and ducks *(Anas domestica)* of different ages. For being investigated, our materials were fixed in osmium tetroxide buffered with collidine,

according to BENNETH and LUFT (1959), and then embedded in araldite after alcoholic dehydration. We used 3—4 p.c. uranyl acetate for contrasting the material, and lead citrate contrasting, according to REYNOLDS (1963) for staining the sections. The sections were made with ultramicrotome Porter—Blum LKB, and the microphotograms with electron microscope Tesla 242 D.

The electron microscopic investigations were aided by researchers IMRE ZS. NAGY (Institute for Biological Research, Tihany) and ÁRPÁD PÁRDUCZ (Electron Microscopic Laboratory of the Biophysical Institute, Biological Research Centre, Szeged).

Letter clue to the electron microscopic photographs

P	—	perikaryon	Mac	—	accumulation of mitochondria
Cm	—	cell membrane	Cr	—	mitochondrial crest
D	—	desmosome	Ly	—	lysosome (functioning)
Zo	—	zonula occludens	Lpr	—	prelysosome porthposome
Md	—	interdigitating membrane	Lpo		(residual body)
Ip	—	intercellular angle	Gr	—	granule
N	—	cell nucleus	V	—	vesicle
Nm	—	nuclear membrane	Pv	—	pinocytotic vesicle
Er	—	granulated endoplasmatic	Dv	—	dense core vesicle
Nm		reticulum	Bm	—	basal membrane
R	—	ribosome	E	—	endothelial cell
G	—	Golgi apparatus	Mc	—	macrophage
Gt	—	Golgi tubule	Ci	—	cilium
Gv	—	Golgi vesicle	Rci	—	radix cilii
Va	—	vacuole	Pr	—	protrusion
M	—	mitochondrium	Prv	—	protrusive vacuole
Mm	—	mitochondrium membrane	Mvb	—	multivesicular body
Ma	—	mitochondrium matrix	Myc	—	myelin configuration

Results

In the course of our investigations there occurred some interesting structural peculiarities that characterized the pineal organ of the birds investigated particularly and that have not been discussed in this direction so far. These are as follows:

1. Formation of the pineal cell membranes, 2. intracellular cavity systems, vacuole, 3. Golgi apparatus of vacuolar type with vesicles resp. granules of various types and sizes, 4. several lysosomes in transformation, 5. content of the apical surface and of the adjacent cavity system, 6. structure of the pineal vasculature.

Membrane formations

In the pineal organ of the three bird species investigated, between the cells of much the same diameter and building the follicles in more layers, membrane fusions resp. thickenings of more types and of very different length were to be seen. It is peculiar that often in the same cell two or three kinds of cell membrane formations were manifested. It is obvious, too, that the

course of the normal unit membrane is strongly wavy. The wideness of the intercellular space often changes (75 Å–160 Å). At the angles of cells, there are often wide polyhedric intercellular angles (Ip) to be found. At that time, the unit membrane divides, the intercellular space may grow eight to ten times wider forming polyhedric shapes of various forms and length. From among the membrane formations the following forms are characteristic:

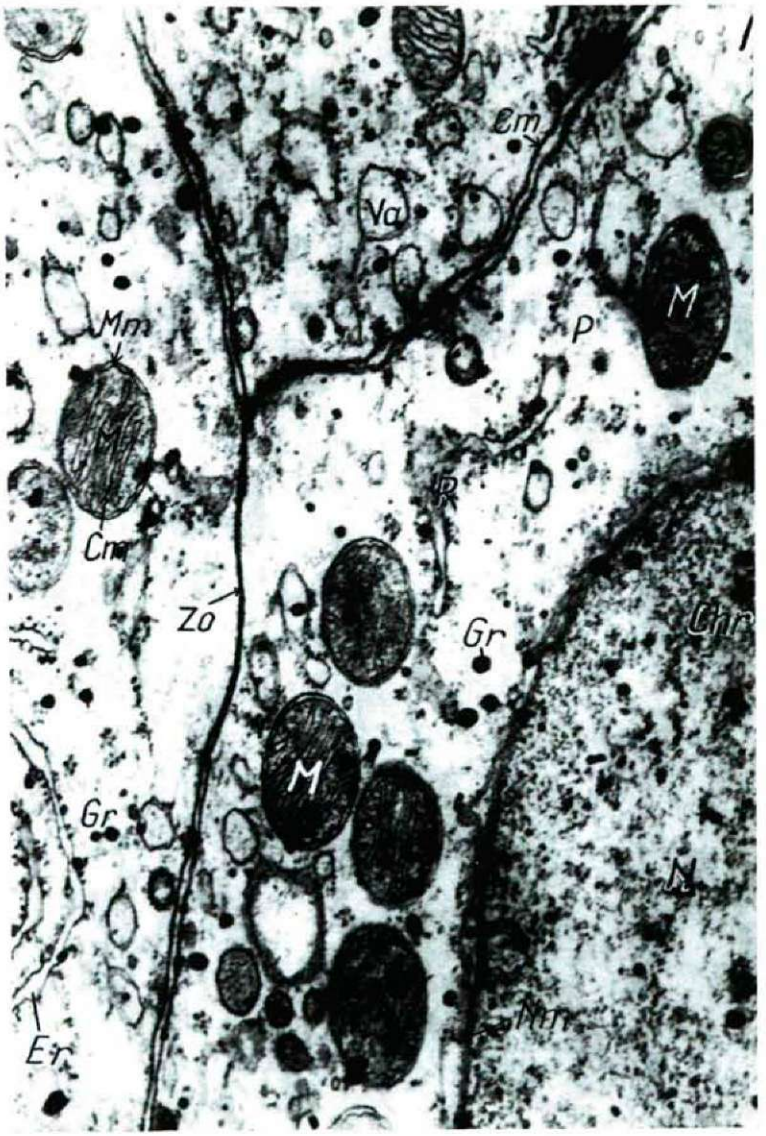

Fig. 1. *Meleagris gallopavo:* formation of the membrane between the pineal cells (zonula occludens). x 35.000

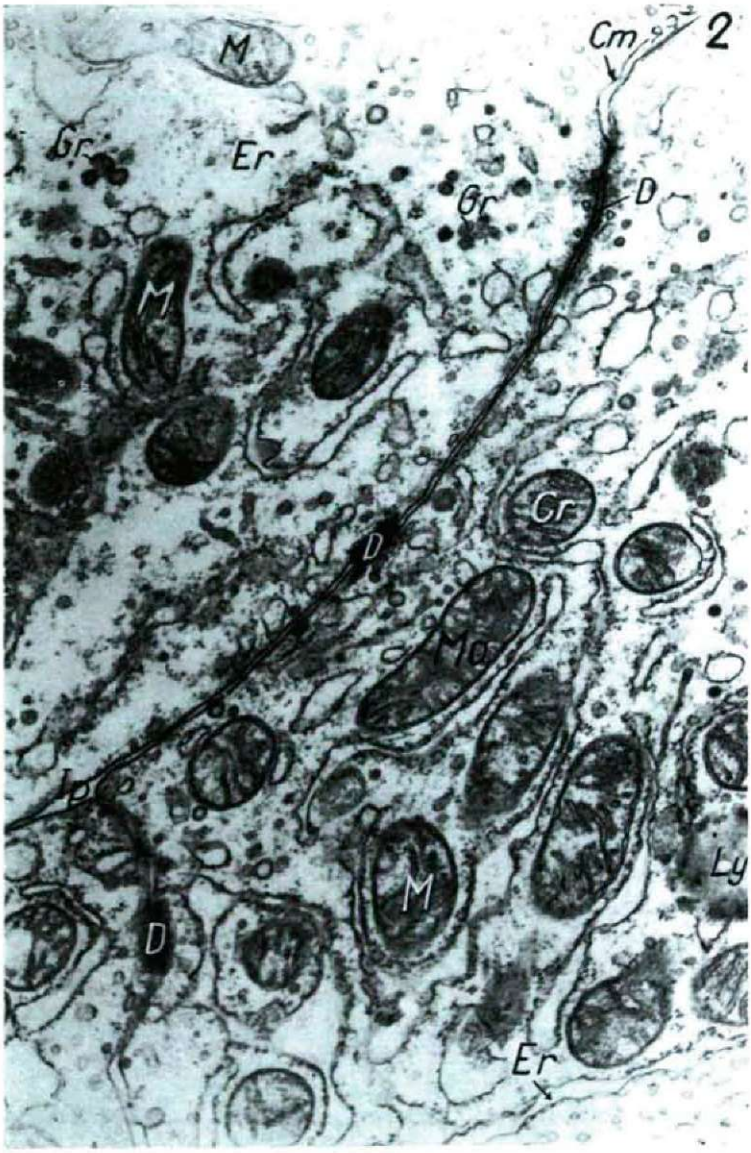

Fig. 2. *Meleagris gallopavo:* formation of the membrane between the pineal cells (desmosome). x 30.000

1. A full fusion (Fig. 1) manifested generally in a long part. At that time, the unit membranes of cells fuse into a thin, dark line (Zo). This change in membrane has every criterion of the notion of occludent zone or closing crest. A fusion like that occurs the most frequently in the lateral walls of the long-shaped cells surrounding the lumen. It never appears near the blood vessels.

2. Desmosomal connection (Fig. 2). It is the most general and obvious thickening of the pineal cells (D). It manifests itself generally in a short region (about 0.6 u). At the desmosomes of pineal cells the intercelluiar space is wide and clear (150 Å). The electron dense filaments (tonofilaments) that can be seen well from the cytoplasm join with the membrane. The length of filaments reaches 400–500 Å. In a longer course there can often be obseved some desmosomal sectors where the intercellular space is dark. The adhesive filaments are usually still longer, 600–800 Å. The following two membrane formations are characterized by this form of thickening.

3. Interdigitating membrane system (Fig. 3). It is entirely peculiar that between the parenchymal cells there were found also some interdigitating cell borders that are characteristic of the cells of myocardium. It is distinctly visible in the picture that the unit membrane has formed large-sized vesicles with strangulations. The vacuoles of various sizes found in the cytoplasm of the cell get into a close connection with these. The interdigitating membrane system is connected with desmosomes in a longer sector.

4. Tubulovesicular connection (Fig. 4). We have often observed this peculiar formation in the deeper layer of follicles, close to blood vessels, in the first line of angular pineal cells of about identic diameter and in many layers. In that place the cell membranes fused long and strongly divide at the angles of cells, forming the particular tubulovesicular system (Tv) seen in the picture. The tubular system may be produced by the digital protrusions of the contiguous cell membranes reaching one another. At the beginning we thought that the canals of the rough endoplasmatic reticulum of the adjacent cells were connected together in these places but that was not possible because the ribosome never appeared on the surface of canal. It becomes clear after investigating the connections that a formation of membrane is in question. This structure that is similar to the biliary capillaries is referring to an absorbing resp. evacuating function. A particular attention is also deserved by the long fused double membrane where the intercellular space completely disappears but from the cytoplasm a filament similar to that of the desmosomes is adhering to the membrane. This dark desmosomal connection extends almost over the entire limiting membrane, interrupted only at the tubulovesicular systems.

The close connection between the pineal cells can be found not only at the pineal cells of birds but also at those of mammals. They were noticed first by HOPSU and ARSTILA (1965) between the pinealocytes of the rat and published under the name somato-somatical synapsis. The authors mentioned above have not found any divergent forms. As according to the literary data there appear occludent zonules between the photoreceptor cells of the retina (DOWLING and BOYKOTT, 1967; DOWLING and GIBBONS, 1962; EAKIN, 1965; HOLMBERG, 1969; 1971) and desmosomal connection between the ependymal cells (BLOOM FAWCETT, 1970), the membrane mutations observed do not give us any argument for deciding the proper place of the avian pineal cells. At any rate, it is sure that the matter in question is a parenchymal tissue of a very close functional collaboration. This is a particularly close functional cennection in the vicinity of blood vessels. The complete fusions, as known well, are meaning

an almost perfect barrier for the macromolecular matters. It is probable that these close fusions extending over a large surface do play an important part among the lumen content and the materials of the blood vessels lying deeper.

Vacuolar cavity systems (Va)

In some of the avian pineal systems there appeared some major cavity systems (Fig. 5). Sometimes the cavity filled up the cell even to the half. These may be vesicles filled in with some fluid. As shown by the figure,

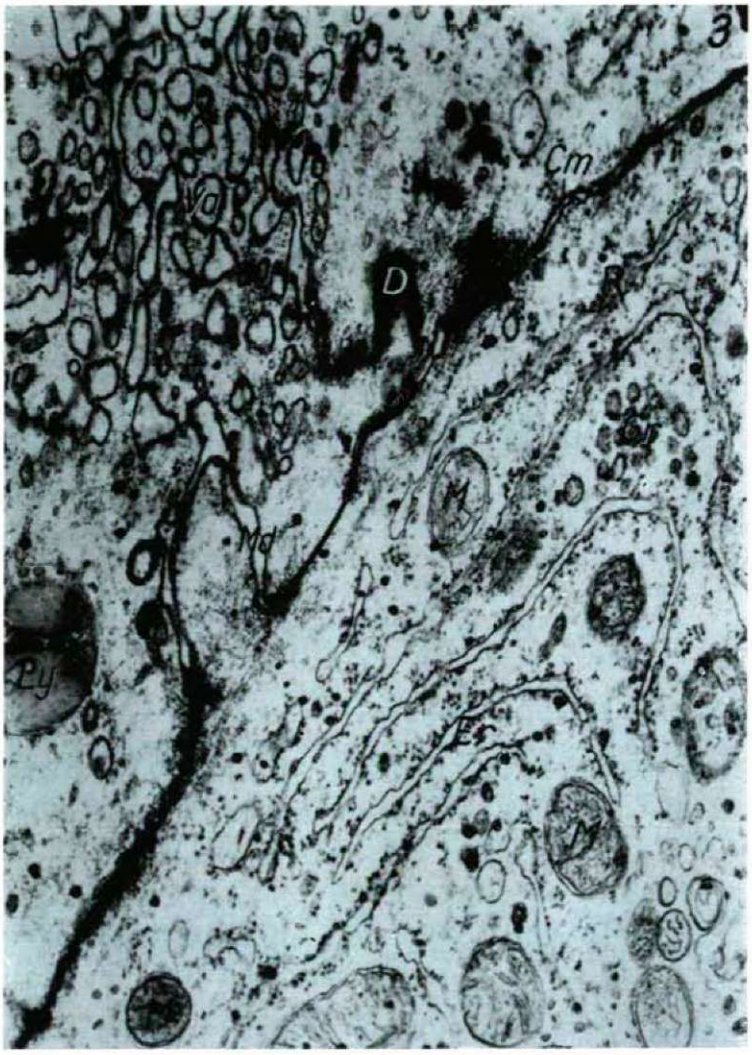

Fig. 3. *Columba domestica:* interdigitating membrane with detaching vesicles. x 35.000

the vacuole is lying in the immediate neighbourhood of the nucleus. These vacuoles of major size may be in connection with lesser vacuolar groupings multiplied in the cytoplasm everywhere but particularly round some major vacuoles and directed towards one another with their protrusions. To be sure, it is possible, as well, that these lesser cavities are the vesicles broken off the large cistern.

In the world of living, the vacuoles of fluid are mainly known in the vegetable cells. From the cells of the animal kingdom they are almost entirely

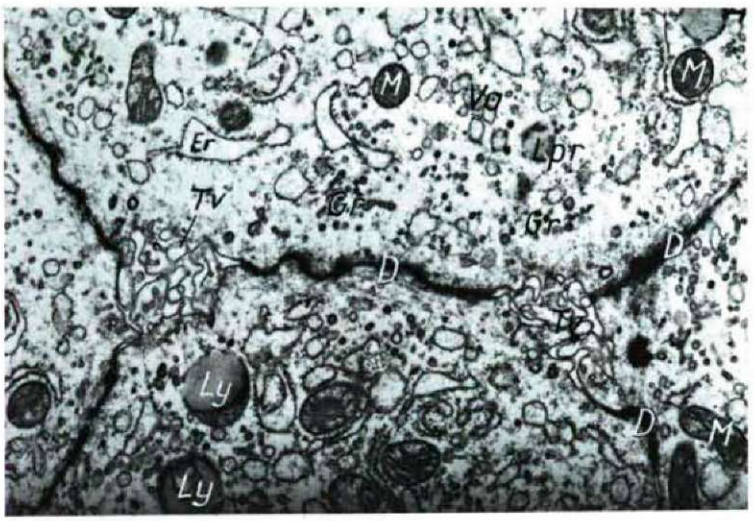

Fig. 4. *Columba domestica:* tubulo-vesicular connection between the pineal cells. x 17.600

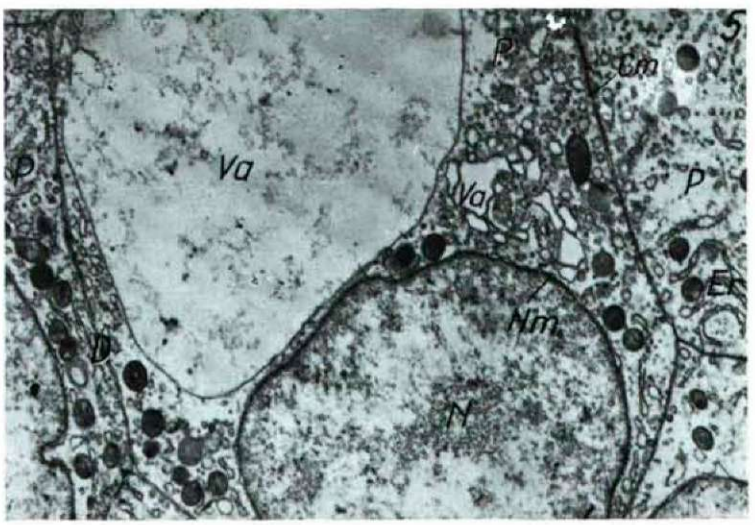

Fig. 5. *Columba domestica:* a large-sized vacuole in the pineal cell. x 17.600

absent. We find only according to the recent literary data some reference to, that there occurred some cavity systems similar to the above mentioned ones in the venticular area of brain, as well, in the ependymal cells containing water (VIGH–TEICHMANN and VIGH, 1969).

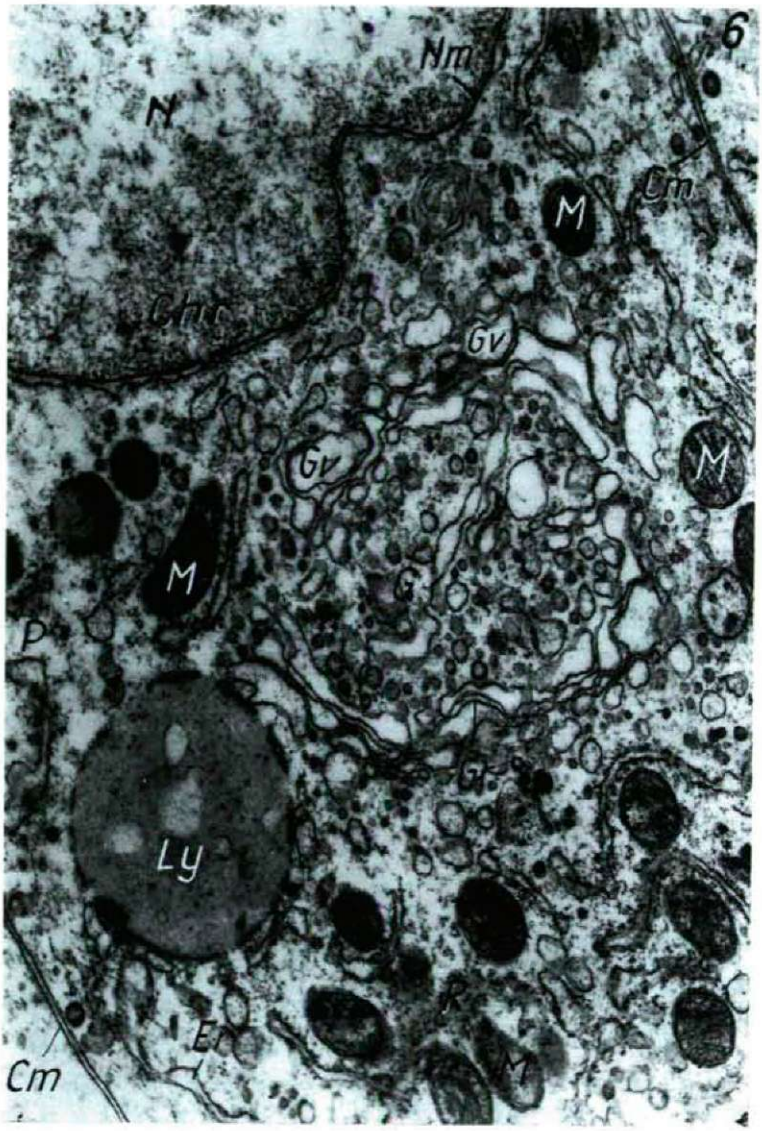

Fig. 6. *Columba domestica*: GOLGI apparatus of the pineal cell. x 22.000

Golgi apparatus (G)

The GOLGI apparatus is mostly present in the form of oblong, narrow vessels (Gv) and of small vesicles detached at their ends (Gv) in the cells. This form was never found in the perikaryon of the parenchymal cells of avain pineal body. Instead of these, a peculiar vacuolar type can be seen (Fig. 6). The Golgi apparatuses are very well developed in the pineal parenchymal cells. Apart from some flat canals at their edges – that perceptibly enter, anyway, the centre, too, – this apparatus is built by very large-sized vesicles of diameters 2500–3500 Å. In the by and large circular apparatus, rich in vacuoles of very various sizes, some vesicles and granules of different size and colour are to be seen. The dark granules are frequent. Among these there are many completely dark granules of about 250–300 Å. In addition to these, there appear also some larger and a little clearer granules of a size 450 Å in a large enough number. From among the dark granules, particularly those of smaller size appeared very frequently even in the cytoplasm scattered, mainly near the endoplasmic reticulum and along the cell membranes, as well. Rather rarely, there appeared vesicles of dense core type, too, sized in the average 800 Å. Besides the dark granules, also a great number of clear vesicles can be found in the Golgi apparatus. The diameter of these is 400–600 Å. They are, as a rule, round but there occur elliptical forms, too. From among the elliptical forms, those of larger size have diameters 850 Å in length and 400 Å in width. In the cytoplasm the clear vesicles are rare. In the vicinity of cell membranes (Cm) they appear usually as pinocytotic vesicle types and they are particularly frequent in the endothelial cells of the blood vessels. There occurred, even if scarcely, also some multivesicular bodies in the GOLGI apparatus, with diameters of 2500 Å. Similar forms were sometimes found in the cytoplasm, too, most of them having appeared in the content of the follicular lumen.

We had first thought the Golgi apparatus of vacuolar type to be some vesicle containing or storing fluid. It was decided only by its vicinity to the cell nucleus, its granulosity and permanent uniform appearance that the matter in question is the GOLGI apparatus. We have often observed lysosomes in the neighbourhood of the GOLGI apparatus and also the open, resp. vacuolarly dilated canals of the endoplasmic reticulum manifested themselves immediately beside the Golgi apparatus.

Lysosomes (Lv)

The lysosomes, these electron microscopic cell-organelles of heterogeneous appearance and function are probably permanent and large-size cell-organelles in the pineal cells of the species investigated. According to their appearance, they are vesicles surrounded by a unit membrane. They are interesting because of their alternating electron density and different size. We regard the lysosomes of the parenchymal cells of the bird as lysosomes rich in hydrolytic enzymes. We could follow even the most different transformed forms of lysosomes. In the cells investigated we have found a great number of forms, from the quite small organelles of 150 mμ till the lysosome of about 3 μ. We consider as prelysosome (Lpr) the small – mostly homogeneous – form (Fig. 7). There

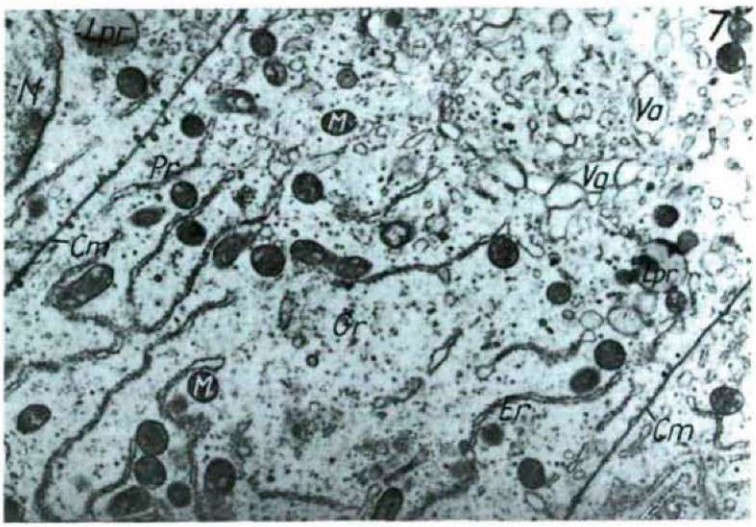

Fig. 7. *Anas domestica:* lysosome in the pineal cell (prelysosome). x 17.600

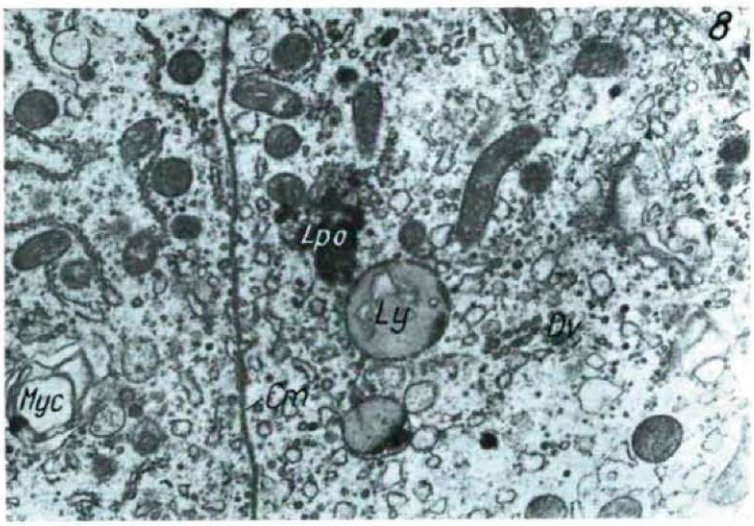

Fig. 8. *Meleagris gallopavo:* residual body in the pineal cell. x 17.600

develop from these the real or proper lysosomes of spotted structure, cap-like loaded with electron dense nodules at the edge or peak (Figs. 6, 8). The latter ones have appeared in the largest number in the pineal cells. They are striking in almost every picture (Ly). In their vicinity we could always observe a dilated, granulated endoplasmic reticulum and a great many pinocytotic vesicles. However in lower number, the residual bodies are nevertheless very conspicuous; as post-lysosomal forms (Lpo), they are probably storing the decomposition products of pineal cells (Fig. 8). In the body surrounded with a membrane, decomposing

dark granules are to be seen. The electron dense granules reminding of melanin or lipofuchsin granules are actually stuffing the matrix of lysosome. There has never appeared any autophagosome containing any cellular element (mitochondrium or granule). We have not observed, in a single case, either, that these residual forms would ever have been discharged by exocytosis throught the cell membrane.

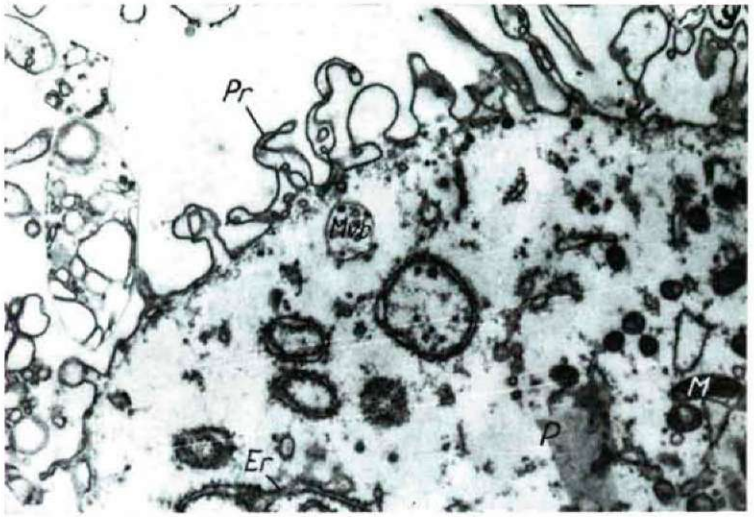

Fig. 9. *Columba domestica* (8-day old): luminal surface of the cell limiting the follicle. Protrusions. x 35.000

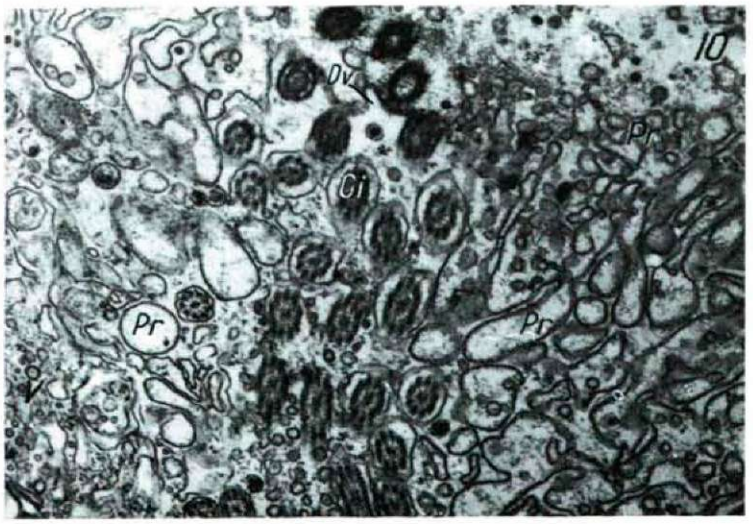

Fig. 10. *Columba domestica* (6-month old): surface of the follicle-limiting cell in cross-section. Cross-sections of protrusions and cilia. x 35.000

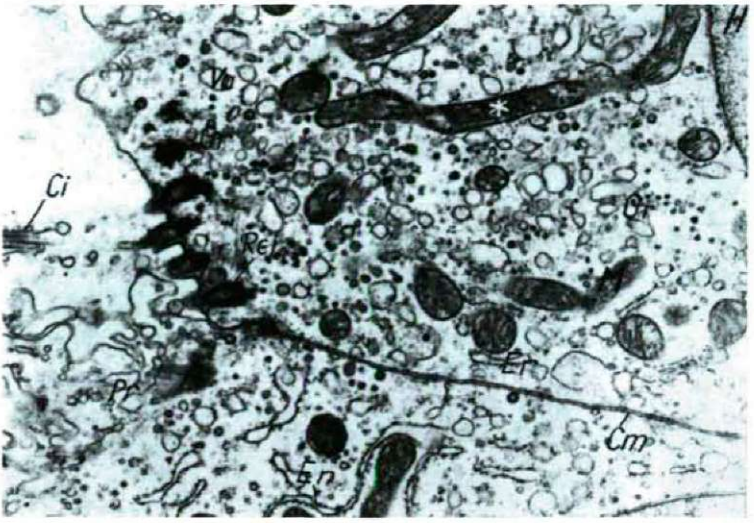

Fig. 11. *Meleagris gallopavo:* surface of the follicle-limiting cells. Radices of cilia. x 35.000 x 35.000

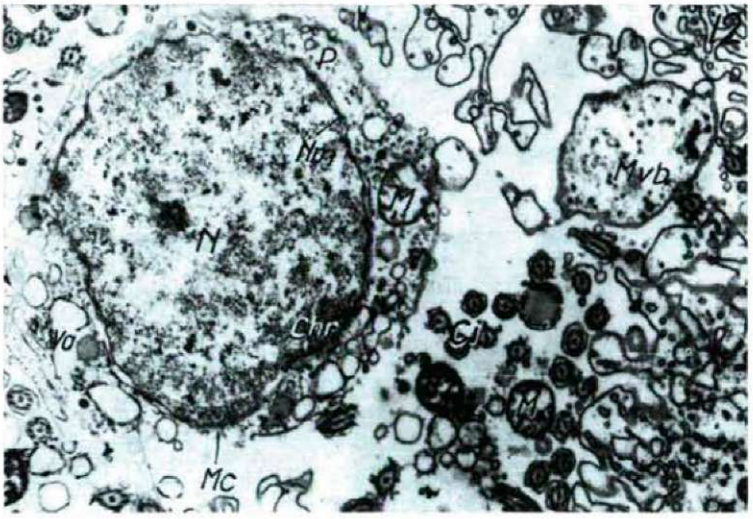

Fig. 12. *Columba domestica:* content of the pineal follicular lumen. Macrophage. x 17.600

Surface and lumen content of the pineal cells

The pineal bodies of all the three bird species investigated are of follicular structure. Protrusions and cilia are reaching down into the lumen of the follicle (Figs. 9 to 12). The protrusions are peculiar twisted formations, filled in with tiny clear vesicles. The matter in question is probably containing pinocytotic vesicles and the essential structural elements of the secernent function of the

pinael cells. We have observed that at the end of protrusions even larger vesicles and protruding pieces, as well, may be detached. The lumen is full of these detached pieces as well as of mitochondria devoted to destruction, of small-sized lysosomes and quite well multivesicular bodies. There often appeared laminated systems similar to myelinic configurations and some independent cells – probably some macrophages – as well (Fig. 12).

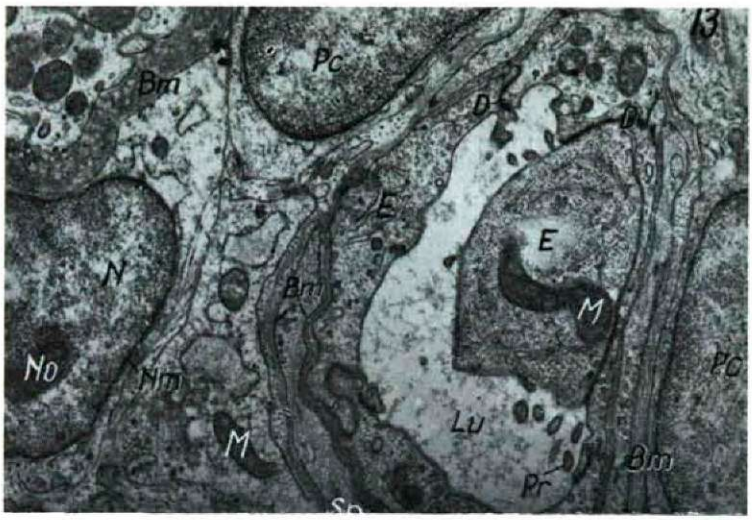

Fig. 13. *Columba domestica:* pineal capillary cross-section. Peculiarly developed basal membrane systems and perivascular spaces. x 17.600

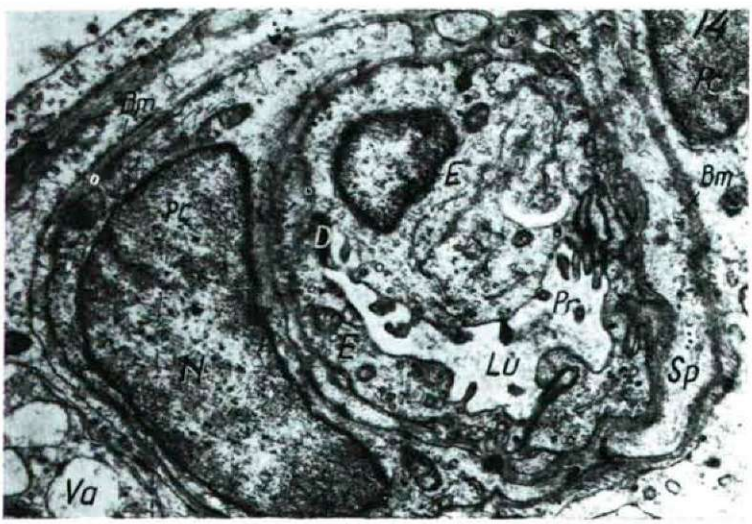

Fig. 14. *Anas domestica:* pineal capillary cross-section. Pinocytotic vesicles and protrusions. An endothelial cell protruding into the lumen. x 22.000

According to our observation, on the surface of the pineal cells, in quite young birds (eight-day old doves) there are only some protrusions (Fig. 9), the cilia appeared only later, after the sixth week (Fig. 10). They usually appear mixed on a cell surface. There are, however, some cell surface only with protrusions and others only with cilia. On this basis, in our opinion, there can ot be told any cells from another. We regard the cilia to have a typical 9 + 2 structure, adhering with conspicuously strong ciliary roots (Rci) to the surface of cell (Fig. 11). Generally a great many vesicles and granules and particularly elongated mitochondria take place in the cytoplasm close to the cell surface.

Blood supply of the pineal cells

The blood vessels between the pineal cells are showing electron microscopically a peculiar structural arrangement, most part of them being small arteries resp. capillaries and they are present, as a rule, only between angular parenchymal cells of equal diameters and of deeper site. The monostratal, long-shaped cells limiting the lumen haven't any independent capillary system more. A characteristic of the pineal small vessels is the obvious thick and dark basal membrane system (Figs. 16, 17). Round the cross-section of one or two blood vessels there are often to be seen double or triple basal membranes with considerable perivascular spaces. The nerve fibres that are of sympathetic origin have only appeared here.

The wall of capillaries is mostly constructed of quite thin endothelial cells attached to each other with desmosomes. The desmosomes between the endothelial cells are long, with thick electron dense filamens and a clear but narrow intercellular space. The cytoplasm of the endothelial cells does contain the general cellular elements and we have not found any difference as compared with the endothelial cells of other capillaries. The nucleus is markedly large and strongly granulated, being in most cases also indented. There are, to be sure, polygonal endothelial cells of larger size, too, reaching into the vascular lumen. It may be supposed about these cells that they play the part of valve in the regulation of blood flow. It is possible that these are characteristic only of the venous capillaries. Apart from the basal membrane system, also the rich protrusive system is a peculiarity of the pineal endothelial cells. From the surface of endothelial cells a great many protrusions reach into the lumen, respectively some empty vacuoles of different sizes may be seen as detached from the protrusions and forming groups either in the lumen or in the perivascular space. Seeing these formations, we think with reason on a particular secretory function of merocrine character.

The large number of pericytes beside the capillaries is remarkable, as well. There may be distinguished two types of these pericytes. At one of the types, the strongly indented cellular nucleus is dark, granulated, the nuclear membrane is smooth and there are to be seen never any nuclear pores. The perikaryon is very narrow, creating many protrusions. At the other type of pericytes a long-shaped nucleus can be seen, with a permanently smooth surface. At these, the cytoplasmic cell part is much larger and wider and they have fewer cellular protrusions. It may be supposed that the two types of cells play two kinds of functions. It is probable that the first one takes a prominent part in contraction and the second one in support.

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