LARS BLOM

RIDGE PATTERN AND SURFACE ULTRASTRUCTURE OF THE OVIDUCAL MUCOSA OF THE HEN (*GALLUS DOMESTICUS*)

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Synopsis

The ridge pattern and the ultrastructure of the mucosal surface in oviducts from three hens (*Gallus domesticus*) in different stages of the egg laying cycle were studied by scanning electron microscopy.

The ridge patterns showed well-defined differences between the five oviducal segments. The topographical relationship between the ciliated and non-ciliated cells was demonstrated. The appearance of the two kinds of epithelial cells was different in the five segments, as regards the length of the cilia, the size and the shape of the hemispheres formed by the luminal part of the mucus secreting cells, and the microvilli covering these hemispheres. No cyclic variations were found in the appearance of the mucosa of the same oviducal segment in connection with the position of an egg in the oviduct. However, evidence of a strictly local discharge of mucus from randomly dispersed areas was found in the magnum segment. Several longitudinal rows of cytoplasmic villus-like sprouts were observed on the lateral epithelial cell wall in the magnum, the isthmus and the uterus.

A pattern of metachronal waves of the coordinated ciliary action was found in the magnum, the isthmus and the uterus. Their function is to distribute the secretory material and to clean the mucosa.

Gland openings all over the surface of the folds were seen in the magnum, the isthmus and the uterus segment. Generally they were funnel-shaped, but in the pouch-like portion of the uterus segment their appearance varied. On cross section of the glands from the magnum and the isthmus, the secretory granules were observed in cavities of cytoplasm. There was no evidence of intergranular connection.

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Introduction

In time past several morphological studies of the avian oviduct have been reported, including light microscopy (LM) and transmission electron microscopy (TEM). Up to now, studies using scanning electron microscopy (SEM) have been comparatively few.

Based on macroscopical, histological and histochemical differences, the oviduct is divided into five segments, with the following now generally accepted names and functions:—

Infundibulum: Engulfs the ovulated ovum, and here fertilization takes place in the funnel-shaped part. Possible participation in the formation of the outer layer of the perivitelline membrane and/or the chalazae in the tubular posterior part (the so-called chalaziferous region).

Magnum: Produces the greater part of the egg-white proteins.

Isthmus: Produces the shell membranes and possibly participates in the egg-white production.

Uterus: Secretes the so-called "plumping fluid" in the anterior tubular part, which dilutes the albumen, distends the shell membranes, and gives the egg its shape. Forms the shell substances, the pigment in the coloured shells, and the shell cuticula in the pouch-like posterior portion.

Vagina: Reservoir for spermatozoa following copulation.

The transitions from one segment to another are gradual (with two exceptions), and mixed epithelia and glands are found in these border areas (Johnston et al., 1963, Schwarz, 1969, Wyburn et al., 1970). The exceptions are the border between the magnum and the isthmus seen macroscopically as a distinct white line (Schwarz, 1969) and the utero-vaginal junction, which is marked by a narrow groove called *Recessus uteri* (Aitken, 1971).

The mucous membrane consists of alternating ciliated and non-ciliated cells throughout the whole oviduct, except for the funnel-shaped part of the infundibulum. Here the foldings are covered by tall columnar ciliated cells, which are replaced by cubic non-ciliated secretory cells in the grooves between the foldings, the so-called "glandular grooves" (Surface, 1912).

Beneath the surface epithelium, glands are found in the lamina propria, except in the anterior part of the infundibulum, the distinct border between the magnum and

the isthmus and in the vagina. In the vagina, glands are found only in a narrow region on the vaginal side of the utero-vaginal junction, so-called utero-vaginal glands where sperms are located following copulation (Bobr et al., 1964). The gland openings are found all over the mucosal folds in the magnum, the isthmus and the uterus (Richardson, 1935, Johnston et al., 1963, Schwartz, 1969, Fertuck & Newstead, 1970, Wyburn et al., 1970, Makita & Sandborn, 1971, Aitken, 1971). The glands have no real ducts in the sense of non-secreting epithelium lined tubes; the glandular epithelium is continuous with the covering epithelium (Schwartz, 1969, Wyburn et al., 1970, Makita & Sandborn, 1971). However, an intermediate zone ("zone de transitions") between the gland cells and the surface epithelium, consisting of cells changing progressively from the serous gland cell type to the mucous epithelium cell type, have been described in the magnum segment by Ulrich & Sandoz (1972).

The gland cells in the magnum and the isthmus are more or less filled with granules, according to the stage in the egg laying cycle, and the secretion is merocrine (Schwarz, 1969, Fertuck & Newstead, 1970, Wyburn et al., 1970, Sandoz et al., 1971). The intracellular structures in these glands have been studied by SEM (Makita & Sandborn, 1970), and have been seen as an interconnected branching network of cytoplasm covering circular profiles. In another SEM study, those authors demonstrated other intracellular components, such as the nuclei in the lining epithelium and the gland cells in the isthmus segment (Makita & Sandborn, 1971).

These few SEM studies of the avian oviduct have not shown any topographical relationship between the different components in the oviducal mucous membrane. SEM has a great advantage for this special purpose because it permits examination of large areas of tissue under different magnifications ranging from approximately 20× and up to the ultrastructural level. The present study was initiated in order to demonstrate the normal components in the oviducal mucosa of the domestic hen and some of their cyclic changes known from LM and TEM studies.

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Material and Methods

Eight active egg-laying hens of White Leghorn breed aged 6–18 months were used in a normal anatomical investigation of the genital organs by means of LM and TEM. Three oviducts at different stages of the egg production cycle were chosen for the SEM studies (I: egg in the magnum, II: egg in the uterus, III: no egg in the oviduct).

Anaesthesia was induced by ether using open mask and continued by Fluothane® (I.C.I.) through an endotracheal catheter. The oxygen flow rate was one litre per minute.

Aldehyde perfusion fixation was performed as described by KJAERHEIM (1969), with 0.9 per cent NaCl solution containing 6 per cent dextran as prerinse fluid (total 500 ml) and 1.7 per cent glutaraldehyde in 0.1 M phosphate buffer at pH 7.3 as fixation fluid (total 3000 ml). The flow rate was 300 ml perfusion fluid per minute. After cessation of the perfusion fixation, the oviducts were excised and samples measuring about 1×1 cm were taken of the five segments from representative areas (see pl. 1, fig. 1). Ribbons 1 mm in width were cut off these samples round the edge of the epithelium. Furthermore, these ribbons were cut up into small pieces measuring about 1 mm^3 for TEM studies. The remaining parts of the samples (each about 1×1 cm) were used for the SEM studies.

Additional fixation of the SEM samples was performed by immersion in 10 per cent glutaraldehyde in 0.1 M phosphate buffer at pH 7.3 for 24 hours, rinsing overnight in 0.1 M phosphate buffer, and postfixation in 2 per cent osmium tetroxide in 0.1 M phosphate buffer containing 4 per cent sucrose for 24 hours at room temperature (NØRREVANG & WINGSTRAND, 1970, ad modum HANSEN, 1972). Finally washing in 0.1 M phosphate buffer containing 4 per cent sucrose was carried out for 24 hours at 4°C.

Dehydration was made through ascending grades of ethanol with final transfer to benzene (NØRREVANG & WINGSTRAND, 1970). The specimens were then freeze-dried at −30°C and coated in a vacuum evaporator, the majority with gold only and the remainder with carbon followed by gold (the conducting layer was estimated to be about 50–70 nm thick).

The specimens were examined in a Cambridge Stereoscan Mk II a SEM with an accelerating voltage between 10 and 30 kV.

The tissues used for TEM studies were post-fixed as described by KJAERHEIM, 1969, dehydrated through ascending grades of ethanol, cleared in propylene oxide, and embedded in TAAB embedding resin (TAAB Laboratories, Reading).

For LM, survey sections of one μm were cut from the blocks, stained with 1 per cent Toluidine blue in 1 per cent sodium borate solution and mounted on glass slides.

Ultrathin sections were double-stained with 5 per cent uranyl acetate at 37°C for 30–60 minutes followed by lead citrate (REYNOLDS, 1963) at room temperature for 1–10 minutes.

The sections were examined in a Siemens Elmiskop 101 TEM at 60 or 80 kV.

Observations

General Description of the Oviducal Mucosa

Plates 1–3

The left oviduct (the only one which functions in the hen) is a convoluted and highly distensible tube approximately 50–70 cm long in active egg-laying, suspended in a fold of peritoneum from the dorsal abdominal wall.

Throughout its whole length the oviducal mucosa is heaped up into slightly twisted folds varying in size and number in a manner characteristic for each of the oviducal sections (pl. 1, figs. 1 a & b).

These mucosal folds start in the funnel-shaped part of the infundibulum, where they are low, simple, slightly winding and interrupted by shallow grooves (pl. 1, fig. 2). It is difficult to examine the folds macroscopically, because the wall in this part of the oviduct is almost transparent and only the blood vessels are visible on pl. 1, fig. 1 a.

The ridges become more prominent and continuous in the narrow tubular posterior part of the infundibulum. Many secondary folds separated by deep clefts can be seen from the top and sides of the major ridges (pl. 1, figs. 3–4). The primary folds divide and fuse, thus making the overall picture an irregular pattern of ridges.

The border between the infundibulum and the magnum is not distinct, but can be recognized macroscopically in the area where the diameter of the oviduct increases and the ridge pattern becomes particularly prominent, with the ridges almost filling up the total lumen. The major simple ridges in the magnum are slightly twisted (approx. one and a half times around the oviduct throughout the magnum segment) and can be followed for a long distance without interruption. Subfoldings are very rare (pl. 1, fig. 1 a, pl. 2, figs. 1–2). The colour is greyish-white, because the lamina propria is entirely filled with glands, in contrast to the brown colour of the infundibulum where glands occur only in the last centimeter.

The junction between the magnum and the isthmus is sharply marked by a white ring (about 0.5 mm wide) where there are no glands in the lamina propria. In this junctional zone, the oviduct becomes constricted and the folds disappear for a short distance (exceptionally long on pl. 1, fig. 1 a). Just behind the border, the ridges again increase in the isthmus segment and become slender, with larger spaces between the single folds than in the magnum. The surface of the folds at the beginning of this segment is smooth but soon becomes more complex, with subfoldings in the posterior portion (pl. 2, figs. 3–4).

The tubular part of the uterus can be distinguished from the isthmus by a change in the colour of the mucosa from greyish-white to yellow-brown. The ridges become high and narrow with numerous deep incisions (pl. 1, fig. 1 a). In the subsequent pouch-like and enlarged posterior part of the uterus, the major longitudinal ridges are cut by deep transverse clefts which give the mucosa an overall pattern of small

folds resembling leaves or tongues (pl. 3, figs. 1–2). The few (5 or 6 in number) rough transverse folds in this pouch (pl. 1, fig. 1 a) are due to the involvement of the tunica muscularis in their formation.

The low winding ridges in the *Recessus uteri* continue in the regular longitudinal folds of the vagina, which have subfoldings lying parallel to the major folds (pl. 3, figs. 3–4).

Detailed Description of the Individual Oviducal Segments

Infundibulum

Plates 4–5

The epithelium of the funnel-shaped part consists of tall columnar ciliated cells covering the summits and the sides of the low ridges. In the shallow grooves between the ridges there are cubic non-ciliated glandular groove cells. Occasionally these cells are also found on the top and sides of the ridges. Pl. 4, fig. 1 shows these glandular groove cells, which are stained strongly with Toluidine blue in contrast to the ciliated cells. The TEM picture (pl. 4, fig. 2) shows their few small electron dense granules, which never cause the luminal surface to bulge into the lumen.

The SEM picture (pl. 4, fig. 3) shows the surface of the ridges covered with cilia, and in the glandular groove a uniform dense layer of short microvilli can be seen. There is no bulging of the luminal surface of the cells as a result of accumulation of secretion, and therefore the cell borders in the glandular groove are difficult to observe (pl. 4, fig. 3).

In the posterior and tubular part of the infundibulum the epithelium changes appearance and at the same time the mucosal folds become more bulky. A single layer of tall columnar ciliated cells can be seen alternating with mucus secreting cells all over the primary and secondary ridges (pl. 5, fig. 1). The clefts between the ridges gradually become deeper, and from the bottom of these clefts the tubular glands are developed in the last centimeter of the infundibulum.

The tall columnar mucous cells contain membrane-bounded electron dense granules which accumulate in the apical part of the cell. Consequently, this part of the cell is distended and bulges into the lumen and forms a hemisphere, and the microvilli covering these hemispheres become correspondingly shorter and more widely spaced. When large hemispheres are seen, the microvilli are only visible in the clefts between the hemispheres (pl. 5, fig. 1).

Pl. 5, fig. 2, shows a part of a major fold divided by irregular clefts between the secondary foldings. The surface is uniformly covered by ciliated cells in the form of tufts of cilia alternating with mucous cells.

On higher magnification, the mucous blebs can be seen clearly covered with a few short microvilli. The cell borders are seen as clefts between the rounded prominences (pl. 5, fig. 3). No pattern of coordinated movements of the cilia (so-called metachronies) is seen in this segment of the oviduct.

Magnum

Plates 6–7

The tunica mucosa of the magnum consists of alternating ciliated and non-ciliated tall columnar cells. The non-ciliated cells secrete mucus and are filled with granules containing a filamentous material which occupies the entire supranuclear portion of the cells, where they fuse (pl. 6, fig. 1). Dependent on the size of the hemispheres, the cell surface is covered by microvilli which are fewer and shorter than those on the ciliated cells. As a possible result of the pressure from the mucous cells, the ciliated cells are tall and slender with an expanded apex carrying the cilia and microvilli.

Throughout the whole oviduct the lateral epithelial cell membranes (i.e. those in direct contact with the adjoining epithelial cells) can be seen interdigitating with each other (pl. 6, fig. 2a) from just beneath the junctional complex to the basal lamina. In the magnum and the next segments of the oviduct (the isthmus and the uterus), the intercellular spaces between the epithelial cells are sometimes wide, and here villus-like cytoplasmic sprouts on the lateral cell wall can be seen stretching out into the intercellular space (pl. 6, fig. 2b).

In artificial disruptions of the magnum epithelium, these cytoplasmic sprouts can be seen clearly on the SEM picture on the lateral epithelial cell wall in longitudinal rows (approx. 5–8 rows per cell) from cell base to cell apex (pl. 6, fig. 2c).

Cyclic variations in the appearance of the mucus secreting cells, dependent on the position of the egg, were difficult to observe because of the random discharge of mucus in the magnum segment also known from previous TEM studies. In this study, no difference could be seen in the appearance of the magnum mucosa in the oviducts with an egg in the magnum (before passage) and with an egg in the uterus (after passage). However, it was possible to observe randomly dispersed areas on both mucosae where the hemispheres of the mucus secreting cells were low and densely covered with microvilli (pl. 6, fig. 3) among areas where the mucous blebs were considerably better developed and had a smooth surface without any microvilli (pl. 6, fig. 4).

The branched tubular glands which determine the thickness of the ridges open into the oviducal lumen all over the surface of the folds. These glands have no real ducts, but the secreting cells are continuous with the surface epithelium (pl. 7, fig. 1) with a "zone de transition" in between. The gland openings could only be observed by SEM in areas where the surrounding cells were of the non-ciliated type (pl. 7, fig. 2). The openings are all funnel-shaped, differ in size, and are lined with microvilli as far down as they can be observed. In most of the cases, there were a few granules with a diameter of approx. 2 μm in immediate contact with the openings.

On cross section of these glands, it is possible by SEM to observe the intracellular secretory granules (diameter 1–2 μm) placed in cavities surrounded by a fixed mass of cytoplasm (Type A gland cells described by Wyburn et al., 1970). Pl. 7, fig. 3a shows the basal part of a gland, and there seems to be connection between the cavities

in the form of holes surrounded by a thickened edge in several walls of the cavities (indicated by arrows). A TEM picture of the membrane-bounded and tightly packed secretory granules in the gland cells is shown on pl. 7, fig. 3b.

Isthmus

Plates 8–9

The lining columnar epithelium is composed of alternating ciliated and non-ciliated cells. The latter are filled with electron dense granules without any tendency to fuse (pl. 8, fig. 1), in contrast to the granules in the mucous cells of the magnum. The luminal surface of the cells is only slightly vaulted and is covered with a few long, slender microvilli. Small electron-dense granules are also found in the ciliated cells, although these are few in number. Between the cilia there are numerous slender microvilli.

The cilia are longer than in the previous segments (approx. 15μm) and for this reason the appearance of the surface is completely dominated by cilia (pl. 8, fig. 2; pl. 9, fig. 2). Only with high magnification is it possible to observe the secretory cells between the ciliated ones (pl. 8, fig. 3).

In both the isthmus and the magnum and uterus, metachronies can be seen forming slight curved lines representing the top of a ciliary wave. The length of the wave is not constant but varies between 10 and 20 μm. In places where two such metachronies with different directions meet, a "honeycomb" pattern of interference is formed, composed of tips of cilia connected with each other (pl. 8, fig. 2; pl. 9, fig. 2).

As in the magnum, the isthmic glands open all over the surface of the folds, where the gland cells are directly connected with the covering epithelial cells (pl. 9, fig. 1). On account of the dense layer of cilia in this segment, it is very difficult to get a clear picture of these openings by means of SEM. In this study they have only been observed as shallow depressions in the surface of the mucosa sometimes filled with clusters of secretion granules (granulum diameter approx. one μm) (pl. 9, fig. 2).

Pl. 9, fig. 3, shows a cross section of an isthmic gland. The different size of the granules can be seen, the smaller ones appearing centrally beneath the luminal surface of the gland cells. The gland lumen is lined with long and slender microvilli, which can also be seen by TEM.

Uterus

Plates 10–11

The uterine epithelium is pseudostratified and consists of alternating ciliated and non-ciliated cells with the nuclei of the epithelial cells arranged in two zones (pl. 10, fig. 1). The cells with an apically placed nucleus have cilia interspersed with long, slender microvilli. These ciliated cells always contain a few electron-dense granules. The appearance of the cells with basally placed nuclei is different in the tubular and

pouch-like parts of the uterus. In the former, they often contain large secretory masses which cause the cell surface to bulge into the lumen. This is never seen in the pouch-like portion, where the surface is generally densely covered with microvilli (pl. 10, fig. 1). For that reason, the ultrastructure of the mucosal surface in the pouch-like portion is characterized by a uniform dense layer of microvilli without any visible borders between the cells and here and there tufts of cilia (pl. 10, fig. 2).

The tubular uterine glands are more branched than elsewhere in the oviduct. Their openings are found all over the surface of the ridges and their appearance varies. On the SEM picture, some of them are funnel-shaped (pl. 11, fig. 2), while others form distinct holes in the mucosa (pl. 11, fig. 4) with the surrounding cells all at the same level or even elevated as compared with the mucosal surface. The different shapes of the openings are confirmed by the LM findings (pl. 11, figs. 1 and 3). Both types of gland openings are narrow tubes stretching down through the epithelium, limited by specially arranged epithelial cells, and only their width on the mucosal surface is different.

Vagina

Plate 12

The vaginal epithelium is pseudostratified and has the greatest height in the oviduct. It is mainly composed of tall columnar ciliated cells with apical nuclei. In between, there are mucous cells with basally placed nuclei, mostly in the posterior part of the vagina (pl. 12, fig. 1). The latter contain membrane-bounded secretory granules which are characteristic in having an electron-dense core surrounded by a light zone. These secretory cells have a very small apex which does not bulge into the lumen. Although they can be found all over the mucosal folds by means of LM and TEM, it is impossible to demonstrate them by even high magnification by SEM because the cilia cover the whole epithelium (pl. 12, figs. 2–3).

Metachronies have not been observed in this segment, but the cilia at the top of the parallelly arranged secondary folds appear to have been moving very uniformly in the same direction (pl. 12, fig. 2).

Discussion

The generally accepted division of the avian oviduct into five different segments was also observed in the present SEM study, on the basis of the ridge pattern, which shows well defined differences between the five segments. These five different ridge patterns can be correlated with the different functions in the five sections. The folds increase the secretory surface, especially when the primary folds are provided with a large number of subfoldings or secondary ridges, as in the tubular part of the infundibulum, in the isthmus, in the tubular part of the uterus and in the vagina. These four parts have the smallest diameter of the oviduct, and the strongly folded mucous membrane also provides the possibility of expanding, this is particularly necessary in the vagina where the egg is hard-shelled. The slightly twisted voluminous folds in the magnum will force the egg to rotate slowly while it passes through the magnum. This gentle rotation twists the mucin fibres in the albumen together to form the chalazae (Scott & Huang, 1941). The folds of the pouch-like part of the uterus provide this section with the strength needed to expel the egg, because the tunica muscularis is located in the large cross folding (Schwarz, 1969). The small tongue-like secondary foldings give an intimate contact surface to a passing egg, even though the large cross foldings are so massive that they are only slightly compressed while the egg is in that part of the oviduct.

The typical appearance of the surface of the oviducal mucosa found in this SEM study is dominated by cilia from the ciliated cells, and only by high magnification is it possible to observe the apical surface of the mucus secreting cells between the tufts of cilia. However, scattered areas dominated by or consisting of mucous cells are observed on the mucosa at all levels of the folds, except for the funnel-shaped part of the infundibulum and the vagina, where the foldings are lined with a dense layer of cilia.

The marked differences in the appearance of the two kinds of epithelial cells from the five oviducal segments observed by LM and TEM have been observed in this SEM study only to a minor degree. Here the cilia show differences in length, and both the mucous hemispheres and the microvilli covering them show variations in size and shape. The long complex cytoplasmic processes between the microvilli described by Aitken & Johnston (1963) were not observed in this study.

In TEM studies, cyclic variations in the size of the mucous hemispheres, especially in the tubular part of the infundibulum and the magnum, have been described as being only weak. The mucous cells are never completely discharged and are restored rapidly (Aitken & Johnston, 1963, Schwarz, 1969, Wyburn et al., 1970, Fertuck & Newstead, 1970, Sandoz et al., 1971). In this study, there were no differences in the appearance of the same segment in the two oviducts before and after passage of an egg. The appearance of the hemispheres and the relationship between the number

of the two kinds of epithelial cells were constant. A possible transformation of the ciliated cells to non-ciliated cells or vice versa, observed by RICHARDSON (1935), was not observed. However, in the magnum it was possible on the same tissue block to find randomly dispersed areas where the hemispheres were low and densely beset with microvilli while the surrounding mucosa showed the highly developed hemispheres generally found in this section. This suggests a total discharge of mucus in small isolated areas.

For obvious reasons, the variations in width of the intercellular space reported from TEM studies (SCHWARZ, 1969, WYBURN et al., 1970) were not found in this SEM study. However, it was possible to show villus-like cytoplasmic sprouts (called microvilli by WYBURN et al., 1970) on the lateral epithelial cell walls between disrupted cells, probably as a result of the freeze-drying. The lateral cell walls were so well preserved that these cytoplasmic sprouts could be seen clearly. On the SEM pictures, the sprouts are arranged mainly in longitudinal rows from the base to the apex of the epithelial cells, with only very few sprouts present on the lateral epithelial cell walls between these rows. According to DIAMOND (1971), these features are ubiquitous of fluid transporting epithelia, and this is in agreement with the observations of WYBURN et al. (1970), who found evidence of a movement of extracellular fluid into the lumen of the magnum.

The freeze-drying method preserved the metachronal waves of the ciliary action, previously described by ECHLIN (1971), who used the far more complicated critical point drying method. Metachronies are seen in many different ciliated epithelia (HANSEN, 1972) and in the oviduct they are found in the magnum, the isthmus and the uterus segments, where the cilia are long (approx. 10–15 μm) and the ciliated cells are placed in a regular pattern. The metachronies are considered to have a function in distributing the secretory material and in cleaning the mucosa, rather than participating in the movement of the egg. No metachronies were found in the funnel-shaped part of the infundibulum and in the vagina, i.e. the two segments which participate least in the formation of secretion. Here the foldings have a dense layer of cilia (approx. 10 μm), all of which appear to move in the same direction, and all cilia seem to be in the same phase. In the tubular part of the infundibulum the cilia are shorter (approx. 6–8 μm) and the ciliated cells more dispersed. Here the cilia show a pattern of individual movements.

Gland openings all over the mucosal folds were observed clearly in this SEM study in the magnum and the uterus, while they were hidden by the cilia all over the isthmic mucosa and only indicated by grooves in the epithelium filled with clusters of secretion material. Both in the magnum and the uterus funnel-shaped openings were observed in places where the surrounding cells mainly consisted of the secretory type. In the pouch-like portion of the uterus, there were variations in the appearance of the gland openings. In addition to the funnel-shaped openings, some openings were observed as distinct holes in the mucosa surrounded by cells all at the same level or even elevated in contrast to the funnel-shaped form. The LM pictures show that the varia-

tions only concern the width of the gland openings at the mucosal surface, while the glands beneath are alike.

Generally, the mucosa was surprisingly clean and only in a few areas, especially in the magnum segment, the structure of the surface was obscured by fixed secretory material. This absence of mucus could be a result of rinsing in sucrose after post-fixation, while this should have a softening and loosening effect on mucosubstances covering the mucosal surface according to Landboe-Christensen & Parapat (1972). However, material of supposed proteinaceous origin was found at several places on the mucosal surface, especially in the magnum and the isthmus, where it took the form of granular structures. As a rule, the granules were found near the gland openings and were of the same size as the granules observed on cross sections of the glands from the same oviducal section.

As mentioned in the introduction, the intracellular structures observed on the cross section seen on pl. 7, fig. 3a have been described previously by Makita & Sandborn, 1970, assuming intergranular connections in the form of cytoplasmic bridges covering branching granules. This feature was not confirmed in the present study. In their SEM study, those writers used other fixatives and especially another drying method, i.e. vacuum drying. This is obviously responsible for the quite different appearacce of these structures in their study as compared with the results of the present study. It is improbable that the granules seen on pl. 7, fig. 3a, could exist without being enclosed by a membrane, and the holes in the walls of the cavities on pl. 7, fig. 3a, are therefore interpreted not as intergranular connections, but as fixation artifacts. Because the secretory granules are packed so tightly that very little of the cytoplasmic matrix remains between the membrane-bounded secretory granules where they meet (pl. 7, fig. 3b), the fixation of the cytoplasm gave the appearance shown on pl. 7, fig. 3a.

The granules found near the openings of the glands might be a result of an artificial disruption of some of the gland cells and a liberation of membrane-bounded granules through the gland openings.

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PLATES

PLATE 1.

Fig. 1a: Oviduct from a hen in active egg laying. The places where the tissue blocks for SEM were taken are indicated by crosses (approx. $^1/_4$ of actual size).

Fig. 1b: Schematic drawing of fig. 1a, showing the five different segments of the oviduct.

infundibulum, magnum, isthmus, uterus, vagina.

Fig. 2 From the funnel-shaped part of the infundibulum. Low slightly winding folds interrupted by shallow glandular grooves. SEM. 90×

Fig. 3: From the tubular part of the infundibulum. Three major folds are divided by many deep irregular clefts between the secondary folds. SEM. 22×.

Fig. 4: Cross section of fig. 3. (E) epithelium, (F) lamina propria in a major fold, (f) a secondary fold, (M) tunica muscularis, (V) vein. SEM. 70×.

1a

10 cm

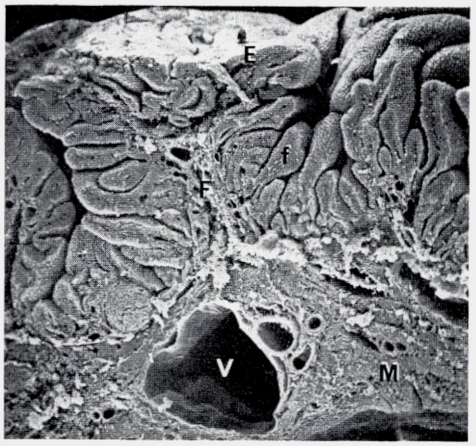
1b

200 μ

2

1mm

3



200 μ

4

PLATE 2

Fig. 1: From the magnum segment. The surface of the simple major folds has many small artificial disruptions, probably resulting from the freeze drying. SEM. 21×.

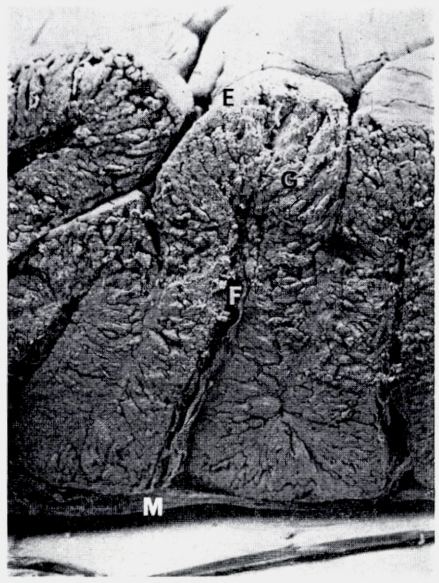
Fig. 2: Cross section of fig. 1. (E) epithelium, (F) lamina propria in a major fold, (G) glands in lamina propria, (M) tunica muscularis. SEM. 27×.

Fig. 3: From the isthmus segment. The surface of the major folds is divided by clefts between the secondary folds. SEM. 19×.

Fig. 4: Cross section of fig. 3. (E) epithelium, (F) lamina propria in a major fold, (f) a secondary fold, (G) glands in lamina propria, (M) tunica muscularis. SEM. 32×.

1 mm

1

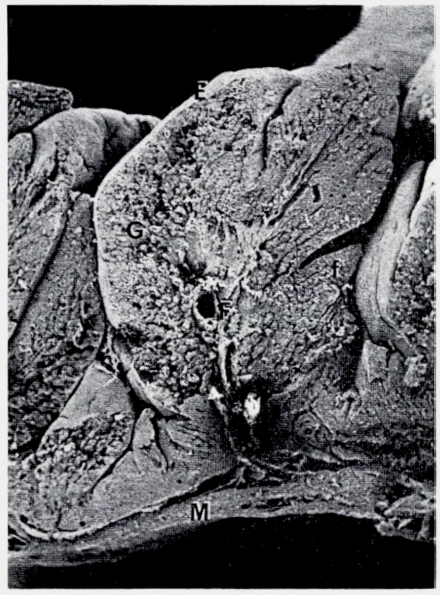


1mm

2

1mm

3



1mm

4

PLATE 3

Fig. 1: From the pouch-like part of the uterus segment, showing a tongue-like fold. SEM. 47×.

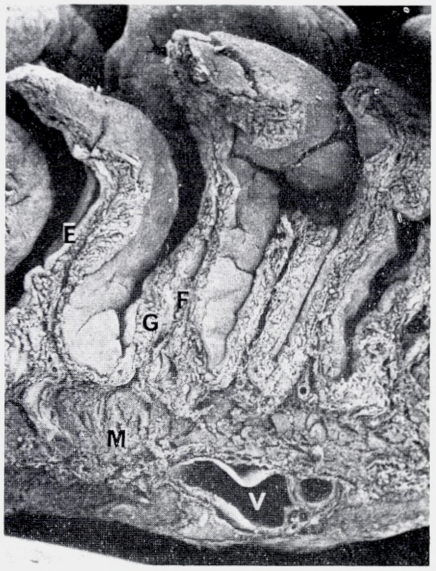
Fig. 2: Cross section of fig. 1. (E) epithelium, (F) lamina propria in a major fold, (G) glands in lamina propria, (M) tunica muscularis, (V) vein. SEM. 32×.

Fig. 3: From the vagina segment. The surface of the major folds is divided by parallel clefts between the secondary folds. SEM. 83×.

Fig. 4: Cross section of fig. 3. (E) epithelium, (F) lamina propria in a major fold, (f) secondary fold, (M) tunica muscularis. SEM. 62×.

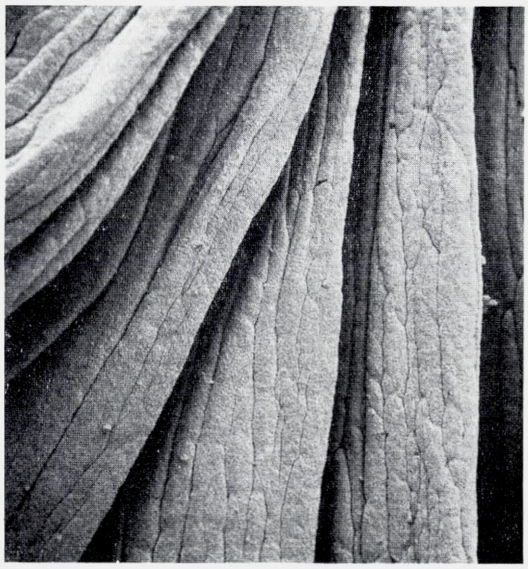
500μ

1



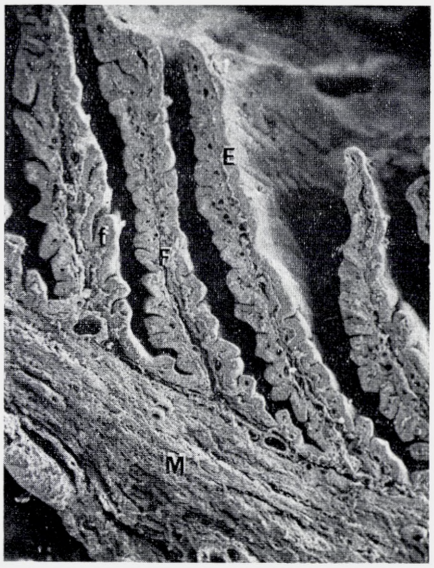
500μ

2



500μ

3



500μ

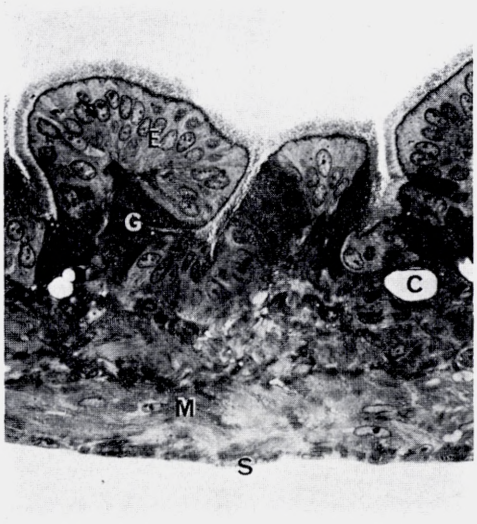
4

PLATE 4

Fig. 1: The low ridges in the funnel-shaped part of the infundibulum. Several glandular grooves can be seen in the bottom of the clefts between the folds. Occasional single glandular groove cells (strongly stained by Toluidine blue) are found between the ciliated cells on the sides of the ridges. (E) ciliated epithelium, (G) glandular groove, (C) capillary, (M) tunica muscularis, (S) serosal covering. LM. 440×.

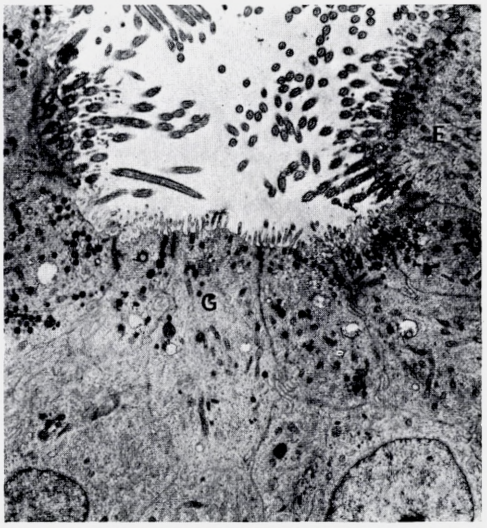
Fig. 2: A glandular groove between two ciliated folds. The glandular groove dells contain small electron dense granules which never cause any bulging of the apical surface. (E) ciliated epithelium, (G) glandular groove. TEM. 6250×.

Fig. 3: Detail of pl. 1, fig. 2. A glandular groove covered by a uniform dense layer of microvilli can be observed between two folds covered by cilia. Cell outlines are not observed. SEM. 2800×.



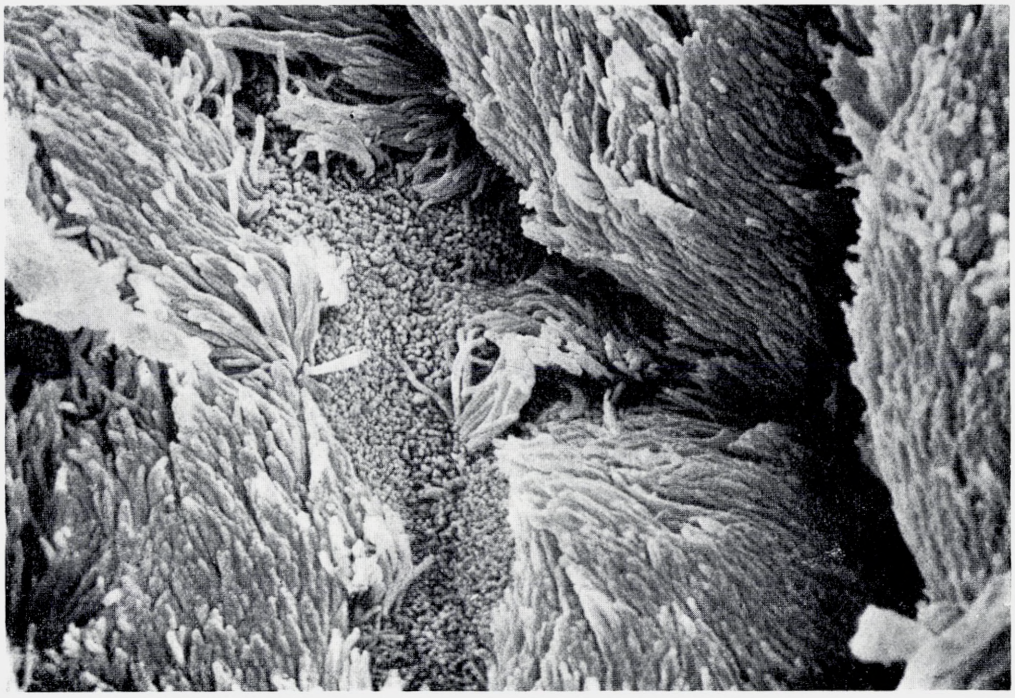
50 μ

1



4 μ

2



5 μ

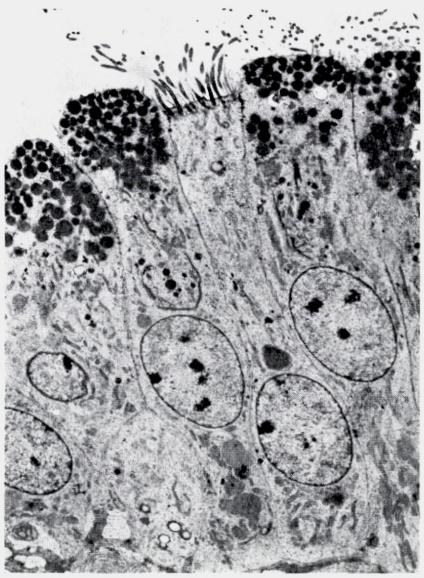
3

PLATE 5

Fig. 1: From the tubular part of the infundibulum. The lining epithelium consists of alternating tall columnar ciliated and non-ciliated (mucus secreting) cells. TEM. 2900×.

Fig. 2: Detail of pl. 1, fig. 3. The surface of a major fold in the tubular part of the infundibulum, divided by irregular clefts between the secondary folds. SEM. 195×

Fig. 3: Detail of fig. 2. The hemispheres from the secretory cells (M) alternate with tufts of cilia (C) from the ciliated cells. There are small scattered microvilli on the hemispheres. SEM. 9000×.

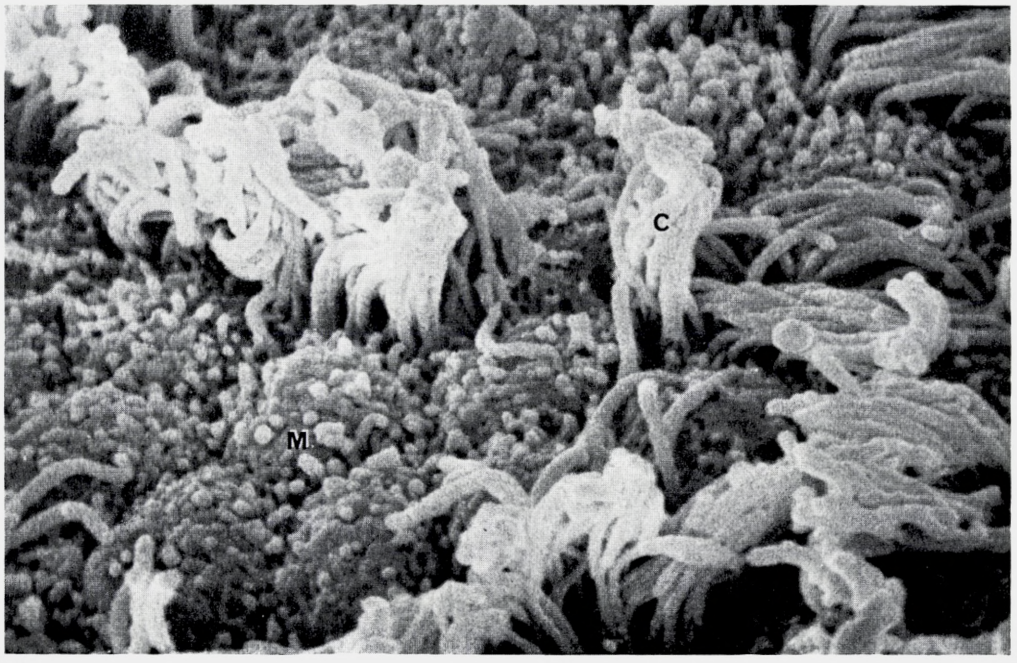


5 μ

1

100 μ

2



2 μ

3

PLATE 6

Fig. 1: The lining epithelium from the magnum segment. Mucus secreting cells alternate with ciliated cells. TEM. 3400×.

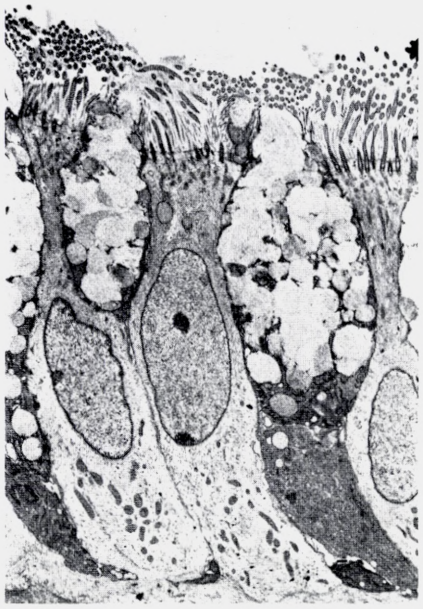
Fig. 2a: Detail of fig. 1. The lateral cell membranes interdigitate. (G) secretory granule, (N) nucleus. TEM. 34000×.

Fig. 2b: From the same part as fig. 2a. In a stage with wide intercellular spaces, where cytoplasmic sprouts (CS) stretch out. (G) secretory granule. TEM. 34000×.

Fig. 2c: The lateral cell walls can be seen in an artificial disruption of the magnum epithelium. There are rows of villus-like cytoplasmic sprouts (→). SEM. 1850×.

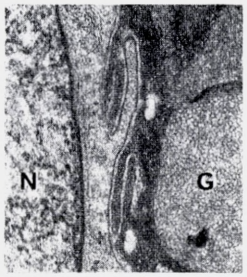
Fig. 3: Detail of pl. 2, fig. 1. The lining epithelium from the magnum segment *after* secretion. The hemispheres of the mucous cells (M) are low and densely covered by long microvilli. Between, tufts of cilia (C) from ciliated cells can be seen. SEM. 4700×.

Fig. 4: From the same part as fig. 3. *Before* secretion. The mucus secreting cells are bulging with secretory material in the form of hemispheres between the cilia from the ciliated cells. The surface of the hemispheres shows some finer structures, possibly remnants of microvilli. SEM. 4500×.

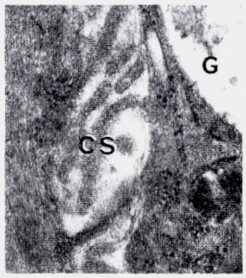


5 μ

1

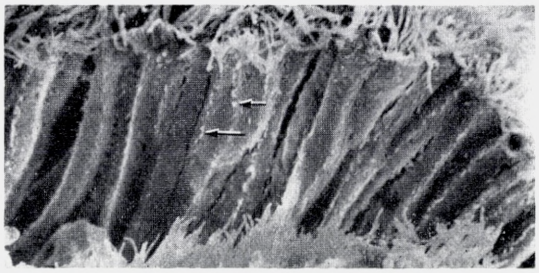


2 a



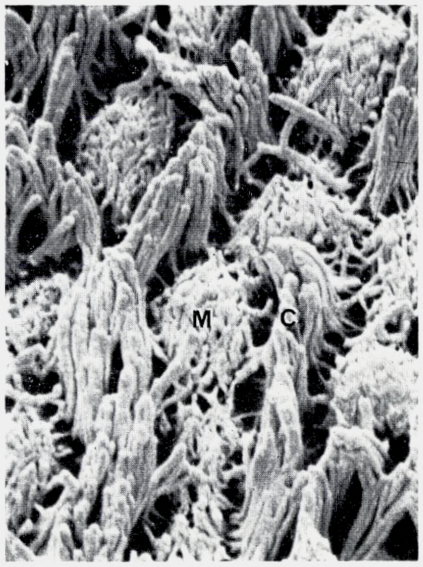
0.5 μ

2 b



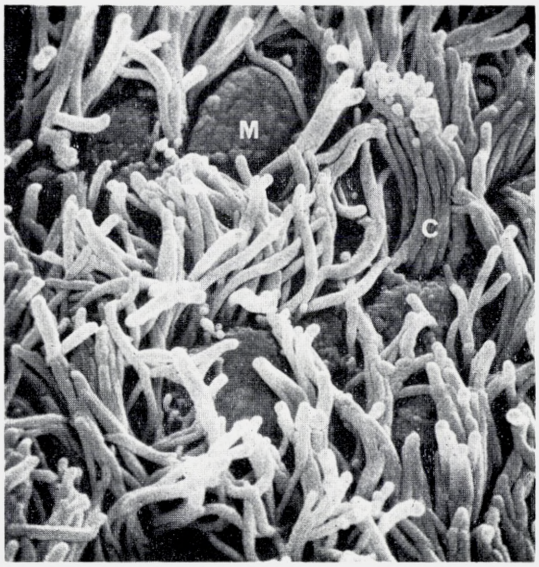
5 μ

2 c



5 μ

3



5 μ

4

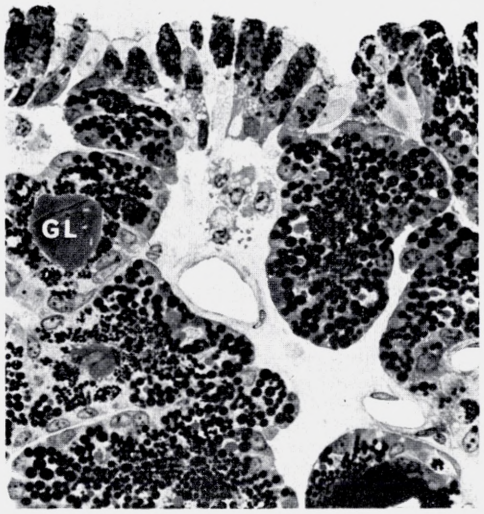
PLATE 7

Fig. 1: Three magnum glands open into the oviducal lumen. The gland lumen is filled with amorphous material (GL). LM. 500×.

Fig. 2: A funnel-shaped magnum gland opening. The surrounding cells are densely covered with microvilli. Three secretory granules (G) can be seen in intimate contact with the opening. SEM. 5000×.

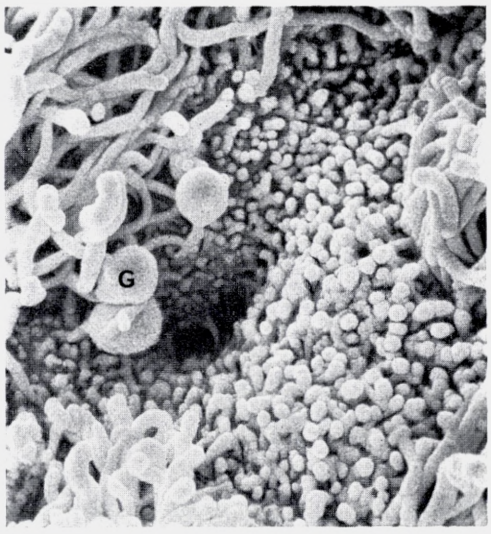
Fig. 3a: Detail of pl. 2, fig. 2. Cross section of the basal part of a gland cell from the magnum segment. Albumen granules (G) can be observed in cavities surrounded by a fixed mass of cytoplasm covering all other organelles. On several walls in these cavities there are holes surrounded by a thickened edge (→). SEM. 8750×.

Fig. 3b: From the same part as fig. 3a. The secretory granules (G) are enclosed by membranes, and packed so tightly that very little of the cytoplasmic matrix remains between adjoining granules. TEM. 13000×.



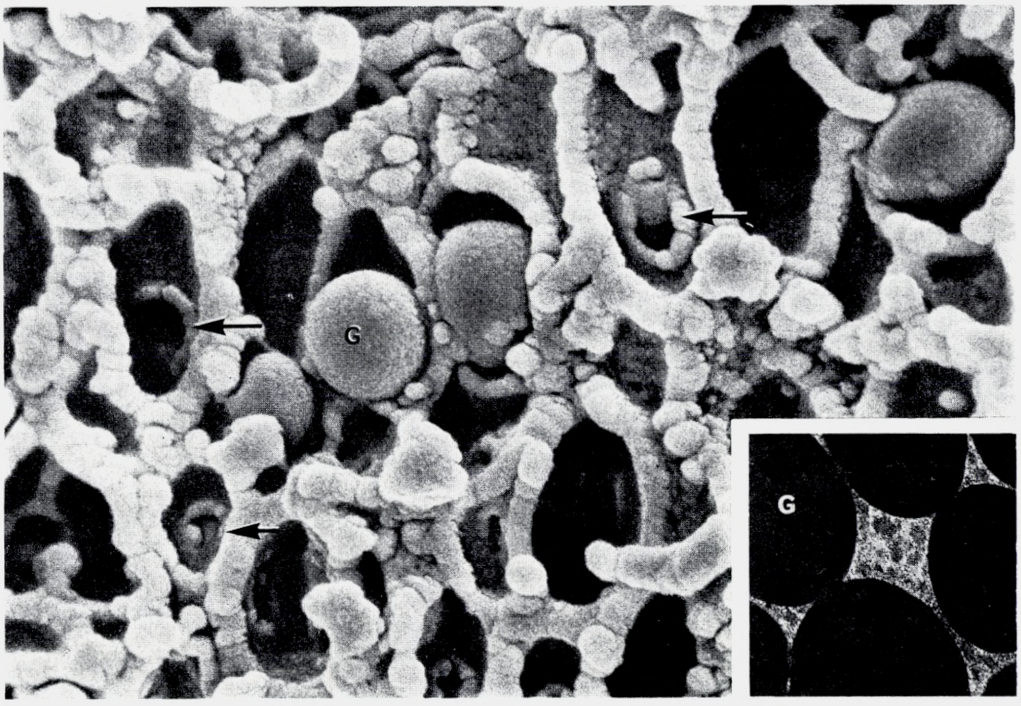
50 μ

1



5 μ

2



2 μ

3 a

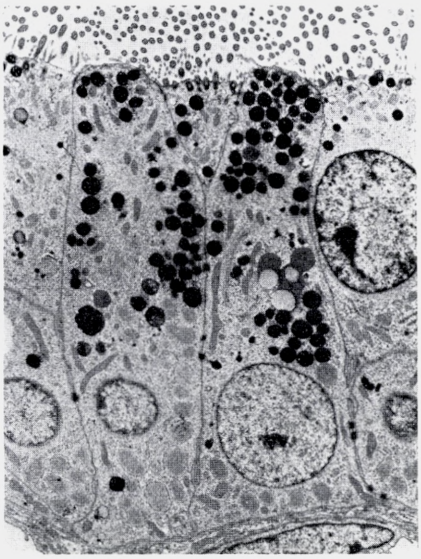
3 b

PLATE 8

Fig. 1: The lining epithelium from the isthmus segment. Secretory cells filled with electron dense granules, but with no bulging of the apical part, alternate with the ciliated cells. The latter contain very few electron dense granules. TEM. 4300×.

Fig. 2: Detail of pl. 2, fig. 3. Surface of a secondary fold from the isthmus segment. A pattern of metachronies (M) can be seen all over the surface. Where metachronies with different directions meet, interference pattern (honeycombs) occurs (J). SEM. 420×.

Fig. 3: Detail of fig. 2. Between the cilia, low hemispheres from the secretory cells covered by long slender microvilli (M) can be observed. SEM. 9000×.

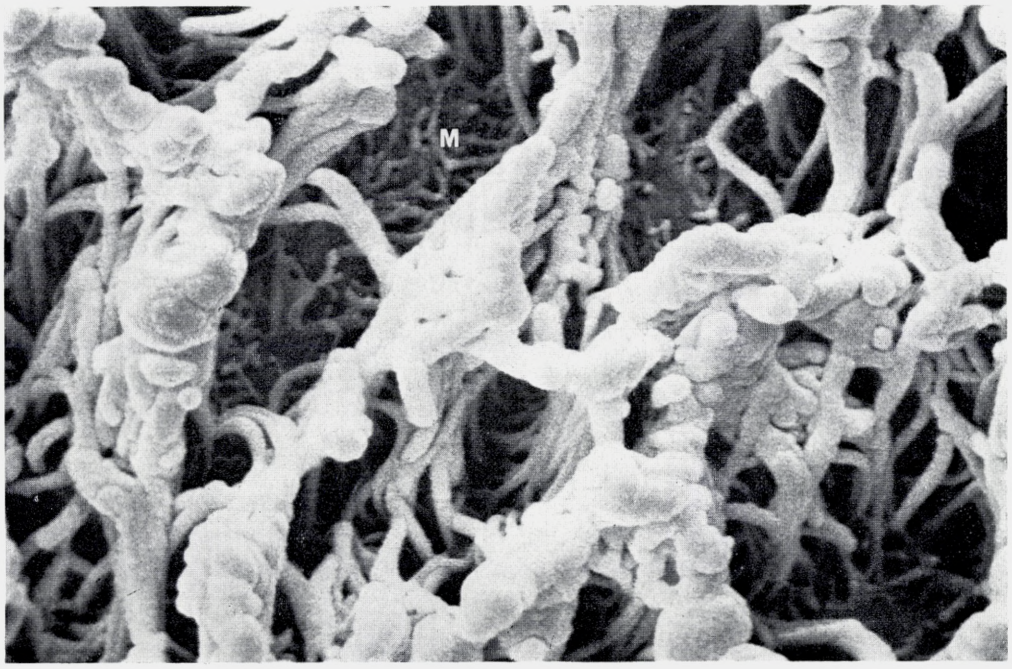


5 μ

1

50 μ

2



2 μ

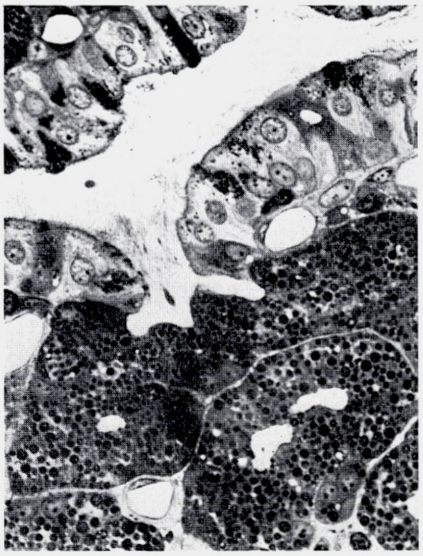
3

PLATE 9

Fig. 1: Several glands from the isthmus segment open together into the oviducal lumen. Cilia from the surrounding cells stretch out into the gland opening. LM. 560×.

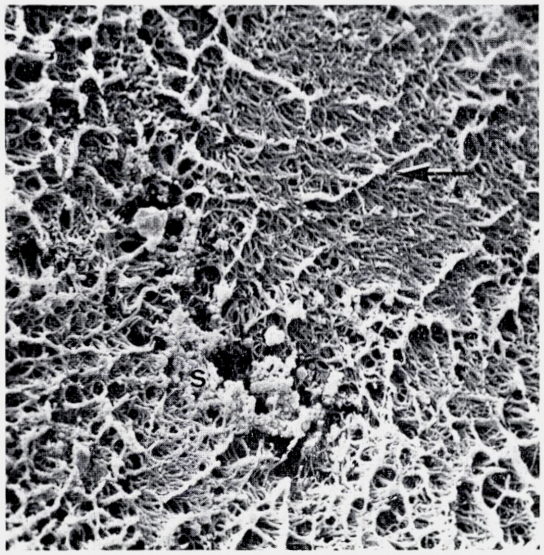
Fig. 2: A gland opening in the isthmus segment filled with clusters of secretory granules (S). Metachronies are present and secretory granules can be seen exclusively on top of the waves (→). SEM. 1050×.

Fig. 3: Cross section of a gland from the isthmus segment. Secretory granules of different size can be seen, the smaller ones (G) appearing centrally beneath the luminal surface of the gland cells. The gland lumen (L) is lined by long microvilli (M). SEM. 3400×.



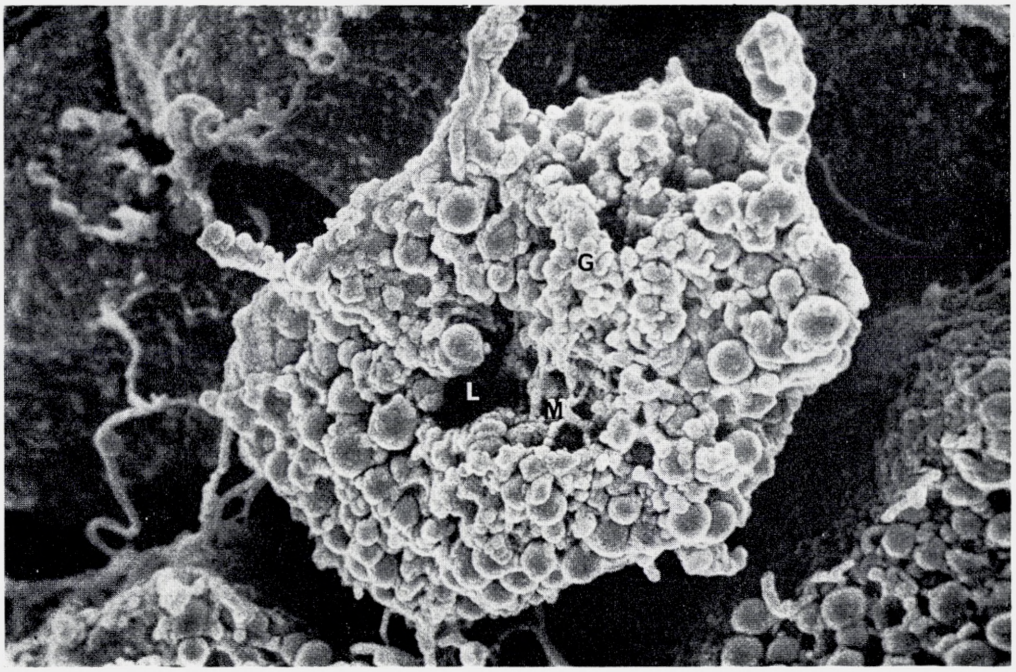
50μ

1



20μ

2



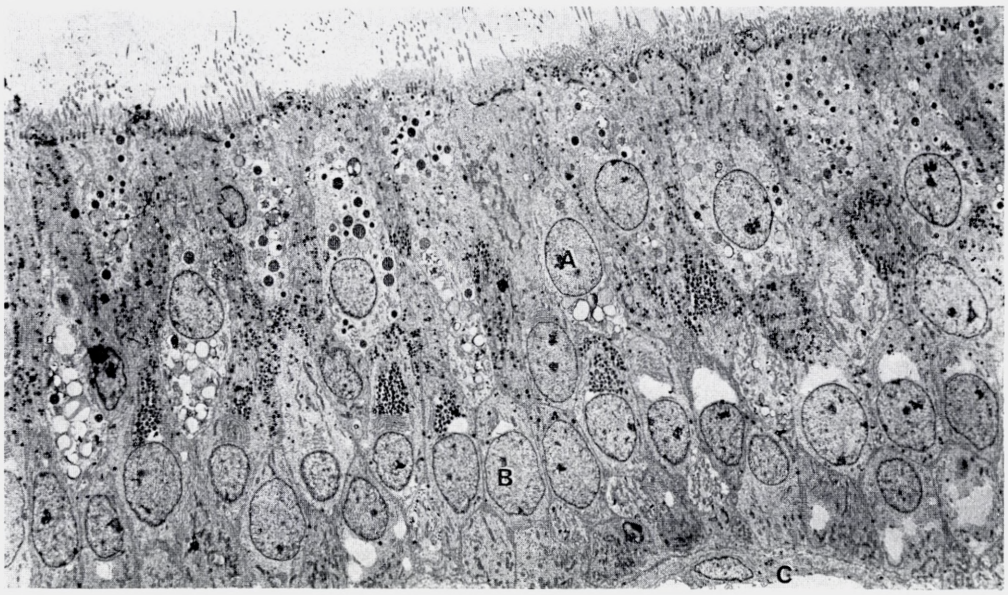
5μ

3

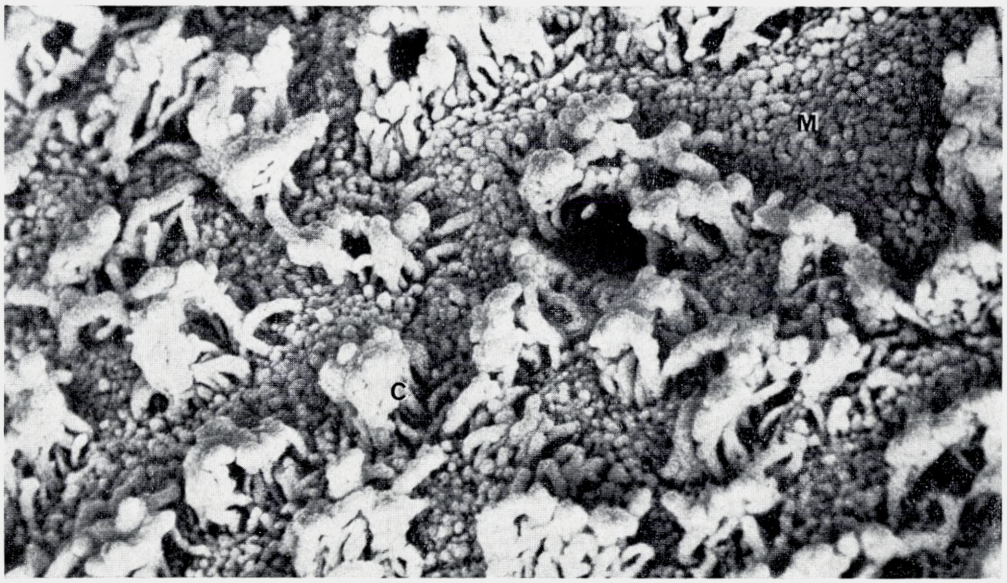
PLATE 10

Fig. 1: Lining pseudostratified epithelium from the pouch-like part of the uterus segment. Basal cells (B) alternate with apical cells (A), some of which are strongly vacuolated. A capillary (C) can be seen beneath the epithelium. TEM. 1950×.

Fig. 2: Detail of pl. 3, fig. 1. The mucosal surface from the pouch-like part of the uterus segment, lined with a uniform dense layer of microvilli (M) and here and there tufts of cilia (C) from the apical cells. SEM. 4100×.



1



2

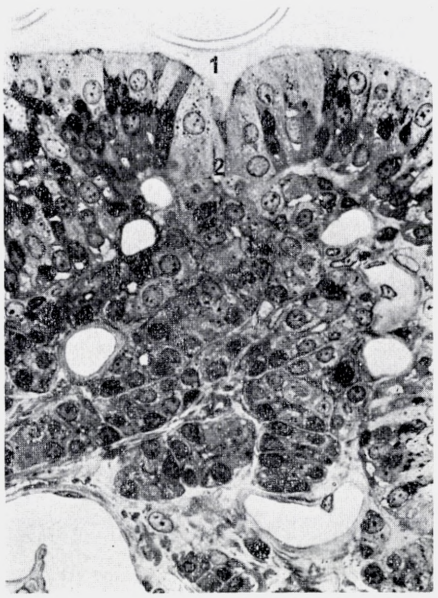
PLATE 11

Fig. 1: Section from the pouch-like part of the uterus. A uterine gland end in the oviducal lumen through a funnel-shaped opening. The gland opening is much wider at the level of the mucosal surface (1) than in the bottom of the tube at the level of the basal lamina (2). LM. 440×.

Fig. 2: The funnel-shaped opening observed from the mucosal surface in the same part of the oviduct as fig. 1. SEM. 5250×.

Fig. 3: Another type of gland opening from the pouch-like part of the uterus. This gland opening is also (as in fig. 1) a narrow tube stretching down through the epithelium limited by specially arranged epithelial cells. However, in this case the gland opening has nearly the same width at the level of the mucosal surface (1) as in the bottom of the tube at the level of the basal lamina of the epithelial cells (2). LM. 440×.

Fig. 4: Gland openings from the same part of the oviduct as fig. 3. The openings are seen as distinct holes in the mucosal surrounded by slightly elevated non-ciliated cells. SEM. 5250×.

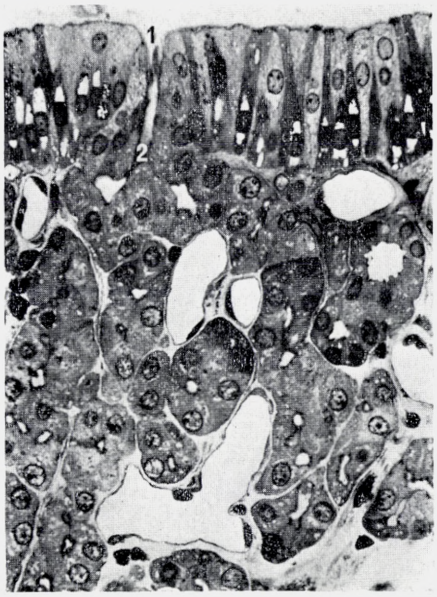


50μ

1

4μ

2



50μ

3

4μ

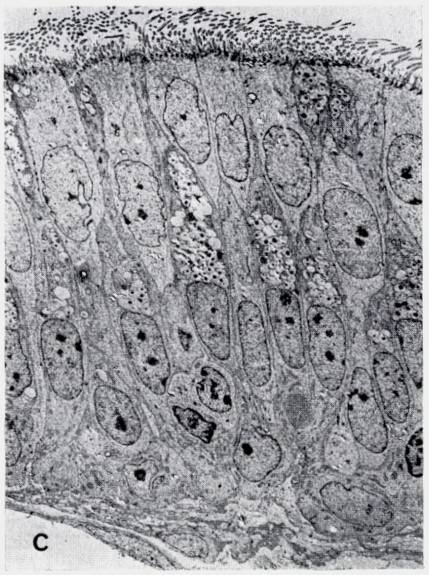
4

PLATE 12

Fig. 1: The lining pseudostratified epithelium of the vagina, composed of tall columnar ciliated cells (with apical nuclei) and tall columnar secretory cells (with basal nuclei). (C) capillary beneath the epithelium. TEM. 1700×.

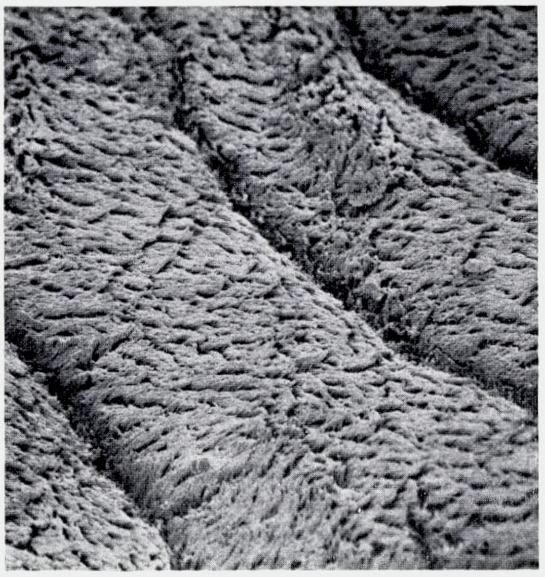
Fig. 2: Detail of pl. 3, fig. 3. Surface of a major fold from the vagina. Parallel clefts run between the secondary folds. The cilia cover the whole surface. SEM. 900×.

Fig. 3: Detail of fig. 2. Even with high magnification, the mucosal surface is dominated by cilia and there is no evidence of the secretory cells. SEM. 21000×.



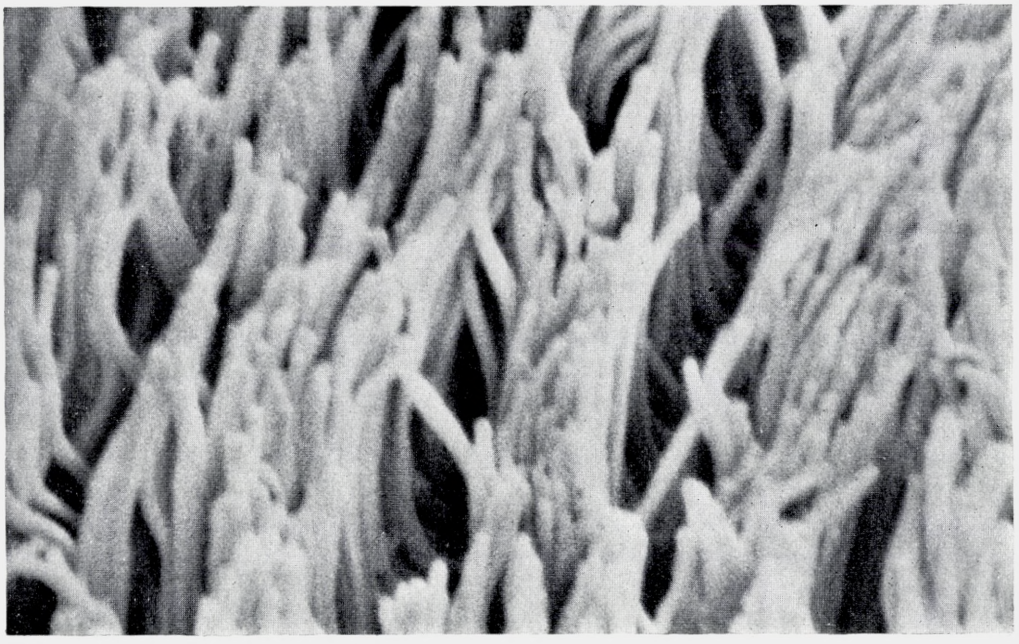
10 μ

1



20 μ

2



1 μ

3