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SECRETORY CELLS AND MORPHOLOGICAL MANIFESTATION OF SECRETION IN THE MOUSE OVIDUCT

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A b s t r a c t

The structure of secretory cells and granules has been described in the mouse Fallopian tube during sexual maturation and oestrous cycle. The oviducts of newborn mice were lined with a simple columnar epithelium in which only tall indifferent cells of uniform appearance were present. In some of these cells, marks of ciliogenesis were observed. The occurrence of secretory cells showing proteosynthetic activity and formation of secretory granules was registered in the oviducts of mouse females at the age of 14 days after birth for the first time. Secretory granules were formed but not released from the cells during sexual maturation, which takes the first 6 to 7 postnatal weeks. Secretory granules and vesicles of several types were found in secretory cells in the oviducts of adult animals. The granules were released into the lumen by way of apocrine secretion. The morphological signs of eccrine secretion of the content of vesicles were occasionally observed.

The ratio of secretory cells in the oviduct epithelium and the production of secretory products were increased around and after ovulation in cycling animals. The processes of secretion in the oviduct epithelium are dependent on the level of ovarian hormones. The influence of these hormones was studied in animals treated with exogenous hormones during their sexual maturation.

K e y w o r d s

Oviduct, Secretion, Oestradiol, Progesterone, Mouse

INTRODUCTION

The mammalian oviduct and tubal fluid represent together an optimal microenvironment and an essential medium for processes associated with fertilisation and early embryonic development. The special composition of oviductal fluid supports viability of the gametes, and nutrition of the cleaving zygote and early blastocyst formation. Selective transudation from the blood capillaries and an active proteosynthesis in the secretory cells of the oviduct epithelium are involved in fluid production (*8*). Participation of components of peritoneal and follicular fluids (at the time of ovulation) and of factors produced by the gametes, the cells of cumulus oophorus, and by the embryo (after ovulation) in tubal fluid composition was mentioned by *Hunter* 1988. The quality and quantity of this fluid is influenced by circulating steroid hormones of the ovary (*15, 20, 31, 33, 34*).

The ultrastructure of secretory cells, the appearance of their secretory granules, the luminal content, and the morphological manifestation of secretion have been studied.

MATERIALS AND METHODS

The oviducts of laboratory mice (C 57 BL/10 x CBA (F1)) were used as the model in the present study. The animals were divided into groups of sexually mature and immature females. The phases of the oestrous cycle (prooestrus, oestrus, metoestrus, and dioestrus) were determined on the basis of the evaluation of vaginal smears, stained with Ehrlich's hematoxylin and eosin, and of the appearance of vaginal introitus in accordance with the experience of *Champlin et al.* (1973) in adult mice. Sexual maturation from birth to the age of 49 days was followed in 7-day intervals; thus the subgroups of young animals were marked according to age in days: 0 (newborn), 7, 14, 21, 28, 35, 42, and 49. From these subgroups, females aged 14, 21, and 28 days were chosen for evaluation of the hormonal influence on the secretory activity of the tubal epithelium. An overview of the groups and numbers of evaluated animals is shown in *Table 1*. These mice were treated with exogenous steroid hormones of the ovary. Microcrystalline water suspensions of steroids, Agofolin-Depot /Biotika/ (estradioli benzoas 10 mg/2 ml) and Agolutin-Depot /Biotika/ (progesteronum 50 mg/2 ml), were administered subcutaneously in the suprascapular region of the experimental animals. Aqua pro injectione /Biotika/ served as a vehicle for the dilution of both hormones and was used for the control animals. The hormone formulas were applied in one daily dose for a period of 4 days. The protocol of the treatment is shown in *Table 2*.

The oviducts were taken in toto after decapitation of animals and processed for electron microscopy (double fixation in 300 mmol/l glutaraldehyde and 80 mmol/l osmium tetroxide in 100 mmol/l cacodylate buffer; embedding into Durcupan ACM (Fluka) after dehydration; cutting on Ultratome III ultramicrotome, and staining with uranyl acetate and lead citrate according to *Reynolds* (1963). The ultrathin sections were viewed and photographed by a transmission electron microscope Tesla BS 500 or Morgagni 286 D (FEI) (90 kV).

Table 1

An overview of groups and numbers of evaluated animals

Adult animals		Sexually immature animals							
Oestrus cycle phase		untreated age		control		oestradiol		oestradiol + progesterone	
prooestrus	5	0 (at birth)	4						
oestrus	5	7 days	6						
metoestrus	5	14 days	5	14 days	3	14 days	5	14 days	5
dioestrus	5	21 days	5	21 days	3	21 days	5	21 days	5
		28 days	5	28 days	3	28 days	5	28 days	5
		35 days	6						
		42 days	5						
		49 days	4						

Table 2

Protocol of hormone administration

	1st day	2nd day	3rd day	4th day
Oestradiol	50 μg/kg.d	50 μg/kg.d	50 μg/kg.d	50 μg/kg.d
Oestradiol + progesterone (P)	50 μg/kg.d	50 μg/kg.d	25 μg/kg.d 0 μg/kg.d (P)	525 μg/kg.d 50 μg/kg.d (P)
Aqua pro inj.	1 ml	1 ml	1 ml	1 ml

RESULTS

Secretory cells

The oviducts of newborn mouse females were lined with a simple columnar epithelium including tall indifferent cells of uniform appearance in all tubal segments (the preampulla, the ampulla, and the isthmus). Transformation of indifferent cells into ciliated cells represented by ciliogenic activity was observed in some of them. The presence of secretory cells or morphological marks of their differentiation were not registered during the first two weeks after birth.

The first secretory cells occurred in the epithelium of the ampulla and the isthmus of animals aged 14 days. Differentiation of secretory cells was characterised by an intensive proteosynthetic activity in the cytoplasm of some indifferent cells. Proteosynthesis was ultrastructurally expressed by an increased number of profiles of the Golgi apparatus and the rough endoplasmic reticulum, and by a small amount of secretory granules. Compact or reticular nucleoli (2–4 in number) were usually found in the nuclei of such cells. According to the fine ultrastructural differences, three types of secretory cells were distinguished during the period of sexual maturation (i.e., days 14–35 after birth). They were marked as 1/ immature, 2/ active mature, and 3/ inactive mature secretory cells (resting cells). Immature cells were characterised by the presence of only a few secretory granules of different level of their maturation. These granules were of different electron density and size (0.15–0.30 μm). They were dispersed in the cytoplasm and did not show cumulation in the cell apexes. A small Golgi apparatus and short, narrow cisternae of endoplasmic reticulum occurred in the cytoplasm. Concentric bodies (1 or 2 in number) localised below the nucleus were observed in some of these cells. The bodies were composed of concentrically arranged narrow, smooth cisternae. Some of them reached about 3 μm in diameter. The luminal surface of these cells projected to numerous longer microvilli. On the contrary, mature secretory cells were irregularly covered with very short microvilli. The active and mature secretory cells were characterised by the occurrence of well-developed cisternae and vesicles of the Golgi apparatus,

sometimes forming a large Golgi field. The granular endoplasmic reticulum was usually dilated and formed a dense network of cisternae in the supranuclear parts of the cytoplasm. Concentric bodies were also found in some of these cells. The inactive mature cells were fully differentiated and showed apical protrusions of the cytoplasm filled with numerous mature secretory granules. Only a small Golgi apparatus near the nucleus and several short, narrow cisternae of the endoplasmic reticulum were present in the cytoplasm. Concentric bodies were not observed in inactive cells.

The occurrence of mature secretory cells (both active and inactive) increased during sexual maturation so that they prevailed, while immature cells were only occasionally found in the oviductal epithelium of animals aged 35 and more days. The same results were observed in the oviducts of adult mouse females.

The administration of exogenous ovarian steroids, especially of oestradiol, showed an acceleration of differentiation and maturation of the secretory cells. The ultrastructural characteristics of the tubal epithelium of young hormone-treated mice (aged 14, 21, and 28 days) were the same as in the oviducts of adult females.

Secretory granules

The appearance of secretory granules was also studied. The most frequent type of granules occurring in many cells contained finely granular material of high electron density (*Fig. 1*). Their diameter was maximally 0.5 μm. The other types of granules or vesicles were occasionally observed. The small, lipid-like granules measured 0.2–0.4 μm in diameter. The dark, electron dense centre of such a granule was surrounded by a homogenous mass of middle electron density (*Fig. 2*). The large and very light granules of a diameter of up to 0.8 μm were filled with coarsely granulated material (*Fig. 3*). Large, electron-lucent vesicles and vacuoles of dilated rough endoplasmic reticulum measured 1.0 to 1.5 μm in diameter and contained fine, granular material. Small vesicles (*Fig. 4*), which appeared to be ”empty” and had 0.5 μm in diameter, were usually observed in close vicinity of plasma membrane. Both large and small vesicles were surrounded by a distinct biological membrane. Except for the above-mentioned types of granules and vesicles with a secretory product, lamellar structures and lipid droplets rarely occurred in some secretory cells (*Figs. 7, 8*) and also in the oviduct lumen. Elimination of lamellar particles, but not of lipid droplets, by exocytosis was monitored (*Fig. 8*).

Secretion

No marks of secretion from the cytoplasm of mature secretory cells were found in the epithelium of sexually immature mouse females during the whole period of their physiological sexual maturation. The secretory product was stored

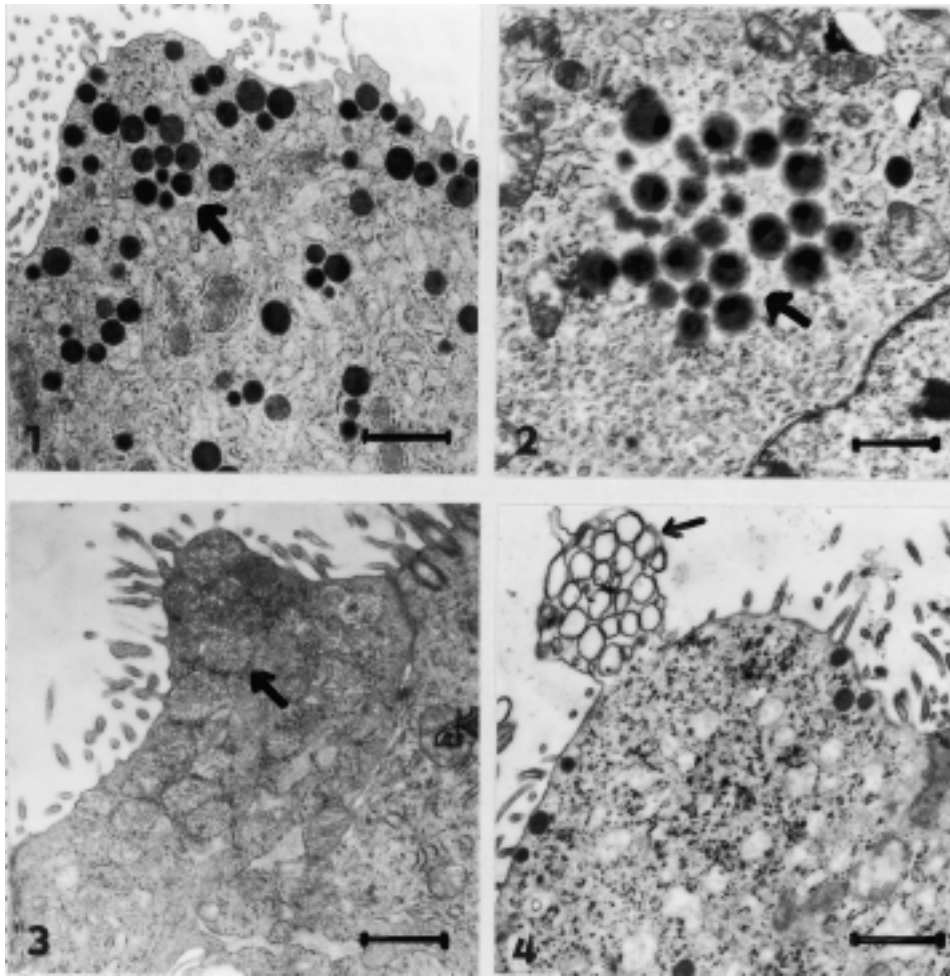

Fig. 1
Isthmus; oestrus: The most frequent type of granules containing finely granular material of high electron density. (Barr = 1 µm)

Fig. 2
Isthmus, prooestrus: Lipid-like granules with electron-dense spot surrounded by a homogenous mass of middle electron density. (Barr = 1 µm)

Fig. 3
Preampulla; age 28 days, oestradiol: Large and light granules filled with coarsely granulated material. (Barr = 1 µm)

Fig. 4
Preampulla; age 28 days, oestradiol + progesterone: Light vesicles appearing as "empty", in constricted protrusion of cell apex. (Barr = 1 µm)

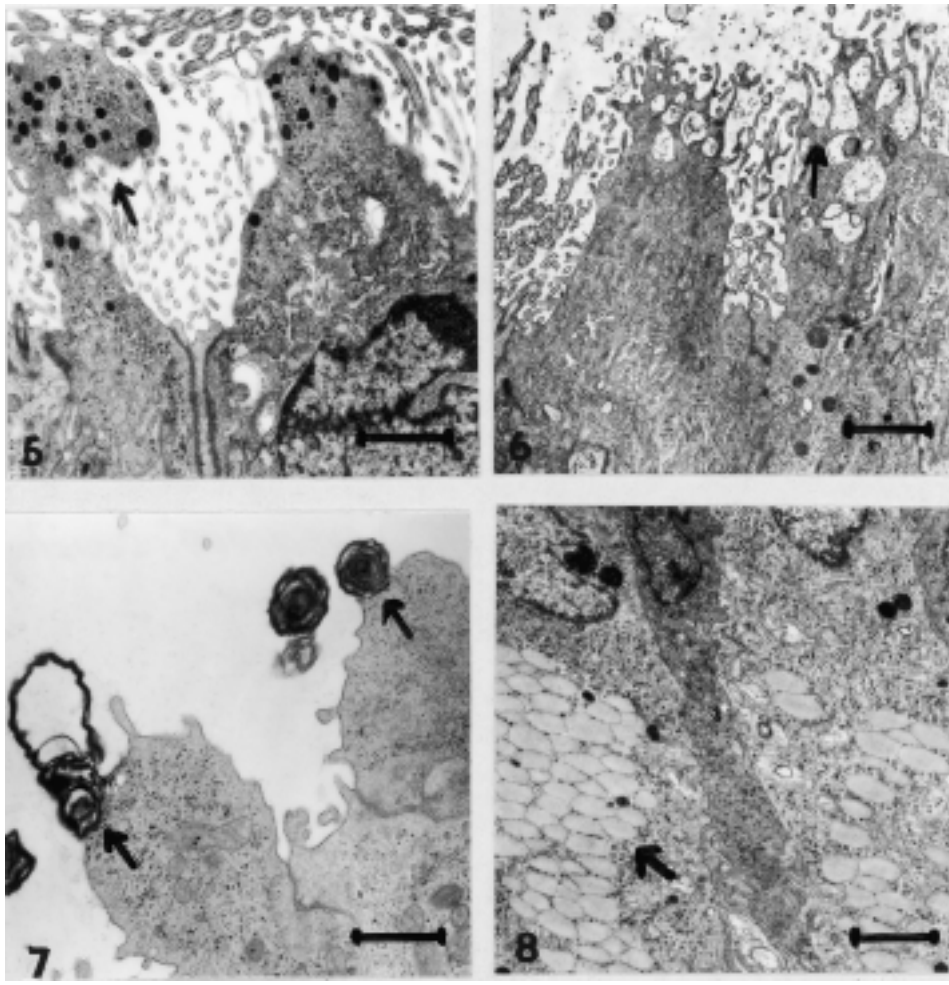

Fig. 5
Ampulla, oestrus: Constricted apical protrusion (→) containing secretory granules. (Barr = 2.5 μm)

Fig. 6
Ampulla, metoestrus: Cell apexes showing signs of eccrine secretion of the content of light vesicles (→). (Barr = 2.5 μm)

Fig. 7
Isthmus, age 42 days, untreated: Lamellar structures (→) eliminated by exocytosis. (Barr = 1 μm)

Fig. 8
Isthmus, oestrus: Aggregates of lipid droplets (→) in basal portions of the cytoplasm of secretory cells. (Barr = 2 μm)

in protruding cell apexes, but was not released into the lumen of the oviduct. In the oviducts of all pubertal animals treated with oestradiol together with progesterone, signs of constriction and separation of apical cytoplasmic protrusions containing secretory granules were manifested. Cytoplasmic fragments of secretory cells were regularly present in the tubal lumen.

Similar morphological signs of releasing the secretory material were monitored in the epithelium of adult females after ovulation in metoestrus (i.e. at the time of progesterone production by the corpus luteum in the ovary). These signs corresponded to apocrine secretion. Cumulation of granules or vesicles in the apical cytoplasmic protrusions and their strangulation were observed on the luminal surface of the epithelium (*Fig. 5*). Free cell fragments containing granules and/or vesicles were found in the lumen of the oviduct. Marks similar to eccrine secretion, but not direct releasing of the product, were monitored in some secretory cells with vesicles (*Fig. 6*).

DISCUSSION

The mammalian oviduct is not only a conducting tube for the passage of gametes and embryos, but it is also a sophisticated secretory organ that maintains and modulates the dynamic fluid-filled environment, which is necessary for fertilisation and early embryonic development (*19*).

The oviductal fluid is transparent, colourless, and lightly alkaline (pH 7.7–8.2 depends on concentration of bicarbonate). Specific gravity is less than 1.0 and osmolality is 310 mOsm (*14*). From the point of view of chemical composition, tubal fluid contains ions, amino acids and proteins, growth factors, enzymes and hormones (*2, 8, 9, 10*), the source of energy – lactate, pyruvate and glucose (*30*), the gamete- and embryo-protective and immunosuppressive components – taurine and hypotaurine *(2, 11, 12, 26*). The tubal epithelium also produces a lubricating substance which facilitates the passage of the oocyte and blastocyst in the narrow isthmus (*5*). Most of the above-mentioned components of tubal fluid originate from blood plasma and pass into the lumen via transudation from the blood vessels. Participation of secretory cells in the production of special proteins and amino acids was studied and described by some authors (*21,9,30*). The best-known proteins are oestrogen-dependent oviduct-specific glycoproteins (*2, 33, 34*), placental protein PP14 (*26*), or avidin in birds.

Secretory cells are tall columnar cells containing secretory granules in their cytoplasm. The marks of proteosynthetic activity are represented by numerous, well-developed profiles of the Golgi apparatus and granular endoplasmic reticulum. This simple morphological characteristic was given by many authors mentioned above in the text. The first secretory cells appeared in the mouse oviduct epithelium of the ampulla and the isthmus on day 14 after birth (*17*). Three types of secretory cells, named as 1/ immature, 2/ active mature, and 3/ inactive

mature cells, were described during the period of sexual maturation. Concentric bodies were observed in some of the immature and active mature cells. The same bodies were observed by some authors in different cell types (*3, 23, 25, 27, 28, 29, 32*). Most of these authors considered the bodies as a specialised form of smooth endoplasmic reticulum. Their function is not clear and the hypotheses about it are not unified. Participation in steroidogenesis and/or glycogenogenesis is assumed by some of the authors. The occurrence of immature and mature secretory cells (both active and inactive) changed during sexual maturation and was different in adult mouse females. Steroid hormone dependence was observed after hormonal treatment in groups of young animals (*18*).

The secretory products were kept in granules or vesicles of several types. The most frequent granules with finely granular material and high electron density were also described in different species by many authors (*6, 16, 30, 31*). The other types of granules were occasionally found in the mouse oviduct epithelium. Small, lipid-like granules of moderate density contained an electron-dense spot and were mentioned in golden hamster by *Abe and Oikawa* (1989). Large and very light granules with coarsely granulated material occurred in several secretory cells. Very large, electron-lucent vesicles or vacuoles containing fine, granular material occurred in the dilated cisternae of the rough endoplasmic reticulum and were observed in primates (*16, 22*) and in cow (*7*). Small, seemingly ”empty” vesicles were rarely found in the mouse oviduct. They were not mentioned by any of the authors whose works we have read.

Lamellar structures were found in some secretory cells and in the oviduct lumen. Lamellar particles were similar to myelin figures composed of phospholipid membranes and were not identical or similar to the lamellar secretory granules described in primates by *Odor et al.* (1983) or in cow by *Uhrín* (1992) and *Eriksen et al*. (1994). These particles were released by exocytosis into the oviductal lumen. Subnuclear aggregates of lipid droplets were a typical cytoplasmic compartment of some non-ciliated cells in the isthmus and free lipid droplets were found in the lumen of the oviduct. Their release via the secretory pathway was never seen in the mouse oviduct. Neutral lipids and phospholipids of tubal epithelium origin were detected by *Henault and Killian (*1993) in the bovine oviductal lumen. The importance of lamellar particles and lipid droplets for oviduct fluid composition is not clear.

In the mouse oviduct we have also studied how the secretory product is released from the cells into the lumen. Apical protrusions of secretory cells cumulating secretory granules or vesicles and their constriction and detaching from the cell surfaces were the most frequent signs of this process. In the lumen of the tube, free cell fragments of an ultrastructure identical to the cell protrusions were observed. In the view of these findings, the apocrine secretion seems to be the main way by which secretions are released from the cells. According to the

papers of the above-mentioned authors, the hypothesis about the type of secretion is not unified and they take a different view of it. Some of them incline to the opinion that the secretory product is released by apocrine secretion only, others describe only exocytosis. However, most of them permit of both these ways of secretion. In our material, we have observed broken surface on some secretory cells with irregular cytoplasmic processes and deeper invaginations of plasmalemma. This picture resembled the cell surface after exocytosis, but no released material was detected in any case. Although immediate marks of eccrine secretion were never seen in the mouse epithelium, we can neither exclude nor confirm it.

The results of this work will be used in a detailed histochemical study of the secretion and analysis of secretory granules and vesicles.

Lauschová I.

SEKREČNÍ BUŇKY A MORFOLOGICKÉ PROJEVY SEKRECE VE VEJCOVODU MYŠI

S o u h r n

Ve vejcovodu laboratorní myši byla popsána ultrastruktura sekrečních buněk a jejich granul, a to jak u pohlavně nezralých samiček v průběhu dospívání, tak u dospělých jedinců v průběhu pohlavního cyklu. Vejcovody novorozených myší jsou vystlány jednovrstevným cylindrickým epitelem s vysokými indiferentními buňkami uniformního vzhledu. V některých buňkách byly pozorovány morfologické známky ciliogeneze. Výskyt sekrečních buněk vykazujících proteosyntetickou aktivitu a tvorbu sekrečních granul byl poprvé zaznamenán ve vejcovodech zvířat starých 14 dní. V období pohlavního zrání, které trvá 6–7 týdnů po narození, jsme pozorovali tvorbu sekrečních granul, nikoliv však známky jejich uvolnění do lumina. V sekrečních buňkách dospělých jedinců jsme pozorovali několik typů sekrečních granul nebo váčků. V nich obsažený sekreční produkt byl uvolňován z cytoplazmy buněk do lumina vejcovodu apokrinním způsobem. Ojediněle jsme zaznamenali známky připomínající ekrinní sekreci.

Podíl sekrečních buněk v tubárním epitelu se zvětšoval a produkce sekrečních granul byla rovněž intenzivnější v periovulačním a postovulačním období pohlavního cyklu dospělých samiček. Proces tvorby a uvolnění sekretu je regulován hladinou ovariálních steroidů. Vliv hormonů byl sledován u pohlavně nezralých zvířat po podání exogenních hormonů ze skupiny estrogenů (estradiol) a gestagenů (progesteron). Zjistili jsme tak, že estrogeny navozují cytodiferenciaci tubárního epitelu a syntézu proteinů v sekrečních buňkách a progesteron, po předcházejícím ovlivnění epitelu estrogeny, podporuje uvolnění sekrečních produktů do lumina vejcovodu.

REFERENCES

1. *Abe H, Oikawa T.* Differentiation of the golden hamster oviduct epithelial cells during postnatal development: An electron microscopic study. J Exp Zool 1989; 252: 43–52.
2. *Boatman DE.* Responses of gametes to the oviductal environment. Hum Reprod (Natl Suppl JBFS 2) 1997; 12:133–149.
3. *Carr I, Carr J.* Membranous whorls in the testicular interstitial cells. Anat Rec 1962; 144: 143–147.
4. *Champlin AK, Dorr DL, Gattes AH.* Determining the stage of the estrous cycle in the mouse by the appearance of the vagina. Biol Reprod 1973; 8: 491–494.
5. *Chatkoff ML.* A biophysical model of the mechanisms regulating ovum transport in rates. In: Ovum transport and fertility regulation (WHO symposium, San Antonio, Texas, 1975). Harper M J K, Pauerstein C J (eds), Copenhagen, 1975, 27–40.
6. *Cigánková V, Krajničáková H, Kokardová M, Tomajková E.* Morphological changes in the ewe uterine tube (oviduct) epithelium during puerperium. Vet Med (Czech) 1996; 41: 339–346.
7. *Eriksen T, Terkelsen O, Hyttel P, Greve T.* Ultrastructural features of secretory cells in the bovine oviduct epithelium. Anat Embryol 1994; 190: 583–590.
8. *Gandolfi F, Modina S, Brevini TAL et al.* Oviduct ampullary epithelium contributes a glycoprotein to the zona pellucida, perivetelline space and blastomere membrane of sheep embryos. Eur J Bas Appl Histochem 1991; 33: 383–392.
9. *Gandolfi F, Modina S, Brevini TAL et al.* Activin beta A subunit is expressed in bovine oviduct. Mol Reprod Dev 1995; 40: 286–291.
10. *Grippo AA, Way AL, Killian GJ.* Effect of bovine ampullary and isthmic oviductal fluid on motility, acrosome reaction and fertility of bull spermatozoa. J Reprod Fertil 1995; 105: 57–64.
11. *Guerin P, Guillaud J, Menezo Y.* Hypotaurin in spermatozoa and genital secretions and its production by oviduct epithelial cells in vitro. Human Reprod 1995a; 10: 866–872.
12. *Guerin P, Menezo Y.* Hypotaurin and taurin in gamete and embryo environments: De novo synthesis via the cystein sulfinic acid pathway in oviduct cells. Zygote 1995b; 3/4: 333–343.
13. *Henault MA, Killian GJ.* Synthesis and secretion of lipids by bovine mucosal explants. J Reprod Fertil 1993; 98: 431–438.
14. *Hunter RHF.* The Fallopian Tubes. Springer Berlin, 1988, 1–191.
15. *Jaffe RC, Arias EB.* Oday-Bowman M.B., Donnelly K.M., Mavrogianis P.A., Verhage H.G. Regional distribution and hormonal control of estrogen-dependent oviduct-specific glycoprotein messenger ribonucleic acid in the baboon (Papio anubis). Biol Reprod 1996; 55: 421–426.
16. *Jansen RP.* Ultrastructure and histochemistry of acid mucus glycoproteins in the estrous mammal oviduct. Microsc Res Tech 1995; 62/1: 24–49.
17. *Lauschová I.* Ultrastructural changes in the oviduct epithelium of sexually immature mouse during postnatal development. Scrip Med (Brno) 1996; 69: 251–261.
18. *Lauschová I.* Influence of estrogen and progesterone on ultrastructural indices of oviductal epithelium in sexually immature mice. Acta Vet (Brno) 1999; 68: 13–21.
19. *Kapur RP, Johnson LV.* Ultrastructural evidence that specialized regions of the murine oviduct contribute a glycoprotein to the extracellular matrix of mouse oocytes. Anat Rec 1988; 221: 720–729.
20. *Malette B, Filion B, St-Jacques S, Kan FW, Bleau G.* Hormonal control of the biosynthesis of hamster oviductin. Microsc. Res Tech 1995; 31: 470–477.
21. *Nancarrow CD, Hill JL.* Co-culture, oviduct secretion and the function of oviduct-specific glycoproteins. Cell Biol Int 1994; 18: 1105–1114.
22. *Odor DL, Gaddum-Rose P, Rummery RE.* Secretory cells of the oviduct of the pig-tailed monkey, Macaca nemestrina, during the menstrual cycle and after estrogen treatment. Am J Anat 1983; 166: 149–172.
23. *Petric P, Collet A.* Lamellar bodies in the epithelial bronchiolar cells in the mouse. Z Zellforsch 1970; 103: 232–237.
24. *Reynolds ES.* The use of lead citrate at high pH as an electronopaque stain in electron microscopy. J Cell Biol 1963; 17: 208–212.
25. *Salomon J.C.* Modification des cellules du parenchyme hépatique du rat sous l'effet de la thioacétamide. J Ultrastruct Res 1962; 7: 293–307.
26. *Saridogan E, Djahabarhch O, Kervancioglu ME et al.* Placental protein 14 production by human Fallopian tube epithelial cells in vitro. Human Reprod 1997; 7: 1500–1507.
27. *Sinha AA, Mead RA.* Morphological changes in the trophoblast, uterus and corpus luteum during delayed implantation and implantation in the western spotted skunk. Am J Anat 1976; 145: 331–356.

28. *Steiner JW, Miyai K, Phillips MJ.* Electron microscopy of membrane-particle arrays in liver cells of ethionine-intoxicated rats. Am J Pathol 1964; 2: 169–213.
29. *Stenger RJ.* Concentric lamellar formations in hepatic parenchymal cells of carbon tetrachloride-treated rats. J Ultrastruct Res 1966; 14: 240–253.
30. *Tay JI, Rutherford AJ, Killick SR et al.* Human tubal fluid: production, nutrient composition and response to adrenergic agents. Human Reprod 1997; 11: 2451–2456.
31. *Uhrín V.* Funkčná morfológia epitelov vajcovodu a maternice kravy [Functional morphology of oviductal and uterine epithelia in the cow]. Slovak Academic Press, Bratislava, 1992, 1–169.
32. *Usa M, Ishimura K, Fujita H et al.* Ultrastructural and immunohistochemical studies on the zona-reticularis cells of the adrenal cortex of normal and 3-methylcholanthrene-treated mice. Histochem 1985; 83: 207–211.
33. *Verhage HG, Mavrogianis PA, Boice ML, Li W, Fazleabas AT.* Oviductal epithelium of the baboon: hormonal control and immuno-gold localization of oviduct-specific glycoproteins. Am J Anat 1990; 187: 81–90.
34. *Verhage HG, Mavrogianis PA, Boomsma RA, et al.* Immunologic and molecular characterization of an estrogen-dependent glycoprotein in the rhesus monkey (Macaca mulatta) oviduct. Biol Reprod 1997; 57: 525–531.