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Morphometric and ultrastructural features of the mare oviduct epithelium during oestrus

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Abstract

Morphometric, scanning electron microscopy (SEM) and transmission electron microscopy (TEM) investigations have displayed regional differences in the mare oviductal epithelium. The entire mucosa of the oviduct was lined with a pseudostratified epithelium, which consisted of two distinct cell types, ciliated and non-ciliated. Ciliated cells were predominant in the three different segments of the oviduct and their percentage increased from fimbriae to ampulla and significantly decreased in the isthmus. SEM revealed in the infundibulum finger-like mucosal folds, some of them interconnected, in the ampulla numerous and elaborated branched folds of the mucosa, whereas the isthmus displayed a narrow lumen, short and non-branched mucosal folds. In the ampulla and isthmus the majority of non-ciliated cells showed apical blebs provided or not of short microvilli. TEM displayed different ultrastructural features of ciliated and non-ciliated cells along the oviduct. Isthmus ciliated cells presented a more electron-dense cytoplasm than in infundibulum and ampulla cells and its cilia were enclosed in an amorphous matrix. The non-ciliated cells of infundibulum did not contain secretory granules but some apical endocytic vesicles and microvilli coated by a well developed glycocalyx. Non-ciliated cells of ampulla and isthmus contained secretory granules. Apical protrusions of ampulla displayed two types of secretory granules as well as occasional electron-lucent vesicles. Isthmus non-ciliated cells showed either electron-lucent or electron-dense cytoplasm and not all contained apical protrusions. The electron-dense non-ciliated cells displayed microvilli coated with a well developed glycocalyx. Three types of granules were observed in the isthmus non-ciliated cells. The regional differences observed along the epithelium lining the mare oviduct suggest that the epithelium of the each segment is involved in the production of a distinctive microenvironment with a unique biochemical milieu related to its functional role.
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1. Introduction

The mammalian oviduct is not a simple conduit of the female reproductive tract, but it plays an essential role in mammalian reproduction, human included, since its epithelial cells create a unique environment for gamete transport and maturation, fertilization and early embryonic development [1–3].

The mammal oviduct can be divided into three anatomically and functionally different regions: infundibulum, ampulla and isthmus. The fimbriated infundibulum introduces the ovulated eggs to the oviductal fluid

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and pushes them into the ampulla, where fertilization and early cleavage-stage of embryo development takes place. The isthmus is considered to be a sperm reservoir as well as it plays a key role in sperm transport to the ampulla and in the passage of the embryo(s) into the uterus [4,5].

The oviductal epithelium is a simple columnar, consisting of two types of cells, ciliated and non-ciliated cells. Ciliated cells play a role in the transport of germinal cells [6], whereas non-ciliated cells are considered to be secretory cells mainly involved in the synthesis and release of glycoproteins that dissolve in the oviductal fluid, together with a selective transudate of serum [1,3,7].

Some glycoproteins secreted by non-ciliated cells of oviductal epithelium associate with ovulated ova and developing embryos and may play important roles in fertilization and/or early embryonic development [8–11]. In addition, several oviductal glycoproteins associate with sperm surface and can affect sperm fertility [2].

The ultrastructure of the epithelium lining the mature oviduct has been studied in several mammals [4,12–15]. Transmission electron microscopy studies revealed that secretory granules accumulate in the apical region of non-ciliated cells and the feature of secretory granules varies in relation to the oviduct tract and the species.

Since no transmission electron microscopic (TEM) study regarding the mare oviduct has been performed before, the objective of this study was to examine the ultrastructural features of the mucosal epithelium of infundibulum, ampulla and isthmus during the oestrous phase of the sexual cycle. This report contains also a scanning electron microscopic (SEM) investigation because the morphology of the entire mare oviduct has not been described by means of the SEM [16,17].

2. Materials and methods

Oviducts from four oestrus (n = 4) mares (with a follicle > 35 mm and exhibiting receptivity to the stallion the day before their slaughter) were obtained from a local slaughterhouse. Immediately after collection, the fimbriae of infundibulum, ampulla and isthmus were cut into small pieces and fixed by immersion in 3% glutaraldehyde buffered with 0.1 M sodium cacodylate (pH 7.2) for 4 h at 4 °C. After rinsing, tissues were post-fixed in 1% OsO_4 buffered with sodium cacodylate for 2 h at 4 °C, rinsed and dehydrated in an ethanol series (30%, 50%, 70%, 80%, 95% and abso-

lute for 30 min each) and then processed for transmission electron microscopy (TEM) or scanning electron microscopy (SEM). For TEM, dehydrated specimens were embedded in a mixture of Epon-812. Semithin sections (1 μm thick) were cut and stained with saturated, borax-buffered toluidine blue dye solution and examined under light microscopy to study the general morphology. The number of cells was determined using 10 light microscopy fields captured at 100x magnification and digitalized with a Quantimet 500W image analyser. Data are given as means $\pm$ standard error of the mean. Student's t-tests were performed on data collected.

Ultrathin sections (50–70 nm) with silver interference were cut, picked up on copper grids and stained with uranyl acetate and lead citrate. The sections were observed under a transmission electron microscope (Morgagni 268, Philips). For scanning electron microscopy (SEM) observations, dehydrated specimens were critical point dried using CO_2. Specimens were mounted on stubs, coated with gold–palladium in a sputter coater, and examined using a LEO S420 SEM.

3. Results

3.1. Light microscopy

The mucosa of the entire oviduct was lined with a pseudostratified epithelium, which consisted of two distinct cell types, ciliated and non-ciliated cells (Figs. 1a,b). Non-ciliated cells showed a more intense staining than ciliated cells. Differently from the infundibulum where a clear apical protrusion was not seen (Fig. 1a), in the ampulla and the isthmus most of the non-ciliated cells showed an apical protrusion (Fig. 1b). Ciliated cells were predominant in the three different segments of the mare oviduct (Fig. 2). The percentage of ciliated cells increased from fimbriae to ampulla (62 $\pm$ 2.0% vs 66 $\pm$ 1.8%) and significantly decreased in the isthmus (59 $\pm$ 2.3%).

3.2. SEM

At scanning electron microscope the fimbriae of the infundibulum appeared constituted of finger-like mucosal folds and some of them were interconnected (Fig. 3a), the ampulla showed numerous and elaborated branched folds of the mucosa and a thin muscle wall (Fig. 3b), whereas the isthmus was characterized by a narrow lumen, short and non-branched mucosal folds as well as by a well-developed muscle layer (Fig. 3c). Except for the infundibulum (Fig. 3d), in the ampulla
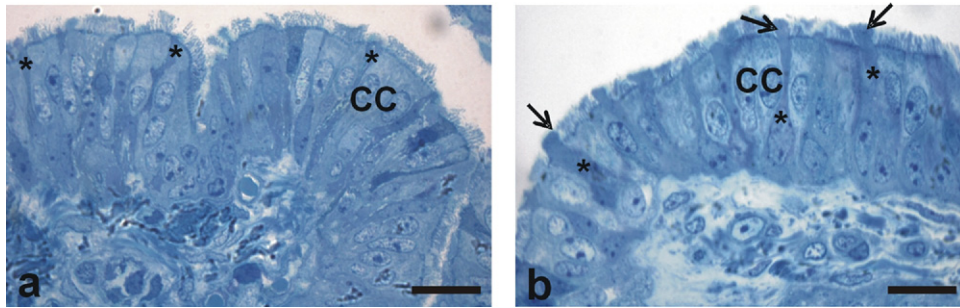
Fig. 1. Light micrographs of the mare oviduct during oestrus phase showing the infundibulum (a) and ampulla (b). Non-ciliated cells were more intensely stained than ciliated cells. Differently from the infundibulum, where apical protrusions were not visible (Fig. 1a), the most non-ciliated cells of the ampulla showed an apical protrusion. Toluidine blue staining. CC, ciliated cells; asterisk, non-ciliated cells; arrow, apical protrusion of non-ciliated cells. Bar: a, 17 μm; b, 13 μm.

and isthmus the majority of non-ciliated cells showed a well developed apical protrusion provided or not of short microvilli protruding from the apical surface (Figs. 3e,f).

3.3. TEM

3.3.1. Infundibulum

TEM observations revealed that the lining epithelium of fimbriae consisted of ciliated cells and two sub-populations of non-ciliated cells (Figs. 4a,c). Ciliated cells were characterized by electron-lucent cytoplasm containing in the middle part a round nucleus which was rich in dispersed heterochromatin (Fig. 4a). Round mitochondria constituted the prominent organelle mainly in the apical zone of the ciliated cells (Fig. 4b). The non-ciliated cells displayed either electron-dense or electron-lucent cytoplasm (Figs. 4a,c). The dark non-ciliated cells did not show an evident differentiated cytoplasm, in which only some scattered mitochondria occurred (Fig. 4a, inset). The nucleus, elongated and with irregular contour, contained abundant heterochromatin and reached the apical region of the cell (Figs. 4a,c). This population of non-ciliated cells could display small apical protrusion provided of microvilli (Fig. 4a). The electron-lucent non-ciliated cells were characterized by a diffuse presence of rough endoplasmic reticulum (RER) throughout the cytoplasm, some endocytic vesicle in the apical region and microvilli surrounded by a well developed apical glycocalyx (Figs. 4c,d). Near the elongated nucleus, which was localized in the middle part of the cell, a small Golgi apparatus, some lysosomes and round mitochondria were located (Fig. 4e). The connection between adjacent cells was assured by junctional complexes consisting of tight junctions, adherens junctions and desmosomes (Figs. 4a,b,c).

3.3.2. Ampulla

The lining epithelium of the ampulla was constituted by electron-lucent ciliated cells and non-ciliated (secretory) cells (Fig. 5a). The secretory cells were characterized by apical protrusions on which very short and sparse microvilli could be seen (Figs. 5a,b). The apical protrusions of the non-ciliated cells contained mostly granules with dark homogeneous matrix and some granules with moderate electron-dense matrix as well as a few electron-lucent vesicles (Figs. 5a,b). The supra-nuclear region contained the Golgi apparatus which was formed by several dyctiosomes (Fig. 5c). Abundant round mitochondria and thin profiles of RER were scattered throughout the cytoplasm (Figs. 5a,c). The elongated nucleus, located in the middle region of the cytoplasm, contained one well evident nucleolus (Fig. 5a).

3.3.3. Isthmus

In the epithelium of isthmus the ciliated cells displayed a dark cytoplasm with nucleus located in its third apical region and the prominent organelles were
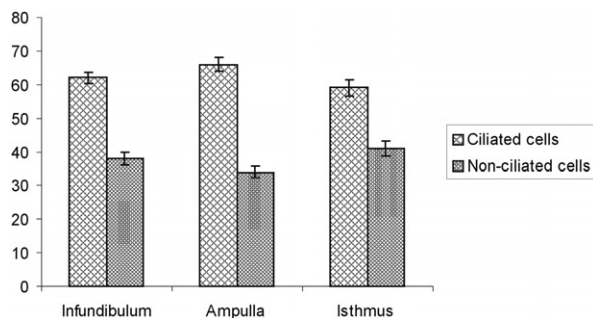

Fig. 2. The mean percentages of ciliated cells and non-ciliated cells in the epithelium of mare oviduct at oestrus phase. Values are expressed as mean ± SEM.
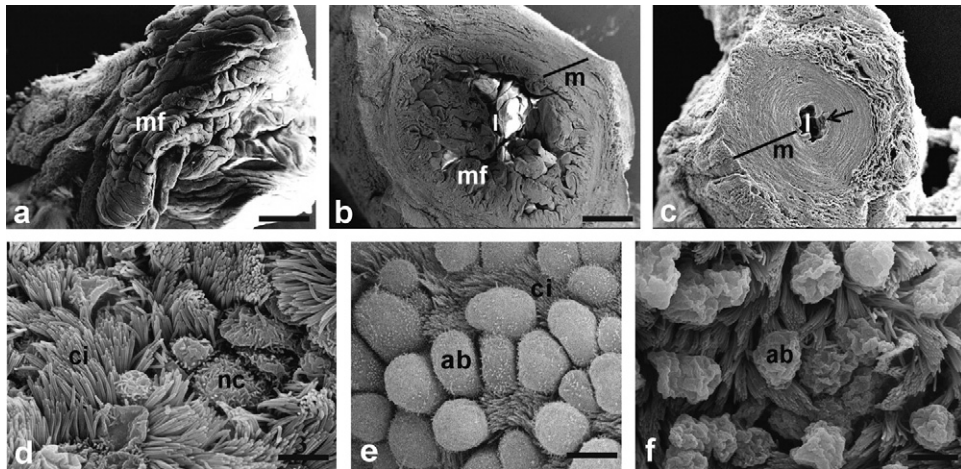
Fig. 3. Scanning electron micrographs of the mare oviduct at the oestrus phase. (a,d), infundibulum; (b,e), ampulla; (c,f), isthmus. ab, apical bleb of non-ciliated cells; ci, cilia; l, lumen; m, muscle layer ; mf, mucosal fold in infundibulum and ampulla; nc, non-ciliated cells; arrow, mucosal fold in isthmus. Bar: a, 450 μm; b, 560 μm; c, 486 μm; d, 3 μm; e, 5 μm; f, 4 μm.

the round mitochondria. The cilia were enclosed in a dense matrix. (Figs. 6a,b).

The non-ciliated cells showed either electron-lucent or electron-dense cytoplasm as well as the presence or not of apical protrusions (Fig. 6). The non-ciliated cells were classified as secretory cells, because their supra-nuclear cytoplasm contained secretory granules (Figs. 6a,b,c,d) and they could lack of apical protrusion. In this case the luminal surface displayed short microvilli covered with a well developed glycocalyx (Fig. 6c).

Three types of secretory granules were found in the non-ciliated cells. The most prominent type of granules was characterized by an electron-dense body surrounded by a less dark and homogeneous matrix; the second type of granules contained an electron-dense matrix and the third type, less numerous, was filled with a moderately electron-dense matrix. The first type of granule was mostly contained in the cytoplasmic protrusions, whereas the other two were more numerous in the apical region of secretory cells without protrusions (Figs. 6b,c). The Golgi apparatus as well as RER were well developed and placed in the supra-nuclear region (Figs. 6d,e).

4. Discussion

This is the first study that demonstrates the regional differences in the mare oviductal epithelium.

SEM investigations revealed that the mare oviductal mucosa consists of finger-like folds in the infundibulum, numerous and elaborated branched folds in the ampulla and non-branched folds in the isthmus.

As in other mammals, the mucosa of mare oviduct was lined with a single layered columnar epithelium constituted of ciliated and non-ciliated cells [4,12–14,18]. The count of ciliated cells and non-ciliated (secretory) cells, carried out on semithin sections, showed differences along the mare oviductal segments. The number of ciliated cells was greater than non-ciliated along the entire mare oviduct. The oviductal segment with lower presence of ciliated cells was the isthmus (59 $\pm$ 2.3%), whereas the one with the major percentage was the ampulla (66 $\pm$ 1.8%). Segmental variations in proportion of ciliated and non-ciliated (secretory) cells have been revealed in the oviduct of other mammals such as golden hamster and bovine [4], goat [12], pig [13].

Cilia are considered to be primarily responsible for gathering up and transporting the ovulated eggs [6]. The lower presence of ciliated cells in the isthmus of mare oviduct could be related to the presence of the well-developed muscle layer surrounding the mucosa. In the mare isthmus the myosalpinx has a plexiform structure [19] which could generate a stirring movement of lumen content [20]. This process can lead to the optimization of the micro-environment and thus favourable conditions for the early embryo development during its flow to the uterus [21].

TEM observations displayed different ultrastructural features of ciliated cells along the oviduct. In particular, isthmus ciliated cells showed a more electron-dense cytoplasm than in infundibulum and ampulla segments. It is noteworthy that this study has revealed that the cilia of the isthmic region are enclosed in an amorphous
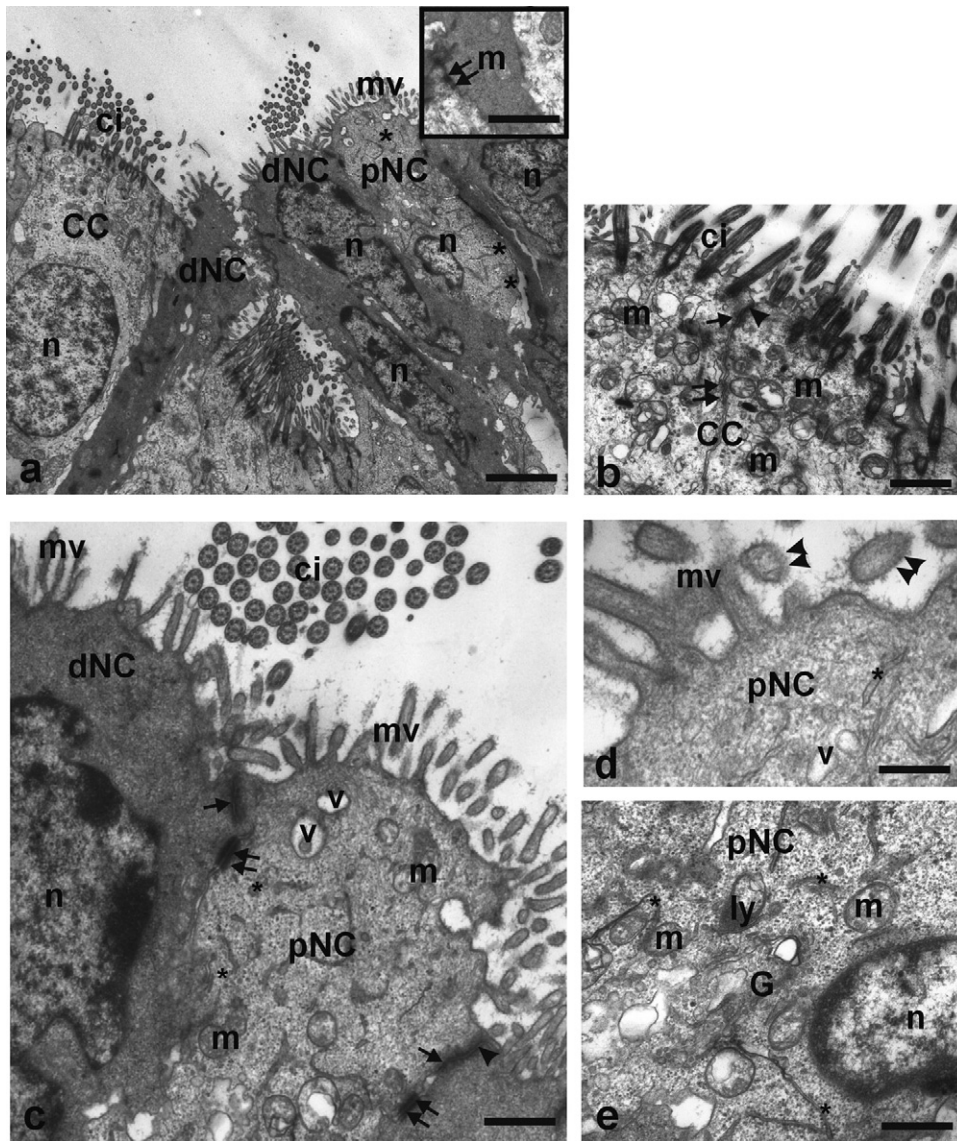
Fig. 4. Electron micrographs of infundibulum epithelial cells of a mare oviduct at the oestrus phase. (a), the lining epithelium consisted of electron-lucent ciliated cells and two sub-types of non-ciliated cells which differed for cytoplasm electron-density and granules. The inset shows junctions between ciliated (light) and non-ciliated (dark) cells; (b), apical region of ciliated cells; (c), two sub-types of non-ciliated cells; (d), apical region of electron-lucent non-ciliated cells; (e), nuclear zone of electron-lucent non-ciliated cells. CC, ciliated cells; ci, cilia; dNC, dark non-ciliated cells; G, Golgi apparatus; ly, lysosome; n, nuleus; m, mitochondria; mv, microvilli; pNC, pale non-ciliated cells; v, vesicle; arrow, adherens junctions; arrowhead, tight junctions; asterisk, rough endoplasmic reticulum; double arrows, desmosomes; double arrowheads, microvilli glycocalyx. Bar: a, 2 μm; b, 0.8 μm; c, 0.8 μm; d, 0.2 μm; e, 0.4 μm.

matrix. This substance consists of material released in the lumen from non-ciliated cells and it could be responsible for the sperm binding to cilia, so it makes the isthmus a sperm reservoir for several mammalian species [5,22–25], including equine [26,27]. However, the main function of isthmic ciliated cells of the mammalian oviduct remains still unresolved since SEM investigations of the oviducts taken from mated pigs [28] and

cattle [24] show sperm associated with microvilli of non-ciliated cells.

The non-ciliated cells of mare oviduct showed regional variations in the ultrastructural features. In the infundibulum, the non-ciliated cells did not show secretory granules and two sub-types were primarily distinguished according to the cytoplasm electron-density. Infundibulum non-ciliated cells did not show a partic-
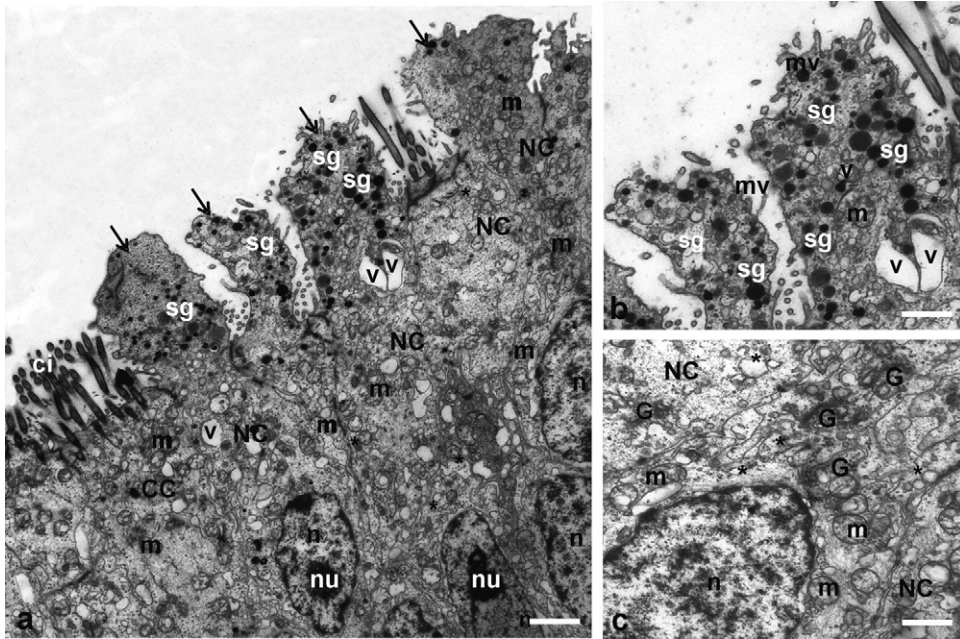
Fig. 5. Electron micrographs of ampullar epithelial cells of a mare oviduct at the oestrus phase. (a), non-ciliated cells showed apical protrusions with secretory granules; (b), apical protrusions contained mostly granules with dark homogeneous matrix, some granules with moderate electron-dense matrix, few electron-lucent vesicles and showed short and sparse microvilli; (c), supra-nuclear region of three non-ciliated cells showing several dyctiosomes in the central non-ciliated cell, round mitochondria and thin profiles of RER were scattered throughout the cytoplasm. CC, ciliated cells; ci, cilia; G, Golgi apparatus; m, mitochondria; mv, microvilli; n, nucleus; NC, non-ciliated cells; nu, nucleolus; sg, secretory granules; v, vesicle; arrow, apical protrusion; asterisk, rough endoplasmic reticulum. Bar: a, 20 μm; b, 0.8 μm; c, 0.8 μm.

ular differentiation of cytoplasm except for the presence in the electron-lucent ones of some endocytic vesicles and microvilli surrounded by a well developed apical glycocalyx in the apical region and thin RER profiles in the supra-nuclear zone. The presence of a well developed luminal surface glycocalyx and endo-
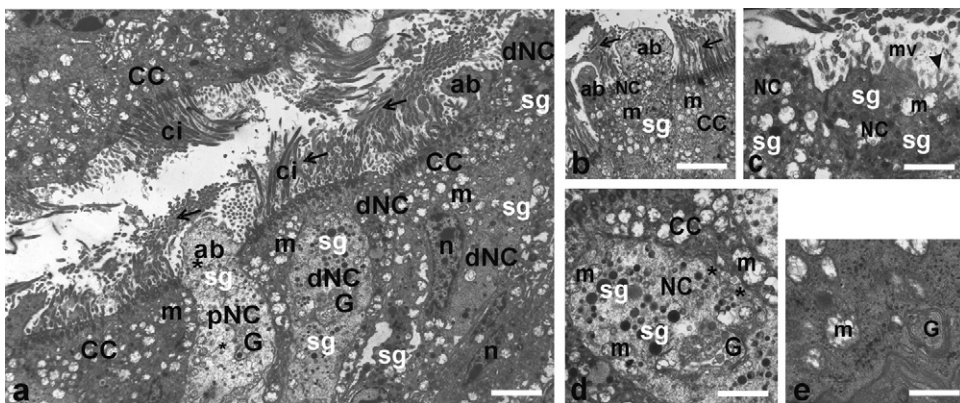

Fig. 6. Electron micrograph of isthmic epithelium of a mare oviduct at the oestrus phase. (a), the ciliated cells displayed a dark cytoplasm, many round mitochondria and the cilia were enclosed in a dense matrix; the non-ciliated (secretory) cells differed in the cytoplasm electron-density and contained secretory granules; (b), apical protrusions of two non-ciliated cells showing different type of secretory granules; (c), apical region of two dark non-ciliated cells showing different types of granules and short microvilli; (d), supra-nuclear region of a clear non-ciliated cell showing Golgi apparatus and secretory granules; (e), supra-nuclear region of a dark non-ciliated cell showing the Golgi zone and some mitochondria. ab, apical blebs; CC, ciliated cells; ci, cilia; dNC, electron-dense non-ciliated cells; G, Golgi apparatus; m, mitochondria; mv, microvilli; n, nucleus; pNC, electron-lucent non-ciliated cells; sg, secretory granules; arrow, dense matrix surrounding the cilia; arrowhead, glycocalyx of the microvilli; asterisk, rough endoplasmic reticulum. Bar: a, 3 μm; b, 2.5 μm; c, 0.8 μm; d, 1 μm; e, 0.4 μm.

cytic vesicles suggests that in the infundibulum of mare oviduct the absorption and manipulation of the luminal fluid may occur. However, the rough endoplasmic reticulum seems to have a role in transforming endocytotic material [29].

Non-ciliated cells of ampulla and isthmus are surely secretory cells because of the presence of secretory granules. The apical region of ampulla non-ciliated cells presented large cytoplasmic protrusion containing secretory granules generally full of dark matrix, as well as some with moderate electron-dense matrix and occasionally electron-lucent vesicles too. In the isthmus the cytoplasm of non-ciliated cells was either electron-lucent or electron-dense and not all the non-ciliated cells showed apical protrusions. The latter cells contained apical microvilli which were covered with a well developed glycocalyx but no endocytic vesicles. This feature indicates that in the isthmus the non-ciliated cells could be involved in absorptive phenomena also. Recent immunohistochemical studies revealed that the luminal surface of the lining epithelium of mammalian oviduct participates in the epithelial fluid movement which lead to the optimization of the luminal microenvironment for fertilization and early embryonic development [30,31]. In the isthmus three types of granules were present. The more diffuse type of granule contained an electron-dense body surrounded by a less dark and homogeneous matrix; the second one displayed an electron-dense matrix and the third type, less numerous, was filled with a moderately electron-dense matrix. The first type of granule was mostly contained in the cytoplasmic protrusions, whereas the other two were more numerous in the apical region of secretory cells without protrusions. Although the difference in granules morphology could depend on their maturation stages, these results suggest that there are differences in the secretory activity and the contents of the secretory granules in each segment of mare oviduct. The ultrastructure of the secretory granules depend on their composition. Dense granules are proteinaceous while less dense granules are mucinous [4].

The observations obtained in mare oviduct are consistent with those in other mammals. Regional differences in oviductal secretory cells have been demonstrated also in other mammals such as goat [12], Chinese Meishan pig [13], woman [32], mouse [33,34], golden hamster [35], rabbit [36], bovine [37], rat [38], and baboon [39]. Regional expression of oviductal secretory proteins seems to be related to the function of the specific oviductal segment that synthesizes these proteins [4,7]. Lectin histochemistry studies revealed the existence of a distinct regional glycoprotein pattern in the mare oviduct as well as the presence of non-ciliated cell sub-types which could be related to their functional differences along mare oviduct [40,41]. In this study we observed that the isthmus contained the highest percentage of cells with secretory granules. This suggests that the epithelium of isthmic region of oviduct actively participates in the production of an unique biochemical milieu able to i) prevent polyspermic fertilization, ii) maintain the fertility of sperm, and iii) regulate capacitation and motility hyperactivation in order to ensure an effective sperm condition during ovulation [42]. The role of the isthmus appear to be of utmost importance in equine where the fertilization may occurs up to 6 days after mating [43].

In conclusion, the oviductal epithelium of mare shows regional variations in morphological features, numbers of ciliated and non-ciliated (secretory) cells, surface morphology and ultrastructural aspect of secretory granules. These differences could be related to the different functions of each segments that constitutes the mare oviduct.

Acknowledgments

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