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Invited Review

The mammalian oviductal epithelium: regional variations in cytological and functional aspects of the oviductal secretory cells

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Summary. The secretory cells in the epithelium of mammalian oviducts produce and release various secretory materials into the lumen. Secretions from such cells provide a suitable environment for the events that occur in the oviductal lumen. This review focuses on the regional differentiation of the secretory cells in mammalian oviducts. Many histological studies have demonstrated regional variations in both the morphological and ultrastructural features of the secretory cells in the oviductal epithelium. Regional differences have been found, for example, in the number of putative secretory granules in the oviductal secretory cells. Histochemical and immunocytochemical studies have also revealed regional differences in the localization of various materials in the oviductal epithelium, suggesting the possibility of regional specificity in the production of various secretory materials by the oviductal epithelial cells. Recent biochemical and immunoelectron microscopical studies have shown that biosynthesis of specific proteins or glycoproteins is associated with region-specific variations in epithelial cells in different oviductal segments. In particular, certain oviduct-specific glycoproteins are produced by secretory cells in specific regions of the oviduct and these glycoproteins may affect fertilization, embryonic development, and sperm functions. The oviductal epithelial cells also provide physiological support to gametes and embryos. The interactions of oviductal epithelial cells with gametes support the development of embryos and the maintenance of sperm functions in vitro. Some studies using coculture systems have suggested regional differences associated with such physiological support by oviductal epithelial cells. Moreover, the expression of functional proteins, such as growth factors, show segmental variations within the oviduct. The regional variations demonstrated in these studies may reflect distinct functional differences among the various segments of the mammalian oviduct. The proposal is presented that despite the fact that the mammalian oviductal tissue is not very complex in terms of structure, the oviductal secretory cells may be highly differentiated along the length of the oviduct.

Key words: Immunocytochemistry, Oviductal epithelium, Secretions, Reproduction

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Introduction

The oviducts (uterine tubes and Fallopian tubes) of mammals are simple tubular conduits that are derived embryologically from the cranial region of the primitive Müllerian ducts. The oviduct is a highly specialized structure during the reproductive period in females and it assumes one of the most basic roles in the reproductive process. The mammalian oviduct functions as more than a simple conduit for the transport of ovulated ova, spermatozoa, or developing embryos between the ovary and the uterus. The oviduct in its functional state is an active organ that maintains and modulates a dynamic fluid-filled milieu. Tubal (oviductal) fluid provides the necessary environment for the final maturation of gametes, fertilization, and subsequent embryonic development.

The epithelium of the oviduct is of the simple columnar type and consists of two kinds of cell, namely ciliated and nonciliated (secretory) cells. The ciliated cells play important roles in the transport of gametes (Odor and Blandau, 1973), while the nonciliated secretory cells synthesize and release specific secretory products (for review, see Oliphant, 1986). The secretions from secretory cells form the oviductal fluid together with a selective transudate of serum (Leese, 1988). Some of these secretory products associate with the gametes and/or the embryo and may play important roles in various reproductive events (for reviews, see Hunter, 1994; Gandolfi, 1995; Malette et al., 1995). Furthermore, the oviductal epithelial cells produce various functional molecules, such as enzymes and growth factors (Morishita et al., 1992; Carlsson et al., 1993). It

has been suggested that the interaction between oviductal epithelial cells and gametes might play an important role in the final maturation of male gametes (Ellington et al., 1993a,b).

The oviduct is a long, convoluted organ. The degree of convolution varies among species. The classification of the parts of the oviduct is based mainly upon macroanatomical features. In general, the oviduct can be divided into several parts, such as the fimbriae, ampulla, isthmus, and utero-tubal junction. The fimbriae are mainly involved in the transport of eggs from the ovary to the oviduct. The ampullar region is the part with the greatest diameter, and it is the site of fertilization in most mammals. The ampulla tapers down to the isthmus, which is the site of a sperm reservoir in some species. Thus, the biological events that occur along the length of the oviduct vary among the regions of the oviduct.

Marked regional variations in the morphological, histochemical, and biochemical characteristics of the oviductal secretory cells have been demonstrated in many species. However, the biological significance of such regional differences is not fully understood. The present review focuses on the regional variations in the morphological, histochemical, immunocytochemical, and physiological features of the secretory cells in the mammalian oviduct and a discussion is presented on the relationship between the regional variations and the biological functions of the oviductal epithelial cells in reproductive events.

Regional variations in morphological features of oviductal secretory cells

Several reviews of studies of mammalian oviductal epithelial cells by light and electron microscopy have been published (Nilsson and Reinius, 1969; Fredericks, 1986; Salamonsen and Nancarrow, 1994). Electron microscopic studies have revealed, in particular, that there are greater differences than might otherwise be expected in the oviducts of various species, among the various segments of a single oviduct, and within a given segment of an oviduct under various hormonal conditions. The present review refers mostly to electron microscopic studies for descriptions of regional variations in the morphological features of the oviductal secretory cells in mammals.

We shall also discuss the relationship between oviductal epithelial cells and the gametes or embryos in an attempt to correlate the structural variations in oviductal epithelial cells with the specific aspect of the reproductive process.

Classification of oviductal segments

The classification of the segments of the mammalian oviduct is based mainly upon the microscopic appearance of the oviduct. In general, this classification is consistent with the common macroanatomical features in most mammalian species. The oviduct can be divided into several regions by reference to the characteristic histological features (Nilsson and Reinius, 1969). Four major segments of the oviduct can be distinguished from differences in the structure of the epithelium: the preampulla, the ampulla, the isthmus, and the utero-tubal junction. The preampulla includes both the fimbriae and infundibulum, which merge gradually into the ampulla. Figure 1 shows the morphology of the mucosal epithelium in three regions of the oviduct of the golden hamster. The fimbriae are visible finger-like mucosal folds (Fig. 1a). In the ampulla, the mucosa forms numerous elaborately branched folds (Fig. 1b). The ampulla is the region with the largest diameter and the most intricate folding of the mucosal epithelium. In the

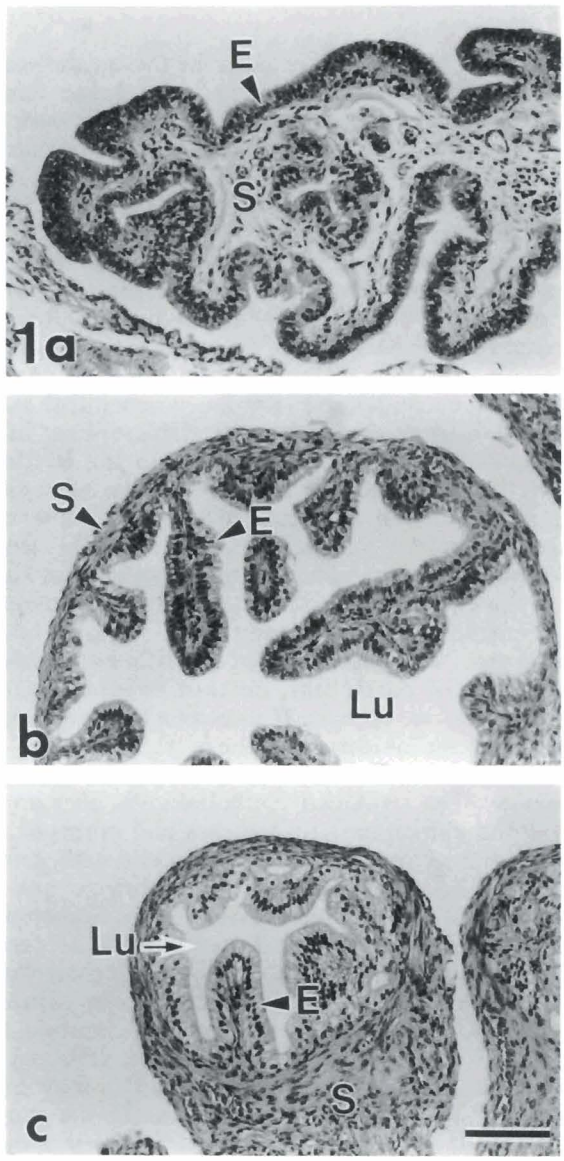

Fig. 1. Light photomicrographs of the oviduct of the golden hamster in cross-section, showing the fimbriae **(a)**, ampulla **(b)**, and isthmus **(c)**. E: Epithelium; Lu: lumen; S: stroma. Bar: 100 μm.

isthmus (caudal region), the longitudinal folds are much less extensive and less highly branched and the muscle layer is well developed (Fig. 1c). The utero-tubal junction has well-developed muscle layers and the narrowest lumen of the entire oviduct.

Relative numbers of secretory and ciliated cells

Without exception, two types of cell are always present in the epithelium of the mammalian oviduct, namely, ciliated and nonciliated (secretory) cells. The relative numbers of these cells have been examined in a variety of species during the estrous (or menstrual) cycle and under various experimental conditions (Verhage et al., 1979, 1990; Odor et al., 1980; Abe and Oikawa, 1989, 1991b, 1992, 1993a,b; Abe, 1994; Odor and Augustine, 1995). The percentages of secretory and ciliated cells in the oviductal epithelium of the golden hamster and the cow are shown in Figs. 2, 3, respectively. In the oviduct of the golden hamster, the number of ciliated cells in the fimbriae is very large compared to that in other regions. The secretory cells account for 65% and 97% of all the epithelial cells in the ampulla and isthmus, respectively. In the cow, the ciliated cells are predominant in the fimbriae, as they are in the golden hamster. In contrast, secretory cells predominate in the ampullar and isthmic epithelia. Half of the epithelial cells are secretory cells in the ampullar and isthmic regions of the bovine oviduct. There is no discernible regularity in the distribution of these cells, but ciliated cells are more abundant in the preampullar region and secretory cells predominate in the lower parts of the oviduct, such as the isthmus.

Distinct changes associated with the estrous or menstrual cycle have been observed in the relative numbers of secretory and ciliated cells in some species (Brenner, 1969; Rumery et al., 1978; Odor et al., 1980; Abe and Oikawa, 1992). In the cow, there is a significant decrease in the number of ciliated cells and an increase in the number of secretory cells in the fimbrial and ampullar epithelium during the luteal phase of the estrous cycle (Fig. 3). In contrast, the percentages of secretory and ciliated cells in the other regions do not differ significantly between the follicular phase and the luteal phase. These observations show that the fimbrial and ampullar epithelia are similar in that both undergo partial deciliation during the luteal phase, while the epithelium in the other regions does not. They suggest, moreover, that there are regional differences in the cyclic changes in ciliation of the cells of the oviductal epithelium. Similar cyclic changes have been observed in the oviducts of primates. In the rhesus monkey, large numbers of cilia are formed during the follicular phase of the cycle and extensive atrophy and deciliation occur during the luteal phase of the menstrual cycle (Brenner, 1969). Odor et al. (1980) showed, in a quantitative study of the oviduct of the pig-tailed monkey, that there is a striking and significant decrease in the number of normally ciliated cells and an increase in the number of nonciliated cells during the late luteal phase. In the epithelium of the golden hamster oviduct, the proportions of secretary and ciliated cells do not change in any region during the estrous cycle (Fig. 2). No cyclic changes in the proportions of secretory and ciliated cells have been found in the rat oviduct (Abe, 1994). It appears that the oviductal epithelium of species with a long-term estrous cycle usually undergoes dramatic cyclic changes in the relative numbers of the two types

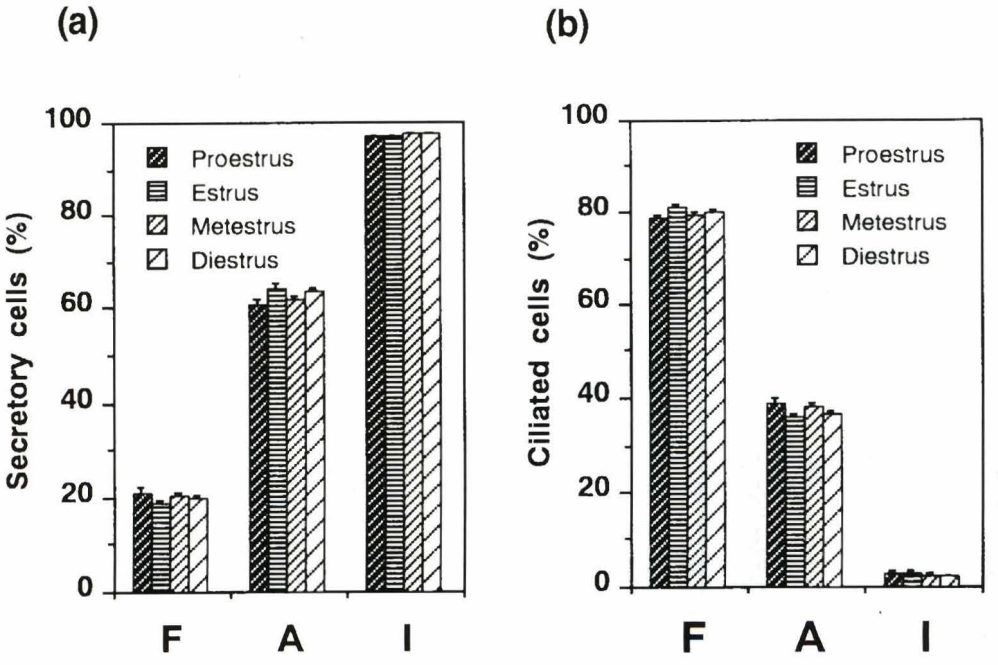

Fig. 2. The mean percentages of secretory (**a**) and ciliated (**b**) cells in the fimbriae (F), ampulla (A), and isthmus (I) of the oviduct of the golden hamster during the estrous cycle. Values are expressed as means±SEM (N=7).

of epithelial cell, but such changes can hardly be detected in species with a short cycle, such as the golden hamster and the rat.

Surface morphology of the oviductal epithelium

Detailed studies by scanning electron microscopy of the oviductal epithelium of many mammals have been reported (Patek et al., 1972a,b, 1973a,b; Patek and Nilsson, 1973; Stalheim et al., 1975; Wu et al., 1976; Nayak, 1977; Rumery et al., 1978; Rumery and Eddy, 1978; Jansen, 1980; Abe and Oikawa, 1992, 1993b; Abe et al., 1993c). Some of these studies have demonstrated regional variations in the cyclic changes associated with the oviductal epithelial cells.

Marked cyclic changes were observed on the surface of the epithelium in the fimbriae and ampulla of the oviducts of the prolific Chinese Meishan pig (Abe and Oikawa, 1992). The cells of the fimbrial epithelium in the follicular phase were densely ciliated, and the cilia partially concealed the bulbous processes of the secretory cells (Fig. 4). During the luteal phase, the secretory cells predominated in the epithelium, and the ciliated cells were hidden by the processes of the secretory cells (Fig. 4a,b). The ampullar epithelium showed similar changes, but to a lesser extent (Fig. 4c,d). In contrast to the epithelium, and in particular the ciliated cells of the fimbriae and ampulla, the isthmus and utero-tubal junction showed few changes between the follicular phase and the luteal phase (Fig. 4e,f). Similar findings have been made in cows (Abe and Oikawa, 1993b) and goats (Abe et al., 1993c).

In the cow, quantitative data revealed that the height of ciliated cells falls dramatically in the fimbriae and ampulla at the luteal phase, while that of secretory cells remains almost unchanged (Fig. 5). We have obtained similar results in our studies of Chinese Meishan pigs and goats (unpublished results). It appears that the dramatic reduction of height of ciliated cells in the fimbrial and ampullar epithelium is responsible for the reduction in the number of cilia on the surface of the oviductal epithelium in these domestic farm animals, even though a partial reduction can also be accomplished by a decrease in the number of ciliated cells. In contrast, the height of secretory and ciliated cells barely changes in the epithelium of the isthmus and utero-tubal junction between the follicular phase and the luteal phase (Fig. 5).

These regional variations associated with the cyclic changes in the ciliation of the oviductal epithelium appear to reflect the function of the various regions in reproductive events. In the fimbriae, the cilia are considered to be primarily responsible for the gathering up and transport of ovulated eggs, and the cilia of the ampullar epithelium have a similar function (Odor and Blandau, 1973). A richly ciliated epithelium at ovulation is important. The function of the ciliated cells in the isthmic region has not been clarified. Recently, some studies have demonstrated that spermatozoa usually bind, via the acrosomal region, to the epithelial cells of the oviduct and mainly to the ciliated cells (Pollard et al., 1991; Suarez et al., 1991). After detachment from the epithelial cells, the spermatozoa maintain both their motility and fertilizing capacity (Smith and Yanagimachi, 1989, 1990). A study by Hunter et al. (1991) revealed specific and active interactions between the tips of the cilia and the flagella of bull spermatozoa in the caudal isthmus of the oviduct of mated bovines. The cilia in the isthmus might act to regulate the progression of capacitated spermatozoa via contacts with their flagella. These studies indicate that the isthmus and/or the utero-tubal junction of the oviduct might

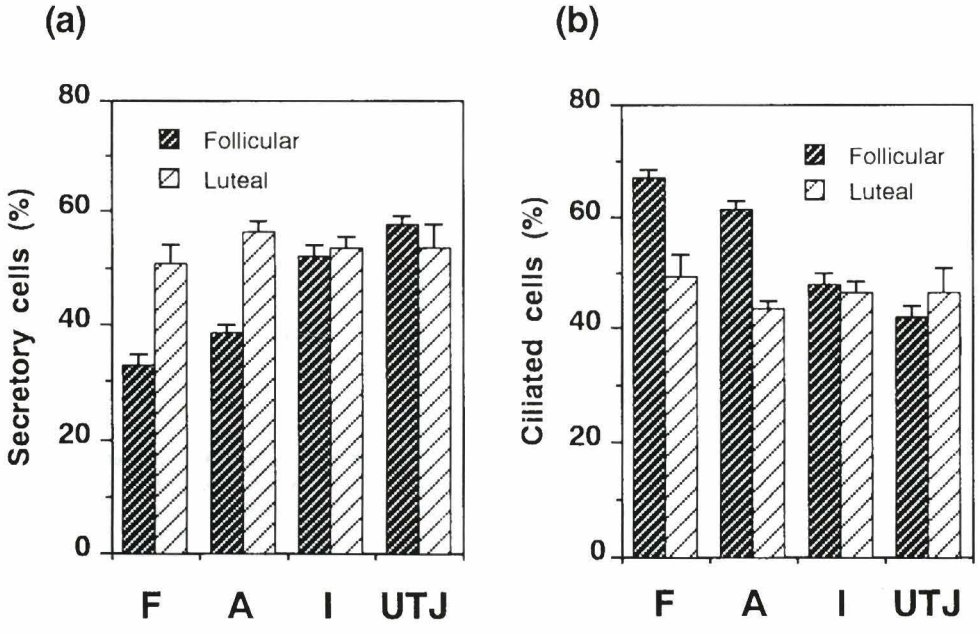

Fig. 3. The mean percentages of secretory (**a**) and ciliated (**b**) cells in the fimbriae (F), ampulla (A), isthmus (I), and utero-tubal junction (UTJ) of the bovine oviduct at the follicular and luteal phases of the estrous cycle. Values are expressed as means±SEM (N=10-25).

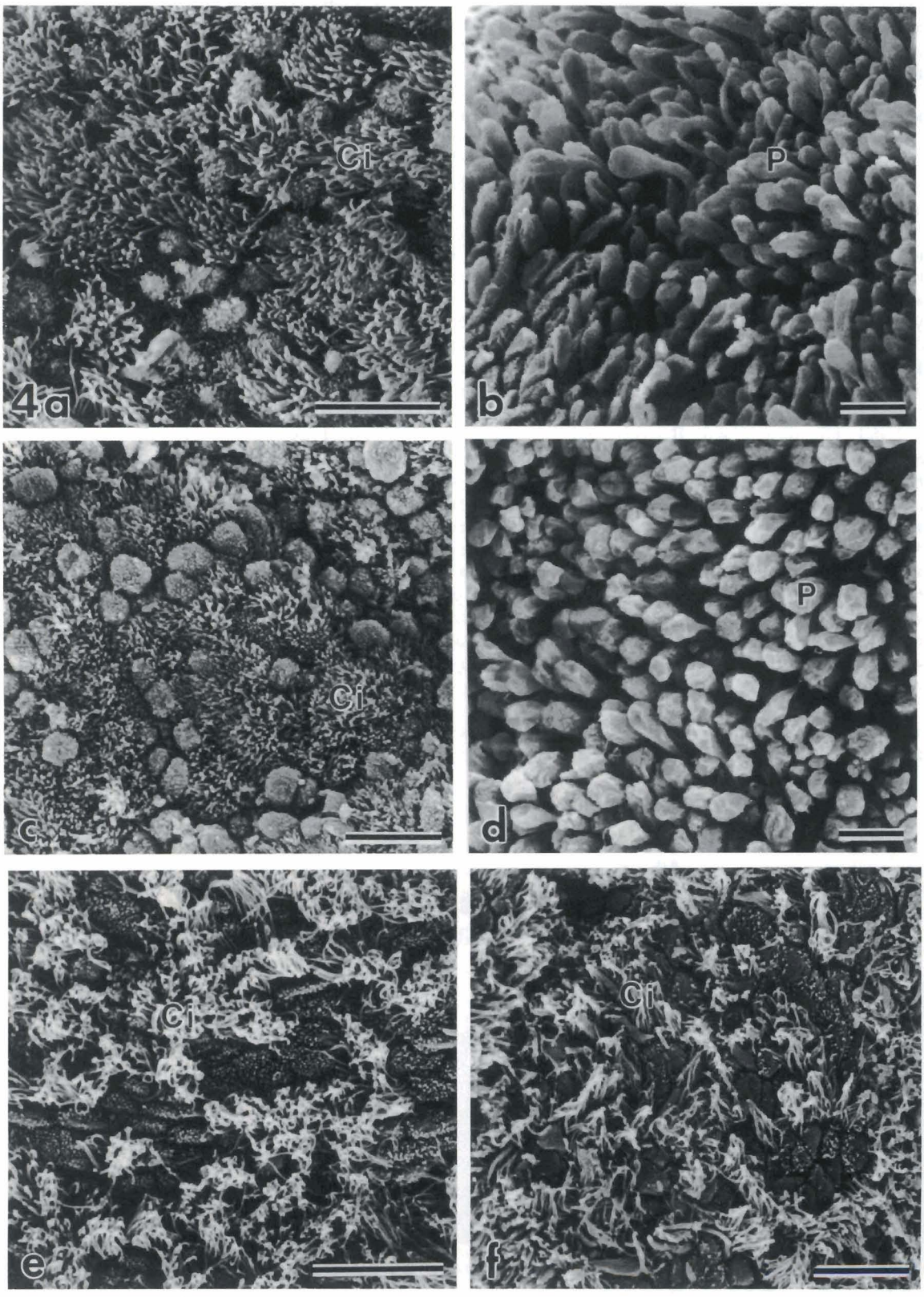

Fig. 4. Scanning electron micrographs of the oviductal epithelium of the prolific Chinese Meishan pig at the follicular phase (a, c, e) and the luteal phase (b, d, f) of the estrous cycle **a, b.** Fimbrial epithelium. The micrograph of fimbrial epithelium at the follicular phase shows the dense ciliation, with variations in the size and shape of the processes (P) of secretory cells. The epithelium at the luteal phase shows the conspicuous processes of secretory cells. Most of the cilia are concealed by the bulbous processes of secretory cells. **c, d.** Ampullar epithelium. The epithelium in the follicular phase is densely ciliated. The cilia (Ci) conceal the bulbous processes of secretory cells. The bulbous apical processes are bigger in this region than in the fimbriae and show greater variations in size and shape. At the luteal phase, most of the cilia are concealed by the bulbous apical processes. **e,f.** Isthmic epithelium. The ciliated and secretory cells are evenly distributed in the isthmic epithelium during the estrous cycle. Conspicuous bulbous processes of secretory cells are not observed in the isthmus. Bars: 10 μm.

serve as a site for storage of spermatozoa and that the epithelial cells in these regions (the ciliated and/or nonciliated secretory cells) might have the ability to maintain the viability and fertilizing capacity of spermatozoa and to regulate the progression of capacitated spermatozoa during the preovulatory period.

Ultrastructure of the oviductal secretory cells

The ultrastructural features of oviductal secretory cells have been investigated by transmission electron microscopy in many species. An early review of the morphology of the secretory cells that line the epithelium of the mammalian oviduct is available (Nilsson and Reinius, 1969). In most mammals studied, the secretory cells of the oviductal epithelium contain putative secretory granules. In several species, it has been suggested that two types of secretory granule, namely, electron-dense and electron-lucent granules, are present in the oviductal secretory cells (Borell et al., 1956; Nilsson, 1958; Fredricsson and Björkman, 1962; Hashimoto et al., 1964; Clyman, 1966; Brower and Anderson, 1969; McCarron and Anderson, 1973; Willemse and Van Vorstenbosch, 1975b; Komatsu and Fujita, 1978; Rüsse and Liebich, 1979; Jansen and Bajpai, 1982; Odor et al., 1983; Hollis et al., 1984; Abe and Oikawa, 1991b; Abe et al., 1993b; Odor and Agustine, 1995), while various observations have shown that there are marked differences among species in the morphological features of the secretory granules.

Marked regional differences in the ultrastructural features of the secretory granules in the oviductal secretory cells have been described. In the bovine at the follicular stage of the estrous cycle, electron microscopy revealed that the nonciliated cells of the ampullar and fimbrial epithelia contained numerous secretory granules (Fig. 6), some of which contained lamellar structures and some of which did not (Fig. 7a). In the isthmic secretory cells, small secretory granules were present in the cytoplasm, but their structural features were different from those of the granules in the ampulla and fimbriae (Fig. 7b). A more recent study demonstrated that the number and location of secretory granules in the secretory cells of the bovine oviductal epithelium show both cyclic and segmental variations (Eriksen et al., 1994). Numerous secretory granules were found in the infundibular and ampullar secretory cells during the period of transoviduct migration of the zygote and embryo but most of cells at the utero-tubal junction were free of secretory granules.

In the ampullar and infundibular segments of the mouse oviductal epithelium, numerous electron-dense secretory granules were observed in the cytoplasm of epithelial cells (Kapur and Johnson, 1988). Instead, the isthmic secretory cells contained a population of apically located granules with more diffuse and filamentous contents. Marked differences in the type and number of granules in the secretory cells were observed in the oviduct of the golden hamster (Abe and Oikawa, 1991b). These secretory cells contained at least two types of secretory granule, namely, moderately electron-dense and electron-lucent granules. The moderately electron-dense secretory granules predominated in the secretory cells of the golden hamster oviduct, while the electron-lucent granules were observed in a limited region of the fimbriae. In the rat, the secretory granules of the fimbriae and ampulla were small, while those of the isthmus were found to be large and the cells of this region contained numerous secretory granules (Abe, 1994).

The secretory cells of the oviduct of the pig-tailed monkey, *Macaca nemestrina*, have two types of the

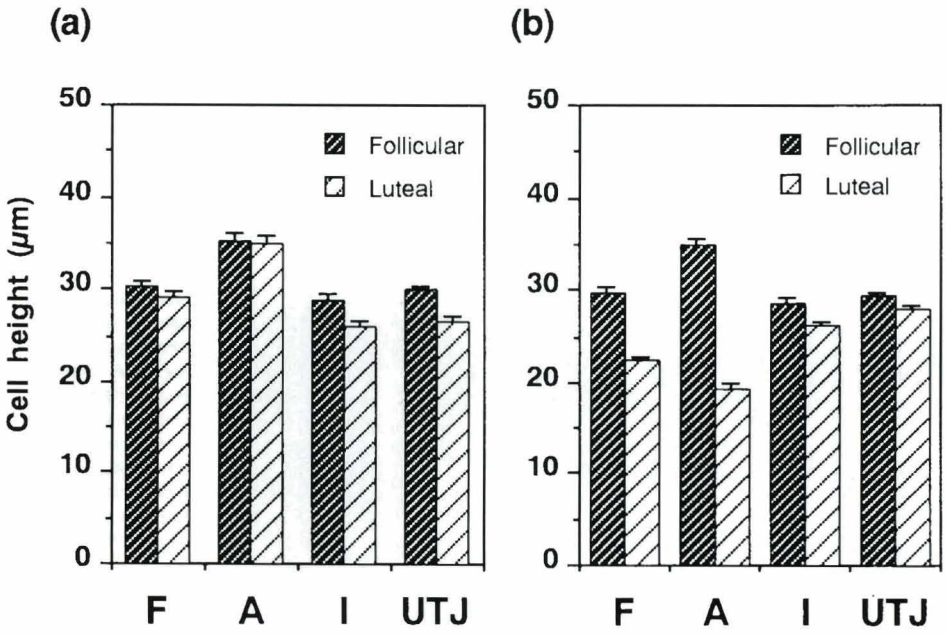

Fig. 5. The height of secretory **(a)** and ciliated **(b)** cells in the fimbriae (F), ampulla (A), isthmus (I), and utero-tubal junction (UTJ) of the bovine oviduct at the follicular and luteal phases. Values are expressed as means±SEM. (N=32-50).

secretory granule: those with an electron-dense, homogeneous matrix; and those with lamellar structures within a moderately electron-dense matrix (Odor et al., 1983). In the ampullar and isthmic secretory cells, secretory granules are more abundant than they are in fimbrial cells during the late preovulatory and early postovulatory periods. The fimbrial secretory cells contain no or only a few small, mainly homogeneous,

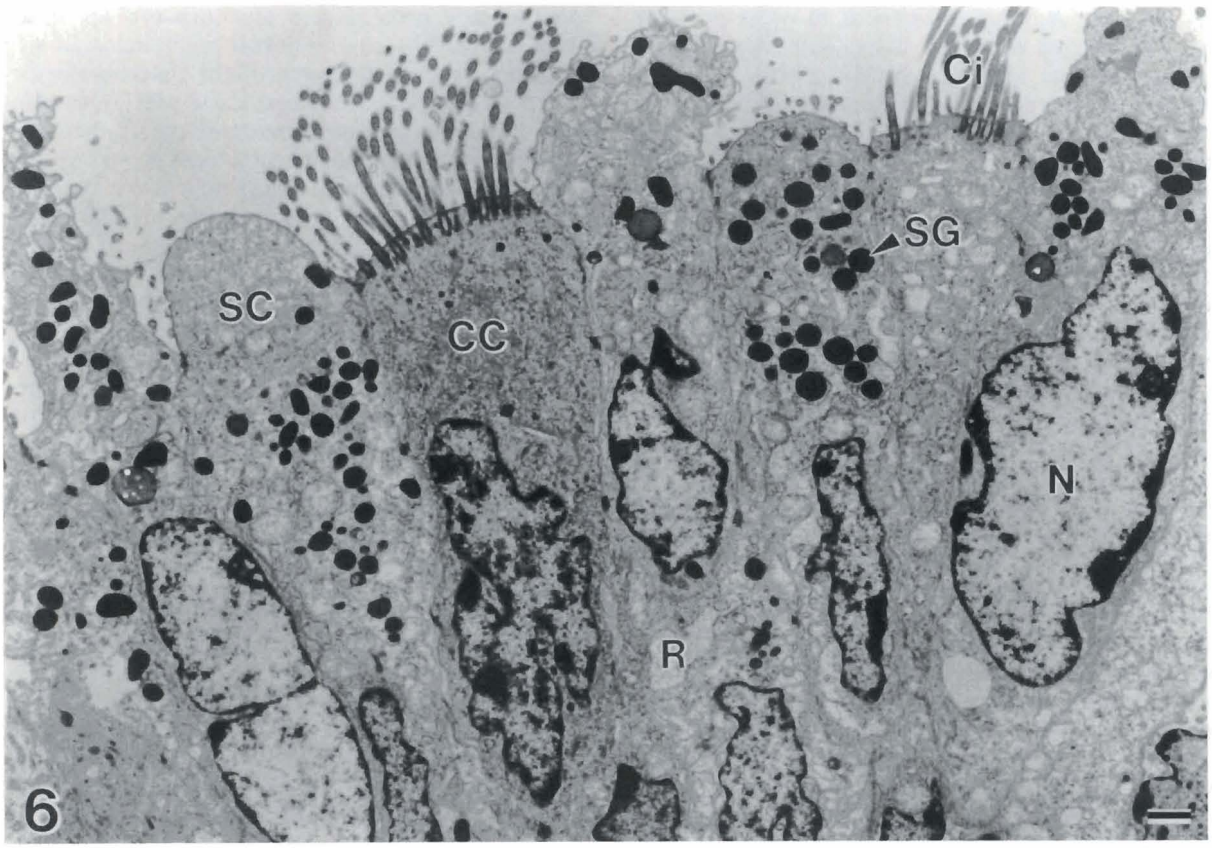

Fig. 6. Electron micrographs of ampullar epithelial cells of a bovine oviduct at the follicular phase. The secretory cells (SC) contain numerous secretory granules (SG) in the supranuclear cytoplasm. Well-developed Golgi apparatus and rough endoplasmic reticulum are present in the cytoplasm. CC: Ciliated cell; Ci: cilia; N: nucleus; R: rough endoplasmic reticulum. Bar: 1 μm.

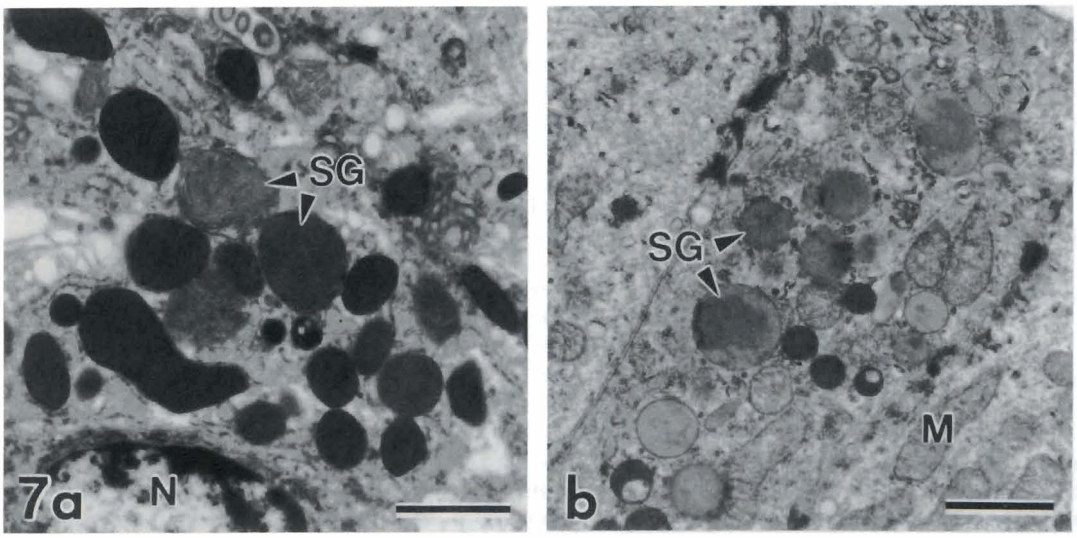

Fig. 7. Parts of secretory cells in the ampulla (**a**) and isthmus (**b**) of a cow at the follicular phase. The ampullar secretory cells contain two types of secretory granule (SG). One type has an electron-dense, homogeneous matrix and the other has conspicuous lamellar structures and a moderately electron-dense matrix. Some secretory granules are present in the supranuclear cytoplasm of the isthmic secretory cell. Most of the isthmic granules are smaller than those of the ampulla and lack a lamellar structure. M: Mitochondria; N: nucleus. Bars: 1 μm.

secretory granules. During the late luteal phase, a few small secretory granules can be found in the apical region of secretory cells in the ampulla, but no fimbrial or isthmic secretory cells have secretory granules.

In addition to the differences among secretory granules, marked regional differences in other granular structures have been observed. Lysosome-like vesicles containing a dense material and/or a fine granular material were observed in the isthmic secretory cells of the golden hamster oviduct (Abe and Oikawa, 1990a, 1991b). Most of these vesicles were located in the infranuclear cytoplasm and they were frequently seen to have fused with the secretory granules. The vesicles were positively stained for acid phosphatase activity and this enzyme is one of the major lysosomal enzymes (unpublished results). Borell et al. (1959) reported vesicles that were partially filled with a dense material in the secretory cells of the oviducts of the rats during estrus. Similar vesicles containing a dense material have been frequently observed in the isthmic secretory cells and occasionally in the ampullar cells of the rat oviduct (Abe, 1994). The vesicles were usually observed in the Golgi areas. Therefore, it seems possible that the vesicles might originate from the Golgi apparatus. The origin of such vesicles and the nature of their contents remain to be fully characterized.

The cells in the mouse oviduct contain some fat granules and vacuoles, and these structures increase in number toward the fimbriated end (Nilsson and Reinius, 1969). In the golden hamster, many electron-dense granule-like structures that resembled lipid droplets were found in the fimbrial secretory cells (Abe and Oikawa, 1991a). Similar structures have been reported in the rat (Abe, 1994). Many large bodies were found in the fimbrial nonciliated cells in the rat oviduct and occasionally it appeared that their contents were released by an exocytosis-like mechanism. Lipid droplets were also observed in the ciliated cells of the fimbrial epithelium in the baboon oviduct (Odor and Augustine, 1995).

The regional variations in the ultrastructure of granules can be ascribed to the secretory functions of the oviductal secretory cells during the reproductive process. The ultrastructure of the secretory granules gives some clues to their composition. For example, dense granules are proteinaceous while less dense granules are mucinous. The regional differences in the ultrastructure and in the numbers of secretory granules in the cells might reflect the fact that the nature of the secretion from oviductal epithelial cells and their secretory activities differ among the various segments of the oviduct.

Secretory products of oviductal epithelium

The fluid present in the oviductal lumen provides an appropriate environment for the final maturation of the male gametes, for fertilization, and for early embryonic development. Therefore, the components and sources of the oviductal fluid are of major interest if we are ever to understand all the details of these events. The oviductal fluid is a combination of secretory products from the oviductal epithelial cells and a transudate of serum (Leese, 1988; Malayer et al., 1988). It has been shown that several proteins and glycoproteins are synthesized and secreted by the oviductal epithelial cells of almost all species studied. Some of the macromolecules have been characterized biochemically and immunologically and attempts have been made to clarify their biological function. Some oviductal secretions appear responsive to the cyclic influence of hormones, while others may be produced at a constant rate. It has also been suggested that there exists a gradient in secretion of these proteins or glycoproteins from the fimbria through the ampulla and into the isthmus, or even some absolute distinctions among these regions. In this section, we shall focus on the regional variations in oviductal secretion in several species and discuss the biological significance of the regional differences in the localization of oviductal secretory products in reproductive events.

Regional differences in the synthesis of oviductal secretory proteins

Regional differences in the biochemical characteristics of secretions from the oviductal epithelium and in the secretory activity of oviductal epithelial cells have been reported in some species. Nieder and Macon (1987) investigated the changes in the protein composition of oviductal secretions during early pregnancy in the mouse. Although secretions from the ampulla and from the isthmic region of the mouse oviduct contained many proteins in common, each region also secreted its own characteristic proteins. Such results suggest that proteins secreted by a particular region might have specific roles in the support of the embryo as it traverses that region even though the functions of these proteins are unknown. The differential secretion of some glycoproteins in the ampulla and the isthmus has been observed in explant cultures of oviducts from cycling pigs and from pigs soon after fertilization (Buhi et al., 1990). These proteins, of 100 kDa, 85 kDa, and 75 kDa, respectively, were synthesized in the ampullar region during estrus but not in the isthmus. Furthermore, differences in the extent of induction or enhancement of the production of estrus-associated glycoproteins by estrogen have been observed between the ampulla and isthmus in the pig oviduct (Buhi et al., 1992).

Findings suggesting a gradient in the synthesis of oviductal proteins have also been observed in the sheep oviduct (Buhi et al., 1991). Murray (1992) examined whether estradiol-17 ß (E_2) alone or in combination with progesterone (P) could induce the biosynthesis of an estrus-associated glycoprotein (90-92 kDa) in the ampulla and/or the isthmus of the oviducts in ovariectomized sheep. This glycoprotein was produced by explants from the ampulla of oviducts or animals that

had been treated with E_2 alone or with E_2 plus P, but not from the isthmus. Subsequently, it was shown that ampullar and fimbrial explants synthesizing this glycoprotein when removed during early pregnancy, but that this glycoprotein was not synthesized in the isthmus obtained from estrus and pregnant sheep (Murray, 1993). Moreover, it has been demonstrated that steady-state levels of mRNA for this glycoprotein are highest in the ampulla and fimbriae at estrus and on day 1 of pregnancy when gamete transport and fertilization occur in the estrogen-dominated oviduct (DeSouza and Murray, 1995). These findings show that the estrus- and estrogen-dependent glycoprotein of 90-92 kDa is synthesized and released by the oviduct in a temporally and regionally specific manner and they emphasize the precise regulation of such synthesis at a time when fertilization and embryonic development are taking place in the oviduct.

A family of glycoproteins of high molecular mass has been identified in the baboon oviduct (Fazleabas and Verhage, 1986). They identified that the ampullar region synthesizes both acidic (100-120 kDa) and basic (120-130 kDa) proteins, whereas the acidic protein is dominant in the fimbrial region and the basic protein is dominant in the isthmic region (Verhage and Fazleabas, 1988). Similarly, a difference in the production of several proteins has been reported between ampullar and isthmic explants of the human oviduct (Buhi et al., 1989b). It has also been shown that explants of the rabbit oviduct are able to synthesize and secrete specific sulphated glycoproteins in vitro and that there is a regional difference in the type and extent of secretion between ampullar and isthmic segments (Hyde and Black, 1986). There appears to be a gradient in the synthesis of these oviductal secretory products. Oviductal secretory activity is greater in the ampullar than in the isthmic oviductal region in many species (Hyde and Black, 1986; Buhi et al., 1989a,b, 1990, 1991; Erickson-Lawrence et al., 1989; Wegner and Killian, 1992; McDowell et al., 1993).

The studies cited above strongly suggest that distinct differences exist in secretions from the different regions of the mammalian oviduct. What is the biological significance of such putative regional differences in the production of oviductal secretions? Some studies have suggested that there are regional differences in the physiological effect of the oviductal secretions on the sperm functions. One study demonstrated that the motility of rabbit spermatozoa was reduced by flushings from the isthmus but was increased by flushings from the ampulla (Overstreet et al., 1980). Recently, Abe and colleagues demonstrated that oviductal flushings and the culture medium of epithelial cells from oviducts of cows at the follicular phase of the estrous cycle support the viability and motility of bovine spermatozoa in culture in vitro (Abe et al., 1995c). The flushings obtained from the ampullar region of oviducts were most effective for the maintenance of viability and of motile activity; for example, the forward motion of spermatozoa. This study suggests that the oviductal fluid in the ampulla at the follicular stage provides a suitable environment for the maintenance of the viability and motility of bovine spermatozoa and that secretory products of oviductal epithelial cells are responsible for this maintenance of both the viability and the motility of spermatozoa.

Prior to fertilization, spermatozoa acquire the ability to undergo the acrosome reaction and to fertilize eggs by a process known as capacitation (Chang, 1951). The isthmic segment of the mammalian oviduct is believed to be a primary site of sperm capacitation (Harper, 1973; Hunter and Nichol, 1988). Parrish et al. (1989) and McNutt and Killian (1991) demonstrated that bovine oviductal fluid causes capacitation of spermatozoa and sustains their motility in vitro. Glycosaminoglycans have been suggested to be the capacitating factor in oviductal fluid at estrus (Parrish et al., 1989). Anderson and Killian (1994) reported the effects of macromolecules from conditioned medium from cultures of bovine oviductal explants on the motility and capacitation of spermatozoa. Conditioned medium from cultures of explants from the isthmus at estrus caused capacitation of significantly more spermatozoa than that from the ampulla. This study also suggested that the proteins, glycosaminoglycans, and proteoglycans in the conditioned medium might be responsible for capacitation of bovine spermatozoa. It appears that secretions from the isthmus might play a major role during sperm capacitation in vivo. The studies cited above suggest that there might be differences in the physiological effects of tubal fluids and secretions(s) in the different regions of the oviduct.

Localization of oviduct-specific glycoproteins

Various oviduct-specific glycoproteins that are present in the oviductal fluid have been identified and characterized in several species. These species include the mouse (Kapur and Johnson, 1985, 1986), golden hamster (Leveille et al., 1987; Oikawa et al., 1988; Abe et al., 1992), rat (Abe and Abe, 1993), sheep (Sutton et al., 1984a, 1986), pig (Buhi et al., 1989a), cow (Malayer et al., 1988; Boice et al., 1990a; Gerena and Killian, 1990), goat (Gandolfi et al., 1993; Abe et al., 1995a), baboon (Fazleabas and Verhage, 1986; Verhage and Fazleabas, 1988; Verhage et al., 1989), and human (Verhage et al., 1988; Wagh and Lippes, 1989). These glycoproteins of high-molecular-mass originate from the oviductal epithelium and some have been shown to associate with ovulated eggs and/or developing embryos (Brown and Cheng, 1986; Hedrick et al., 1987; Kapur and Johnson, 1988; Kan et al., 1988, 1989; Gandolfi et al., 1989, 1991; Abe and Oikawa, 1990b; Boice et al., 1990b, 1992; Wegner and Killian, 1991; Abe et al., 1995a) and with the surface of spermatozoa (Sutton et al., 1984b; Lippes and Wagh, 1989; McNutt et al., 1992; King and Killian, 1994; Abe et al., 1995b). Although the critical biological functions of these oviductal glycoproteins are unknown, it has been suggested that

the oviductal glycoproteins might affect the fertilization and capacitation of spermatozoa (Kimura et al., 1994; King et al., 1994; Boatman and Magnoni, 1995). Most of these oviduct-specific glycoproteins originate from the nonciliated secretory cells in the oviductal epithelium. Immunocytochemical studies with antibodies against these glycoproteins have demonstrated that specific oviductal glycoproteins are present within putative secretory granules of the oviductal secretory cells in the mouse (Kapur and Johnson, 1988), golden hamster (Kan et al., 1988, 1989; Abe and Oikawa, 1990a, 1991a), rat (Abe and Abe, 1993; Abe, 1996), rabbit (Oliphant et al., 1984), sheep (Gandolfi et al., 1991; Murray, 1992), pig (Buhi et al., 1993), cow (Boice et al., 1990a; Abe et al., 1993b), baboon (Verhage et al., 1990), and human (Rapisarda et al., 1993; O'Day-Bowman et al., 1995).

In the mouse, Kapur and Johnson (1986) showed that there are regional differences in the localization of a 215-kDa glycoprotein (GP215), which is secreted by the oviductal epithelium and is subsequently sequestered within the perivitelline space of oocytes and developing embryos. At the ultrastructural level, this glycoprotein was localized in the putative secretory granules only in the cranial segments (infundibular and ampullar epithelium) of the oviduct, again suggesting regional differences in the composition of oviductal secretions (Kapur and Johnson, 1988).

Several groups of researchers have studied the ultrastructural localization of oviduct-specific glycoproteins in the oviductal epithelium of the golden hamster. Kan and colleagues demonstrated by immunoelectron microscopy that the 160- to 250-kDa glycoprotein designated hamster oviductin-1 (Léveillé et al., 1987; Robitaille et al., 1988; St-Jacques and Bleau, 1988; St-Jacques et al., 1992) is localized in the putative secretory granules of nonciliated cells in the golden hamster oviduct (Kan et al., 1988, 1989, 1993). This glycoprotein is transferred to the zona pellucida of the oocyte during transit through the oviduct (Kan et al., 1988, 1989, 1990, 1993) and later appears to be internalized by blastomeres of the embryo and further processed through the endosomal/lysosomal pathway (Kan et al., 1993; Kan and Roux, 1995). In other studies of the golden hamster system, an oviductal glycoprotein of 200-240 kDa has been identified (Araki et al., 1987; Oikawa et al., 1988). Using a monoclonal antibody, Abe and colleagues demonstrated that this glycoprotein is produced and secreted by the secretory cells in the

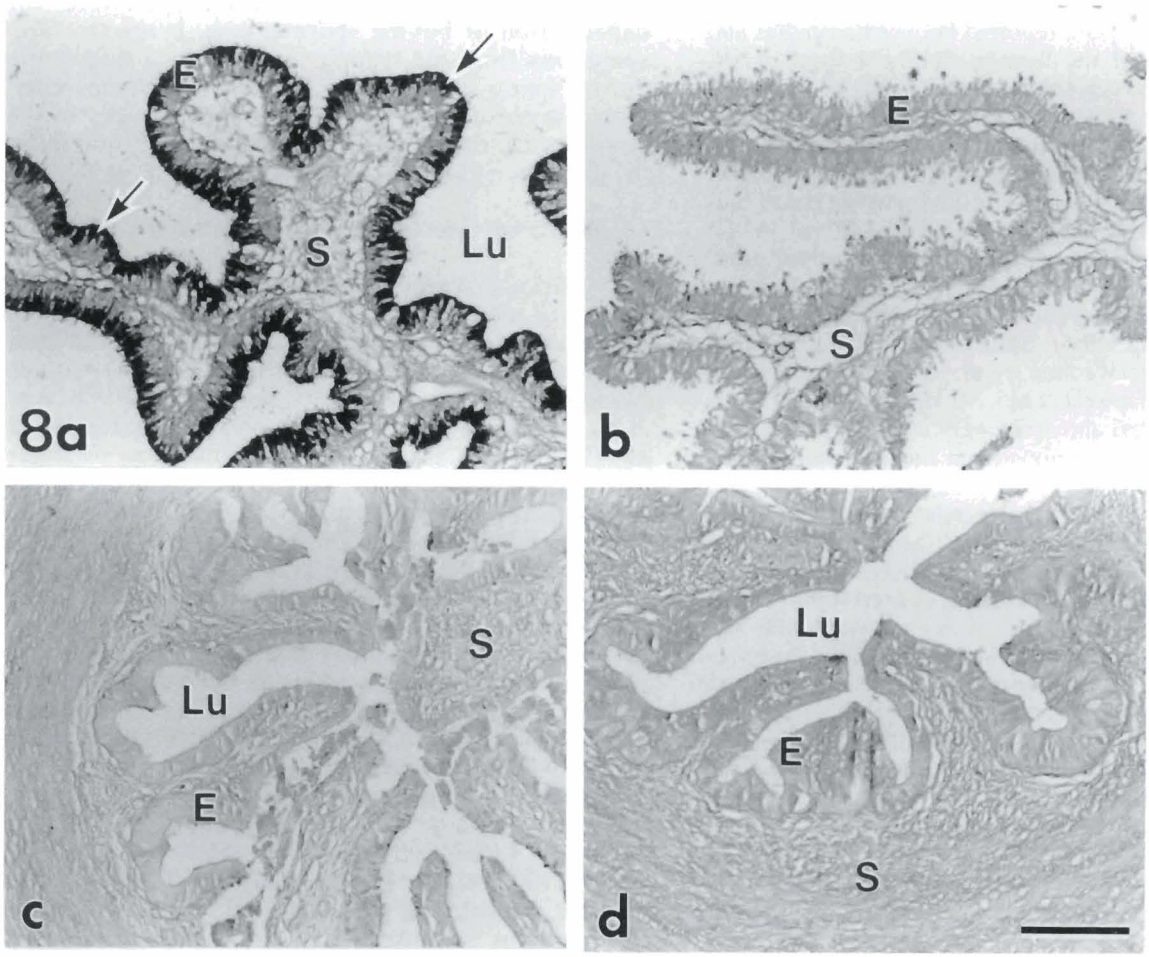

Fig. 8. Immunoperoxidase labeling with a monoclonal antibody against a bovine oviduct-specific glycoprotein (Abe et al., 1993a) of sections of the ampullar (a, b) and isthmic (c, d) regions of the bovine oviduct. **a, c.** Follicular phase. **b, d.** Luteal phase. The monoclonal antibody reacted strongly with the supranuclear cytoplasm of epithelial cells in the ampulla at the follicular phase (arrows in a). No specific staining is visible in the oviductal epithelium of the ampulla at the luteal phase (b) nor in the isthmic epithelium at the follicular (c) and luteal (d) phases. E: Epithelium; Lu: lumen; S: stroma. Bar: 100 μm.

epithelium of the golden hamster oviduct (Abe and Oikawa, 1990a, 1991a) and subsequently becomes associated with the zona pellucida and perivitelline matrix of the ovulated egg (Abe and Oikawa, 1990b; Abe et al., 1992). A detailed study by immunoelectron microscopy showed that this glycoprotein is secreted primarily by ampullar and isthmic secretory cells and to a lesser extent by fimbrial cells, suggesting regional and cellular differences in secretion in the golden hamster oviduct (Abe and Oikawa, 1991a).

In the sheep, Gandolfi et al. (1991) demonstrated immunocytochemically that a 92-kDa glycoprotein is present only in nonciliated secretory cells of the ampulla and not in the isthmus. Murray (1992) demonstrated similarly that the sheep oviduct undergoes region-specific changes in the production of an estrus-associated glycoprotein (90-92 kDa), and these results correspond to those of biochemical studies. This glycoprotein was only found in the secretory granules in the secretory cells of the ampullar region, an indication that this glycoprotein is produced exclusively by the region of the oviduct in which fertilization and early embryonic development take place. In contrast, the glycoprotein was not found in the isthmic region, the site of sperm storage.

In other species, similar regional differences in the localization of oviductal glycoproteins have been observed. The oviductal epithelium of the goat produces an oviduct-specific antigen (glycoprotein) that is immunologically similar to the oviduct-specific glycoprotein of the bovine (Abe et al., 1995a). This antigen is localized in the fimbrial and ampullar epithelium of the oviduct at the follicular phase of the estrous cycle, but not in the isthmus. Moreover, the epithelial cells of the rat oviduct secrete a specific glycoprotein that is immunologically similar to the oviductal glycoproteins of the golden hamster (Abe and Abe, 1993). This glycoprotein is localized mainly in the isthmic secretory cells, a result that again suggests the marked regional specificity of the synthesis of this glycoprotein in the rat oviduct (Abe, 1996).

The biological significance of the regional differences in the localization of oviduct-specific glycoproteins is poorly understood because most of these glycoproteins have not yet been purified and the biological functions of these glycoproteins are still unclear. However, results of a series of studies using the bovine system strongly suggest the possible significance of such regional variations. In the bovine, Boice et al. (1990a) identified a 97-kDa estrus-associated glycoprotein in the oviductal fluid. This glycoprotein was localized within secretory granules of the secretory cells in the oviductal epithelium. Subsequent immunocytochemical studies (Abe et al., 1993a,b), using monoclonal antibodies specific for this bovine oviduct-specific glycoprotein (BOGP), revealed that this glycoprotein is localized in the oviductal epithelium of the ampullar and fimbrial regions at the follicular phase of the estrous cycle, but it is not present in the caudal isthmus or at the utero-tubal junction throughout the estrous cycle (Fig. 8). In an ultrastructural study, putative secretory granules of nonciliated cells in the fimbriae and ampulla were selectively labeled by the monoclonal antibodies (Fig.9a). No specific labeling was detected in the secretory granules of isthmic secretory cells (Fig. 9b). These studies suggested distinct differences in the secretion of this glycoprotein between the different segments of the bovine oviduct. Recently, BOGP (95kDa) was purified and the cDNA corresponding to this glycoprotein was isolated and sequenced (Sendai et al., 1994). Abe and colleagues showed that purified BOGP effectively improved the viability and motility of bovine spermatozoa in culture in vitro, suggesting that BOGP might be a potent factor for the maintenance of sperm viability and motility (Abe et al., 1995b; Satoh et al., 1995). The critical biological function of BOGP in vivo has not been evaluated. However, BOGP is mainly produced by the secretory cells in the ampulla of the

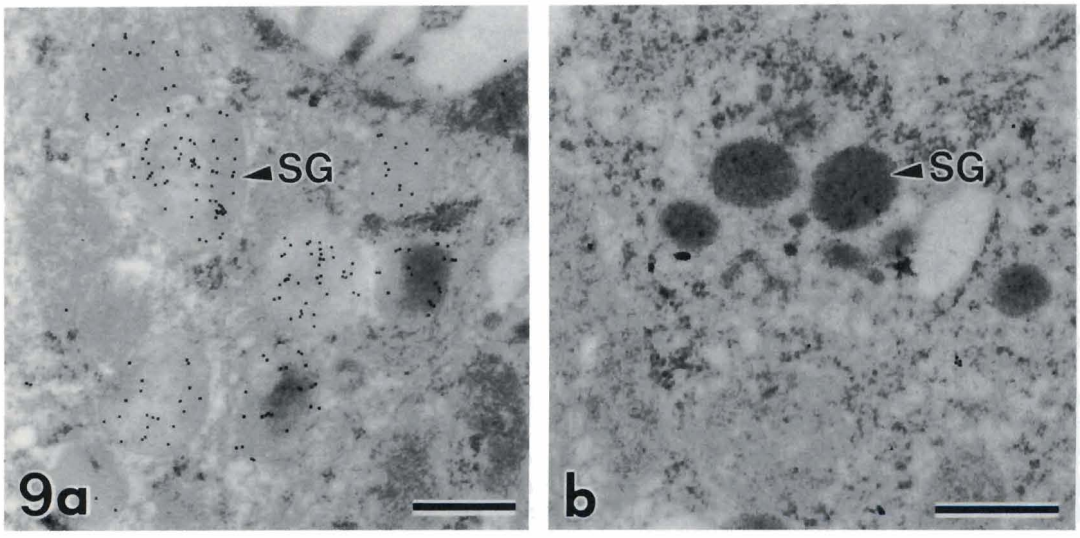

Fig. 9. Immunocytochemical labeling with a monoclonal antibody against the bovine oviduct-specific glycoprotein (Abe et al., 1993a) of secretory cells in the ampullar **(a)** and isthmic **(b)** epithelium from a cow at the follicular phase. Specific labeling with gold particles can be seen on the secretory granules (SG) in the ampullar secretory cell (a). No specific binding of gold particles is visible on the isthmic secretory granules (b). Bars: 0.5 μm.

bovine oviduct, where fertilization takes place (Abe et al., 1993b). It is well known that the mean number of viable spermatozoa in the ampulla is only a few dozen per oocyte (Overstreet and Cooper, 1975; Hunter and Nichol, 1983; Smith et al., 1987; Hunter, 1988). In order to ensure successful fertilization by so few spermatozoa, the oviduct must provide an environment in which they are able to survive and move prior to fertilization. It is possible that BOGP is an oviductal factor that is required for the maintenance of the viability and motility of a few selected spermatozoa in vivo.

Interactions of oviductal epithelial cells with gametes and embryos

The oviduct provides various types of physiological support to both gametes and embryos. Results from coculture experiments and from isolated oviduct culture systems strongly suggest that interactions between oviductal epithelial cells and gametes or embryos might play important roles in the maturation of gametes, fertilization, and embryonic development.

Support of embryonic development

Many studies have demonstrated improvements in early embryonic development upon coculture of early embryos with oviductal cells (for review, see Thibodeaux and Godke, 1992). Early development of sheep embryos is supported by coculture with oviductal epithelial cells (Gandolfi and Moor, 1987; Rexroad and Powell, 1988a,b; Czlonkowska et al., 1991). Improvements in embryonic development in vitro by coculture of embryos with oviductal tissue have also been reported for the mouse (Sakkas et al., 1989; Sakkas and Trounson, 1990; Takeuchi et al., 1992), rabbit (Carney et al., 1990a,b), pig (White et al., 1989), bovine (Eyestone and First, 1989; Ellington et al., 1990a,b; McCaffrey et al., 1991), and goat (Prichard et al., 1992). Medium that had been conditioned by oviductal cells was shown to be as effective as coculture in supporting the development of both ovine and bovine embryos (Rexroad and Powell, 1988b; Eyestone and First, 1989; Eyestone et al., 1991; Mermillod et al., 1993). These studies provided a basis for the hypothesis that the oviductal tissue (epithelial cells) produces and secretes certain factors that support embryonic development. Little is known about the specific products of oviductal epithelial cells that are responsible for the embryonic development in most species studied. However, a recent study by Satoh et al. (1994) demonstrated the existence of two embryogenesis-stimulating activities in medium that had been conditioned by bovine oviductal epithelial cells.

It is well known that the development of embryos in culture in vitro is arrested at a specific stage or is delayed compared with development within the oviduct (Bowman and McLaren, 1970; Harlow and Quinn, 1982). However, an early study showed that mouse zygotes could develop into blastocysts at a normal rate within explanted oviducts maintained in organ culture (Biggers et al., 1962). Whittingham (1968) reported that mouse zygotes developed only in the explanted ampullar region of the oviduct and that the isthmus and the horn of the uterus were unable to support embryonic development. It is likely that the ability of the explanted ampullar region of the oviduct to support embryonic development is related to the fact that it appears to be the most active secretory region of the entire oviduct. The ampullar region probably supplies the necessary nutrients for the early cleavage of embryos. However, little is known about regional differences in the ability of the oviduct to support the development of embryos in most mammals. The differential roles of oviductal epithelial cells and/or their secretions in terms of the support of embryonic development require further analysis.

Maintenance of sperm functions

There is some evidence from several species that the caudal isthmus of the oviduct is the site of a reservoir for spermatozoa during the estrous period (Harper, 1973; Hunter and Nichol, 1983; Hunter and Wilmut, 1983; Hunter, 1984; Smith et al., 1987; Suarez, 1987). In the golden hamster, a short segment of the isthmus, proximal to the utero-tubal junction, is the site of a reservoir for spermatozoa after natural mating and artificial insemination (Smith et al., 1987). The capacitation of golden hamster spermatozoa proceeds at a high rate in the oviduct after ovulation when mating occurs (Smith and Yanagimachi, 1989). Contact between spermatozoa and the oviductal epithelium is considered to be beneficial for sperm survival (Smith and Yanagimachi, 1990) and it may also be necessary for capacitation (Smith and Yanagimachi, 1991). After detachment from the epithelial cells, spermatozoa maintain both their motility and fertilizing capacity. Binding of spermatozoa to oviductal epithelial cells in vivo has also been observed in the mouse (Suarez, 1987). In bovines, spermatozoa have been observed to attach to cultured epithelial cells of the oviduct (Pollard et al., 1991). This study revealed that spermatozoa were bound by the rostral portion of the intact acrosome to the apical surface of polarized epithelial cells and, moreover, that the fertilizing capacity was maintained when spermatozoa were incubated with oviductal epithelial cells. Similar interactions between the spermatozoa and the oviductal epithelial cells have been observed in the pig (Suarez et al., 1991). These studies suggest that the motility and fertilizing capacity of spermatozoa might be maintained and, also, that hyperactivated motility might be induced by oviductal epithelial cells.

The nature of the sperm-epithelial cell interaction is unclear. Uncapacitated spermatozoa from the golden hamster were capable of strong attachment to both the isthmic and the ampullar epithelium, an observation that suggests that there is no major difference in the oviductal

mucosal surfaces between these regions with respect to the attachment of spermatozoa (Smith and Yanagimachi, 1991). Suarez et al. (1991) also demonstrated that the attachment of boar spermatozoa to the oviductal epithelial cells was not related to the oviductal regions (isthmus and ampulla) or to the day of the estrous cycle, but it was increased by addition of estradiol to the medium. However, another study by the same group, using pigs, indicated that more spermatozoa bound to isthmic explants than to ampullar explants of the oviduct, regardless of the presence or absence of steroid hormones (Raychoudhury and Suarez, 1991). Recently, similar observations were made of the interactions of equine spermatozoa with explants of oviductal epithelial cells (Thomas et al., 1994). More equine spermatozoa bound to the epithelium of explants from the isthmus than the ampulla, and more spermatozoa bound to explants at the follicular and postovulatory stages than at the diestrous stage. These studies strongly suggest that the binding of spermatozoa to the oviductal epithelium is influenced by both the region of the oviduct and hormonal status. The effects of bovine oviductal epithelial cells, derived from ampullar and isthmic segments of the oviduct and under various conditions, on penetration of the oocyte by bovine spermatozoa were recently examined in a coculture system in vitro (Chian and Sirard, 1995). Rates of oocyte penetration by spermatozoa that had been cocultured with oviductal epithelial cells derived from the ampullar segment were higher than those by spermatozoa that had been cocultured with the cells derived from the isthmic segment. Spermatozoa were seen to attach to epithelial cells regardless of their origin. Spermatozoa were gradually released from the epithelial cells in the ampullar segment, but they remained attached to isthmic epithelial cells during long-term culture. The motility of unattached spermatozoa in cultures of isthmic cells was higher than that in cultures of ampullar cells. These results suggest that the capacitation of spermatozoa might be enhanced by the attachment of spermatozoa to the ampullar epithelial cells and that the isthmic epithelial cells are important for maintenance of sperm motility. These results also suggest the existence of regional differences in the physiological functions of the epithelial cells of mammalian oviducts.

Regional differences in histochemical characteristics and in the expression of functional proteins in the oviductal epithelium

Detailed descriptions of the histochemistry of the oviduct and of the distribution of various substances in the oviductal epithelium can be found in an early review (Fredricsson, 1969). This section will focus on the regional variations in the histochemical characteristics and in the localization and expression of certain proteins, polysaccharides, enzymes, and growth factors in the oviductal epithelium of various mammalian species.

Mucoproteins and mucopolysaccharides

It has been proposed that the components of the glycocalyx of the oviduct might play important roles in the reproductive process. The histochemical characteristics of the surface of the oviductal epithelial cells in several species have been investigated in detail (Jansen, 1995). The apical surface of the epithelial cells of the isthmus of the rat oviduct is more intensely stained by periodic acid-Schiff (PAS) than those of the ampulla and fimbriae, and no changes are apparent during the estrous cycle (Deane, 1952). PAS-positive material, which was not digested by diastase, was also found on the cell surface of the oviductal and uterine epithelia of rats (Parlanti and Monis, 1975). The luminal surface of the isthmus and ampulla of the rat oviduct can be entirely stained by the PAS procedure and alcian blue, but staining is weak at the fimbriated end, suggesting regional heterogeneity in the characteristics of surface materials. Similar segmental differences have been reported by Lee et al. (1976).

The amounts of mucoprotein and acid mucopolysaccharide present in the secretory cells in the bovine oviductal epithelium differ between the ampullar region and the isthmus (McDaniel et al., 1968). Mucoprotein and acid mucopolysaccharide were found in the largest amounts in the ampullar epithelium of oviducts from estrogen-treated, estrus, and postestrus cows. The relative amounts of mucoprotein in the isthmus paralleled those in the ampulla, but acid mucopolysaccharides in the isthmic secretory cells were either present at negligible levels or were undetectable. The difference in amounts of mucoproteins and acid mucopolysaccharides between the ampulla and isthmus might reflect an actual difference in the composition of secretory products in the two regions.

In goats, the secretory material was found to be strongly PAS-positive and the amount of PAS-positive material decreased towards the isthmus (Joshi et al., 1977). Some regional differences in various histochemical features of the goat oviductal epithelial cells have been reported (Gadegone et al., 1981). The amounts of glycogen, neutral mucins, sulphomucins, and sialomucins were detected in the oviductal secretory cells during the estrous period and they were reduced during early pregnancy. In particular, sulphomucins were absent from the infundibular region and no acid mucins were found in the isthmic region during early pregnancy.

In the rabbit oviduct, the electron-lucent secretory granules in the isthmic epithelial cells exhibit the staining characteristics of highly acid, mucous glycoproteins, but those in the ampullar cells do not (Jansen and Bajpai, 1982). This result clearly shows that the production of highly acid, mucous glycoproteins that coat the ovum is confined to the isthmus and, to a lesser extent, to the mucosal crypts of the ampullar-isthmic junction, in which the ampulla is not involved. It is considered that these regional variations provide important opportunities for interactions of the isthmic

mucous glycoproteins with spermatozoa and with developing embryos during their transport through the isthmus.

Histochemical studies of mucopolysaccharides have been carried out in some amphibians (Kambara, 1956; Shivers and James, 1970; Suvarnalatha et al., 1975; Low et al., 1976). These studies showed regional variation in the mucopolysaccharide content in the oviduct (Kambara, 1956; Low et al., 1976). Recently, regional differences in the distribution of mucopolysaccharides in the oviduct of toad, *Bufo melanostictus*, have been described (Tan et al., 1994). In the oviduct of the toads, the magnum contained the most carbohydrates while proximal infundibulum contained fewer and the isthmus and ovisac the fewest. In the magnum of both the non-ovulating and ovulating toads, segmental differences were noted in the distribution of neutral and acid (sulphated and carboxylated) mucopolysaccharides.

Glycoconjugates

Glycoconjugates have an important role in mediating the interaction between female and male gametes and oviductal environment in reproductive processes of mammals. Plant lectins, which have binding affinity for carbohydrate chains composed of oligosaccharides in specific sequences, have been used to detect and define specific residues in the oviduct (Menghi et al., 1995). Menghi and his colleagues reported that there were no regional differences in the distribution of lectin-binding sites in the oviducts of the rabbit (Menghi et al., 1985, 1989) and the hare (Menghi et al., 1988). However, Fujita et al. (1984) reported that *Canavalia ensiformis* (Con A) lectin-positive mucins were found only in the secretory cells of the isthmic region in the rabbit oviduct, suggesting that the reactivity of secretory cells with lectins varies, depending on the region of the oviduct. An ultrastructural histochemical investigation indicated that secretory activity of glycoconjugates is greater in the isthmus than in the ampulla of the rabbit oviduct during the estrous cycle (Menghi et al., 1984). Neutral glycoconjugates were localized both in the secretory elements of the ampulla and in those of the isthmus, while carbohydrate-containing and sulphated glycosaminoglycans were localized only in the secretory granules of the isthmus.

Three lectins, namely, lectins from Con A, *Triticum vulgaris* (WGA), and *Maclura pomifera* (MPA) were shown to bind to the oviductal epithelium of the mouse (Lee et al., 1983). MPA bound to the epithelium of the proximal oviduct but not to the distal oviductal region. The differential distribution of binding sites for a lectin from *Bandeiraea simplicifolia* (BSA-I) in the oviducts of non-pregnant mice has also been reported (Wu et al., 1983). BSA-I bound strongly to the epithelium of the distal oviduct (isthmus) but not to that of the proximal oviduct (ampullar-isthmic region).

A recent study revealed that WGA and a lectin from *Dolichos biflorus* (DBA) bound more strongly to the isthmus than to the ampulla in cycling pigs (Raychoudhury et al., 1993). Some lectin-staining patterns vary after treatment of animals with estradiol and progesterone or depending on the day of the estrous cycle. These results indicate that there are differences in the glycoconjugates in the pig oviductal epithelial cells that are correlated with both the hormonal state and the region. It is speculated that these variations in glycosylation of protein in the pig oviduct might reflect functional differences of the epithelial cells during the estrous cycle or early pregnancy and might be explained by the increased production of sperm-binding molecules and factors that support the survival of spermatozoa in the isthmic reservoir.

Lipids

Previous studies have demonstrated that droplets composed of neutral lipids are present in the epithelium of the bovine oviduct (Wordinger et al., 1977; Henault and Killian, 1993b). Explants of oviducts can synthesize neutral and polar lipids and release cholesterol that has been synthesized de novo into the culture medium (Henault and Killian, 1993c). Lipids are more abundant in the epithelial cells of the isthmus in the bovine oviduct than in those of the ampulla throughout the estrous cycle (Wordinger et al., 1977). The concentrations of free cholesterol and glycerides appear to be highest in the preampulla and ampulla of the bovine oviduct and lower in the isthmus (Henault and Killian, 1993a,b). Most esterified cholesterol is detected in the isthmic epithelium. These findings indicate that the bovine oviductal epithelium exhibits regional differences in the distribution of phospholipids and neutral lipids. It is though that lipids present in the oviductal lumen might affect fertilization and embryonic development by influencing membrane lipid contents or by providing a source of energy. The regional differences in distribution of oviductal epithelial lipids might reflect changes in the luminal environment and might affect the membranes of both spermatozoa and the developing embryo. In particular, it is suggested that large amounts of esterified cholesterol and phospholipid in the isthmus might play a role in facilitating the attachment of spermatozoa to epithelial cells or the storage of spermatozoa.

Glycogens

The patterns of distribution of glycogen in oviductal epithelial cells have been reported for some species. In the pig-tailed monkey (Odor et al., 1980, 1983) and the rabbit (Schramm and Kuhnel, 1981), glycogen is mainly present in the ciliated cells of the oviductal epithelium. In the human oviduct, glycogen particles were found scattered or in clusters in nonciliated cells in the infundibulum and ampulla after treatment of women with a combination of an estrogenic and a gestagenic steroid (Fredricsson and Björkman, 1973) and in the

ampulla after low doses of a gestagen (Spornitz et al., 1977). Similar findings were made in the ampulla of progesterone-treated, ovariectomized cats (Bareither and Verhage, 1981) and in the isthmus of estrogen-treated, ovariectomized rhesus monkeys (Pathak et al., 1979a). Material that was considered to be glycogen was observed in nonciliated cells of all segments of the bat oviduct shortly before ovulation and its level increased significantly in the ampulla and the isthmus during the tubal transport of early embryos (Rasweiler, 1977). Such material was also observed in the ampullar epithelium of the ovine oviduct (Willemse and Van Vorstenbosch, 1975a). An increase in the activities of the enzyme involved in glycogen metabolism has been reported at fertilization in the oviducts of sheep (O'Shea and Murdoch, 1978). Cech and Lauschova (1991) also reported regional differences in the distribution of glycogen aggregates in the mouse oviduct, while Reinius (1970) had noted sometime earlier that infranuclear aggregates of glycogen particles were present in nonciliated cells of the isthmus and utero-tubal junction of the mouse oviduct. The frequency of glycogen deposits in the cytoplasm seemed to be higher in the isthmus than in the ampulla and preampulla.

Enzymes

Glucose is incorporated and metabolized by oviductal tissue in culture in vitro (Mastroianni et al., 1958, 1961). The incorporation in vitro of U-C^{14}-glucose by oviductal and uterine tissue obtained from rabbits under various hormonal conditions has been examined (Misra et al., 1977). The ampulla of the rabbit oviduct incorporated glucose at a higher rate that the isthmus. The rate of incorporation was increased by the administration of estrogen to rabbits, but it was reduced by treatment with progesterone. Recently, Asaka et al. (1993) examined glucose-6-phosphatase (G6Pase) activity cytochemically in the rat oviduct. The activity of G6Pase was high in secretory cells in the epithelium of the caudal isthmus and the utero-tubal junction at the diestrus phase of the estrous cycle. A high level of G6Pase activity is related to the release of glucose (or fructose) in various organs or cells (Nordlie, 1969). Glucose is utilized by the developing embryo in the oviduct. For example, the mouse embryo can develop beyond the 8-cell stage when glucose is the only available source of energy (Brinster, 1965; Brinster and Thomson, 1966). Moreover, the energy source of the mouse embryo changes from pyruvate to glucose during the early cleavage stage (Leese and Barton, 1984). It is thought that the role of the high activity of G6Pase is to release glucose into the oviductal fluid for use by the embryo as it passes through the caudal isthmus and utero-tubal junction to the uterus.

It has been proposed that prostaglandins (PGs) play an important role in mammalian oviducts, as, for example, in the contractile activity of oviduct smooth muscles (Lindblom and Andersson, 1985; Nozaki and Ito, 1986), in ciliary activity (Verdugo et al., 1980), and in the process of fertilization (Hayashi et al., 1988). In human, $PGF_{2\alpha}$ has been shown to be localized in the oviductal epithelium (Ogra et al., 1974). Other studies have demonstrated that concentrations of PGs are higher in the ampulla than in the isthmus of rabbit (Wakeling and Spilman, 1973) and human (Nieder and Augustin, 1986) oviducts. These studies suggested that the oviductal epithelium might be one of the important sites for production of PGs in the oviduct. PGs are bioactive compounds derived from arachidonic acid, in the final steps of the arachidonate cascades, phospholipase A_2 (PLA_2) functions as a rate-limiting enzyme (Blackwell and Flower, 1983). One of the activities of PLA_2 involved in the biosynthesis of PGs was recognized as being that of a membrane-bound, calcium-dependent enzyme that was active at high pH (Scott et al., 1980). Morishita et al. (1992) demonstrated regional differences in the activity of PLA_2 in the rabbit oviductal epithelium. The activity of a calcium-dependent PLA_2 of this type was significantly higher in the ampullar epithelium than in the isthmic epithelium. This result suggests that the role of production of PGs, which is dependent upon the activity of the arachidonate cascade, might be higher in the ampullar region of the rabbit oviduct than that in the isthmic region. It also suggests that PLA_2 in the ampullar epithelium might play an important role in the regulation of the contractility of smooth muscle and ciliary movement.

The presence of γ-aminobutyric acid (GABA) in rat oviducts has been demonstrated by several groups (Del Río, 1981; Erdö et al., 1982; Apud et al., 1984). The occurrence of glutamate decarboxylase and GABA-transaminase in the oviduct has also been reported (Del Rio, 1981; Apud et al., 1984; Erdö et al., 1984a). GABA may be a neurotransmitter in certain peripheral tissues, such as the myenteric plexus of the gut (Jessen et al., 1979, 1983), but it may have a function in processes other than neurotransmission in other tissues (Erdö, 1985). Furthermore, specific binding sites for GABA (Erdö and Lapis, 1982; Erdö et al., 1983) and receptor-mediated contractile responses (Erdö et al., 1984b; Fernadez et al., 1984) have been demonstrated in oviducts of rats and other mammals. Amenta et al. (1986) showed that the activity of 4-aminobutyrate:2-oxoglutarate transaminase (GABA-transaminase) was present in the epithelial cells of the rat oviduct. Specific GABA-transaminase activity was detected in the ampullar and isthmic regions of the oviducts as well as at the utero-tubal junction. The enzymatic activity was higher in the isthmic or intramural segments than in the ampullar segment of the oviduct and pregnancy induced a significant increase in GABA-transaminase activity in all regions of the oviduct.

Arylsulphatases (arylsulphatase sulphohydrolases) are present in various organs and act physiologically as specific glycosulphatases. Both arylsulphatases A and B have been found in the ampullar and isthmic epithelium of the rabbit oviduct (Vitaioli et al., 1984). At the estrus

stage, the activity of arylsulphatase A increases both in the ampulla and isthmus, but the increase is more marked in the isthmus and less marked in the ampulla.

Alkaline phosphatase activity was found to be more intense at the free margins of epithelial cells in the isthmic region of the sheep oviduct than in the ampullar region (Abdalla, 1968). It is thought that this regional difference might be due to uterine secretions since the histochemical characteristics of the isthmus are more similar to those of the uterus than to those of the infundibulum and ampulla.

Puri and Roy (1981) investigated the activities of some lysosomal enzymes in different parts of the rabbit oviduct at different times *post coitum*. The activities of lysosomal enzymes (acid DNase and acid RNase) increased at the ampullar-isthmic junction and in the isthmus of oviducts 24 h and 70 h *post coitum*, reflecting the increased lysosomal activity in the oviductal fluid produced by the secretory cells. It is thought that this increase in lysosomal factors might help in the process of fertilization and in early embryonic development.

Tissue concentrations of norepinephrine have been measured in the human oviduct in various regions at different stages of the menstrual cycle (Helm et al., 1982). The concentration of norepinephrine was higher in the isthmus than in the ampulla and fimbriae throughout the menstrual cycle. The highest levels of norepinephrine in the isthmus and at the fimbriated end were found at ovulation. These results indicate that regional differences might exist in the density of innervation of smooth muscle sphincters of the oviduct, which seem to be important in the transport of both the egg and embryo.

Growth factors

Several growth factors are known to be important for early embryonic development and differentiation (Rappolee et al., 1988; Paria and Dey, 1990; Wiley et al., 1992). Some studies have suggested that the preimplantation embryo produces growth factors that might act by autocrine an paracrine mechanisms within the preimplantation embryo (Rappolee et al., 1988, 1992; Conquet and Brulet, 1990; Arceci et al., 1992). However, comparisons of growth rates of early embryos in vivo and in vitro have indicated that factors present in the oviduct might be beneficial for early development (Bowman and McLaren, 1970; Harlow and Quinn, 1982). Moreover, it has been reported that the development of embryos can be improved by the addition of growth factors to the culture medium (Paria and Dey, 1990; Kuo et al., 1991). Thus, although growth factors derived from the embryo might participate in some type of autocrine regulation of embryonic development, the full complement of events during development of the preimplantation embryo may require additional paracrine growth factors that originate, perhaps, in the reproductive tract.

Several studies have indicated that insulin and insulin-like growth factors (IGFs) might be important regulators of the growth of preimplantation embryos (Harvey and Kaye, 1988, 1990, 1991a,b). IGF-I is produced by the epithelial cells in the rat oviduct (Carlsson et al., 1993). The expression of IGF-I is dependent on the estrous cycle and can be regulated by estradiol. The mRNA for the receptor for IGF-I has been found in both the oviduct and the preimplantation embryo, suggesting that IGF-I produced by oviductal epithelial cells might support development of the preimplantation embryo via indirect interactions with the embryo, as well as by participating in the regulation of the cyclic activities of the oviduct. However, none of the earlier studies examined whether regional differences might exist in the expression of IGF-I and its mRNA.

Epidermal growth factor (EGF) and transforming growth factor-α (TGF-α) are synthesized and expressed in the human oviductal epithelium. Their expression is specifically linked to stages of the menstrual cycle, and these growth factors may also be involved in early embryonic development (Morishige et al., 1993; Kurachi et al., 1994). An immunohistochemical study demonstrated that both EGF and TGF-α were localized in the ampullar epithelium of the human oviduct at the late follicular and luteal stages, although the localization of these proteins was not examined in other oviductal regions (Kurachi et al., 1994). Another study revealed the presence of EGF, TGF-α, and the receptor for EGF (EGF-R) in the epithelial cells of the human oviduct (Chegini et al., 1994). This study found no differences in the localization of these proteins or of binding of ^{125}I-EGF in the ampullar and isthmic regions or between ciliated and nonciliated secretory cells. However, Lei and Rao (1992) reported regional variations in the distribution and expression of EGF, TGF-α and their common receptor in human oviducts. The expression of all these regulatory molecules seems to be dependent on the oviductal region, cell type, and the reproductive state of the oviduct. In particular, the ampullar segment contains more of these three regulatory molecules than the isthmus. The biological significance of the uneven distribution of these molecules in the human oviduct is unclear. However, all cells (ciliated, secretory and smooth muscle cells) of the human oviduct seem to contain the EGF receptor and its ligands, EGF and TGF-α an observation that suggests that these two growth factors might potentially regulate the vibration of cilia, secretion, contraction, blood flow, cell division, and the differentiation of cells in the human oviduct. The regional variations in the expression of growth factors and their ligands need to be investigated in more detail in other species if we are to clarify the critical roles of growth factors in oviductal functions.

Serum proteins

It has been demonstrated by immunohistochemical methods that serum macromolecules are transferred to the oviductal epithelium in the mouse (Glass and

McClure, 1965). Serum macromolecules were detected immunocytochemically in the mouse oviductal epithelium during postnatal development and complex region-associated and age-associated differences were found in the localization of these antigens within the mouse oviduct. Except in the case of neonatal oviducts, the concentration of serum macromolecules in the ampulla was the same as or as high as that in the isthmus. It is suggested that these regional differences might be attributable to differential transfer by the oviductal epithelial cells or to differential utilization of serum molecules within the oviductal epithelium.

Parr and co-workers studied the pathway for transport of serum protein into the lumen of the mouse oviduct by localizing several tracer proteins in the oviduct after intravenous injection on various days of gestation (Parr et al., 1988). Their study demonstrated that the uptake of serum proteins into luminal epithelial cells occurred mainly in the preampullar region on day 5 of pregnancy, whereas the isthmic region was less active. This study also suggested the occurrence of a cellular vesicular transport system in the preampulla for the transfer of serum proteins to the oviductal lumen in the mouse. The biological significance of this regional difference remains unclear. The oviductal fluid has been shown to contain serum proteins in many species (Shalgi et al., 1977; Oliphant et al., 1978; Sutton et al., 1984a; Gerena and Killian, 1990). In particular, serum albumin may play an important role, for example in the capacitation of spermatozoa (Go and Wolf, 1985) and the acrosome reaction (Fraser, 1985). The transport of serum proteins into the lumen by the preampullar epithelial cells may be important in the reproductive process.

The presence of IgA and IgG in the epithelium of the mouse oviduct has been investigated by a sensitive avidin-biotin immunolabeling technique, and the uptake of intravenously administered fluorescein-conjugated IgA and IgG into the oviductal epithelial cells has been monitored (Parr and Parr, 1986). IgA and IgG were detected by immunolabeling in vesicles in the epithelial cells, for the most part in the preampulla, with lower levels in the ampulla. Fluorescein-conjugated IgA and IgG were found in similar vesicles after intravenous administration. No immunoglobulins were detected in the epithelial cells of the isthmus. These findings suggest that the preampulla of the oviduct might be an important site for the local immune system in the mouse female genital tract.

Villin

Villin, a 95-kDa actin-associated protein that was originally isolated from intestinal microvilli (Bretscher and Weber, 1980) is selectively expressed in the absorptive epithelium of the intestine and kidneys (Bretscher et al., 1981). Horvat et al. (1990) examined the localization of villin in the female mouse reproductive tract by an immunohistochemical methods. The expression of villin was limited to the proximal portion of the oviduct, composed of the preampulla, ampulla, and part of the isthmus, whereas the epithelial cells in the distal portion of the isthmus and at the utero-tubal junction did not express villin. It was suggested that the epithelial cells that line the proximal portion of the oviduct have absorptive functions, since villin is a typical marker of absorptive cells.

Hormonal responses of oviductal epithelial cells

The mammalian oviduct is a target organ for two ovarian steroids: namely, estrogen and progesterone (Jansen, 1984; Brenner and Maslar, 1988). These hormones cause various morphological and biochemical changes in oviductal epithelial cells. The changes in epithelial cells are essential for formation of an environment that can support fertilization and early embryonic development. In particular, estrogen causes hypertrophy, active ciliation, and secretion by atrophied epithelial cells in oviducts of immature or ovariectomized animals (Verhage and Brenner, 1975; Bajpai et al., 1977; Pathak et al., 1979a,b; Abe and Oikawa, 1993a) and during the follicular phase of the estrous or menstrual cycle (Verhage et al., 1979; Odor et al., 1980). In contrast, progesterone usually antagonizes the induction by estrogen of the cytodifferentiation of oviductal epithelial cells (Verhage and Brenner, 1976; West et al., 1976). In several species, the epithelial cells of the ampulla and the isthmus have been shown to undergo region-specific morphological changes in response to estrogen and progesterone (Brenner and Maslar, 1988). The diverse actions of the ovarian steroid hormones on these two anatomically and functionally distinct segments of the oviduct may also be a reflection of the various regional differences along the tube.

The mitotic activity in the tissues of the reproductive tract is estrogen-dependent. Fredricsson and Holm (1974) reported the estrogen-induced regeneration of the oviductal epithelium in various regions in the ovariectomized rabbits. The mitosis of oviductal epithelial cells was most evident in the infundibulum and upper ampulla in estrogen-treated rabbits. The effects in the lower ampulla and the isthmus differed from those in the other regions of the oviduct. There was a lower mitotic frequency and a later response to the stimulatory actions of estrogen in the former regions as compared to the latter. It was suggested that these regional differences in the action of estrogen might have wider implications in the reproductive process as, for example, in the adaptation of the activities of the various oviductal epithelial cells that are associated with ovulation.

Efforts have been made to determine whether various regions (ampulla, ampullar-isthmic junction, and isthmus) respond differentially to estrogen, to progesterone, and to a combination of these hormones in oviducts of the ovariectomized rabbit (Gupta et al., 1969). Estrogen and progesterone cause various biochemical changes in the oviducts of ovariectomized

rabbits and these responses differ among the various regions. The isthmus appears to resemble more closely the uterus in its responsiveness to the hormones than do the ampullar region and the ampullar-isthmic junction. Bajpai et al. (1977) reported the regional responses of oviductal epithelial cells to ovariectomy and estrogen treatment. Ovariectomy caused the degeneration of the cilia of isthmic ciliated cells, but it did not significantly affect the cilia of ciliated cells of the ampulla. The treatment of ovariectomized rabbits with estradiol dipropionate increased the number of cilia per cell in both oviductal segments. However, the isthmic cells seemed to require a higher dosage of estradiol than the ampullar cells. Ovariectomy also led to smaller numbers of secretory granules in the secretory cells in the two regions. Estradiol induced the formation of secretory granules in both regions, and the effect was more marked in the isthmic cells.

Progesterone antagonizes the effect of estradiol on the oviducts of cats when estradiol and progesterone are administered sequentially (estradiol first, then estradiol plus progesterone; West et al., 1976). The combined treatment with estradiol-17ß (E_2) and progesterone somewhat reduced the number of ciliated cells in the fimbriae and ampulla (Verhage and Brenner, 1976). Further treatment with progesterone led to atrophy and extensive ciliation. These antagonistic effects were more marked in the ampulla than in the fimbriae. These results suggest that the ampullar epithelial cells might be more sensitive than the fimbriae to the antagonistic effects of progesterone.

Hyde et al. (1989) determined the cellular distribution of immunoreactivity specific for progestin receptors (PR-IR) in ampullar and isthmic tissues from ovariectomized rabbit that had been primed with E_2 by use of a monoclonal antibody. Estradiol treatment increased the level of PR-IR in cell nuclei of the stroma and muscularis throughout the oviduct. In contrast, while there was little effect on PR-IR in the epithelium of the ampulla, E_2 decreased the numbers of PR-IR in the epithelium of the isthmus. These results suggest a regional difference in the regulation of expression of receptors between the ampulla and isthmus of the oviduct. The biological significance of this regulation of pattern of progestin receptors is unknown. However, it is possible that this variation in the concentration of receptors could be correlated with the differential sensitivity of different segments of the oviduct to progesterone. Hyde et al. (1989) concluded that differences in the concentrations of progestin receptors between segments might be required for successful transport of the ovum during early pregnancy.

Conclusion

Copious evidence for regional variations in the epithelial cells of the mammalian oviduct has accumulated over the years. Studies by light and electron microscopy have revealed that oviductal epithelial cells show regional variations in both morphological and ultrastructural features, which are associated with the stages of the estrous cycle. Histochemical and immunocytochemical investigations have demonstrated that the oviductal epithelial cells produce various secretory materials, and recent studies have confirmed the regional variations in the biosynthesis of such secretory materials. Moreover, several studies have also suggested segmental differences in the physiological effects of the oviductal epithelial cells on gametes or embryos.

Many specific glycoproteins have been found in the oviducts of various species. A glycoprotein (95 kDa) derived from the bovine oviductal epithelium has been shown to act on spermatozoa to support their viability and motility or to enhance capacitation. This glycoprotein is secreted mainly by the secretory cells in the ampullar region of the bovine oviduct and may be a factor that is required for the maintenance of sperm viability and motility at fertilization. The findings suggest a relationship between the regional variations in oviductal epithelial (secretory) cells and the biological functions of oviductal glycoproteins. In other species, the biological functions of the secretory materials synthesized by oviductal epithelial cells should be clarified in the near future. An understanding of the biological functions of these oviductal secretions will contribute to our efforts to define the biological significance of the marked regional differences in oviductal epithelial cells.

Although considerable progress has been made as a consequence of descriptive studies, much remains to be discovered at the molecular level. Now the stage is set for us to examine the regional variations in the localization and expression of various small and large molecules, that are directly involved in the reproductive events within the oviduct. It is hoped that the results of such studies will contribute to an understanding of the critical functions of the oviduct in the reproductive process.

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