THE FINE STRUCTURE OF THE SURFACE EPITHELIUM OF THE HUMAN Ovary

LUCIENNE PAPADAKI AND J. O. W. BEILBY
The Bland-Sutton Institute of Pathology,
The Middlesex Hospital Medical School, London, W. 1, England

SUMMARY

The surface epithelium has been studied on human adult ovarian biopsies, one foetal ovary and an ovarian biopsy from a woman 12 weeks pregnant. In the adult, the surface of the ovary is covered by a single, patchy layer of epithelium which varies from squamous, through cuboidal to columnar in shape. Cytoplasmic projections extend into the peritoneal cavity from the free surface of the cells and their lateral borders are connected by desmosomes. The nucleus is irregular and the dense cytoplasm contains many polysomes, free ribosomes and tonofilaments. Intracellular vacuoles and extracellular channels contain materials of low to moderate density. Lipid droplets and compound aggregates are present and both coated and smooth vesicles occur in the peripheral cytoplasm. Focal degenerative changes may be seen which range from loss of density in the basal cytoplasm to complete desquamation.

In pregnancy the basal surface of the epithelium is deeply infolded with an increase in cytoplasmic lipid. In the foetal ovary the entire surface is covered by an epithelium.

From these studies and the work of others, it seems clear that, although the prime function of the ovarian surface epithelium is its contribution of pregranulosa cells during foetal development, many features remain which suggest that it has an important role in transport. It may also influence follicular development in the foetus and appears to have some potential for steroid metabolism. The patchiness and degenerative changes found in the adult human ovary may be related to fluctuations in hormonal balance.

INTRODUCTION

The surface epithelium of the ovary has long been known as the ‘germinal epithelium’, because of the belief that it gave rise to the primordial germ cells. Evidence is now conclusive that this epithelium does not give rise to germ cells either during development or after birth (Franchi, Mandl & Zuckerman, 1962). The definitive primordial oogonia appear first in the yolk sac entoderm and migrate from there to the medial slope of the genital ridge (Witschi, 1948; McKay, Hertig, Adams & Danziger, 1953). The coelomic epithelium covering the primitive gonad does, however, contribute to the developing ovary; from it the granulosa cells are derived. Cells from the surface epithelium move into the mesenchyme and become associated with the germ cells; the sex cords later break up as the pregranulosa cells encapsulate the oogonia and form the primordial follicles (Gillman, 1948; Franchi et al. 1962). During the last trimester of foetal development, the surface epithelium becomes definitive and separated completely from the cortex by a basement membrane (Pinkerton, McKay, Adams & Hertig, 1961).

The ultrastructure of the surface epithelium has been examined only in the mouse...
L. Papadaki and J. O. W. Beilby

(Yamada, Muta, Motomura & Koga, 1957; Wischnitzer, 1965), hamster (Weakley, 1969) and rabbit (Gondos, 1969a). It therefore seemed of interest to study the fine structure of the surface epithelium of the adult human ovary and to relate the morphology to functional activity during foetal development, through adult life and during pregnancy.

MATERIALS AND METHODS

Ovarian biopsies were taken from 7 patients aged between 14 and 27 years, who were being investigated for amenorrhoea and infertility (Steele, Beilby & Papadaki, 1970). Six specimens were obtained at laparoscopic biopsy and one at laparotomy in which both ovaries were removed. In addition, an ovarian biopsy from a patient 12 weeks pregnant and a foetal ovary were examined; these specimens were obtained at hysterotomy. Because of the scarcity of human foetal material and ovarian biopsies during pregnancy, there was little opportunity for experimentation with different preparative methods. All tissue biopsies were fixed for both histological and electron-microscopical examination.

Electron microscopy

Thin strips of ovarian cortex were fixed in 2% glutaraldehyde, or in 2% formaldehyde (EM grade; Taab Laboratories, Reading)—2.5% glutaraldehyde (one-half strength Karnovsky fixative, 1965), both in 0.1M cacodylate buffer pH 7.4 (Hertig & Adams, 1967). After 2-3 h fixation the strips were sectioned under a dissecting microscope into 0.5-mm cubes each of which contained ovarian surface and/or small follicles. The tissue was fixed for a further 3 h and then washed overnight with 0.25M sucrose in 0.1M cacodylate buffer pH 7.4. The tissue blocks were post-fixed in 1% (w/v) phosphate-buffered osmium tetroxide at pH 7.3 (Millonig, 1961) for 1 h, rapidly dehydrated through graded ethanol/water mixtures and embedded in Epon 812 (Taab Laboratories, Reading); 0.5-μm sections were stained with toluidine blue. Thin sections were cut from the oriented blocks on a Porter-Blum MT2 microtome, mounted on 200-mesh bare grids, stained with uranyl acetate and lead citrate (Reynolds, 1963) and examined in a Siemens Elmiskop I electron microscope.

Histology

A 1-mm thick slice of tissue adjacent to that fixed for electron microscopy was fixed in 4% formaldehyde (EM grade), embedded in paraffin, serial sectioned and stained with haematoxylin and eosin.

RESULTS

A single patchy layer of squamous, cuboidal or columnar epithelium was present on the free surface and in small, shallow crypts of the ovarian cortex. The columnar cells were mainly located in the surface crypts, but all cell types could be seen in any one biopsy.

The surface of the epithelial cells was covered with microvilli and cytoplasmic projections of varying length and undulation (Fig. 1). Many of the projections, which contained homogeneous cytoplasm, were branched and had microvilli on their surface. In general, the cuboidal and columnar cells had more cellular extensions. In 2 or 3 cells, an isolated cilium was found (Fig. 2). The presence of other cilia was indicated by the appearance of a circular arrangement of sectioned filaments in some cytoplasmic projections seen in cross-section. The epithelium was separated from the
Surface epithelium of human ovary

fibrous connective tissue of the tunica albuginea by a basal lamina of varying thickness and moderate electron density (Fig. 1).

The lateral borders of the epithelial cells were parallel to one another and mainly in close apposition (Fig. 2), while invaginations of variable complexity formed an interlocking pattern of cytoplasmic processes from adjacent cells. At intervals, intercellular spaces were seen containing material of low electron density similar to that occurring in adjacent cytoplasmic vacuoles (Fig. 3). Terminal tight junctions on adjoining lateral borders were seen near the free surface of the cells (Figs. 1, 3). The lateral cell surfaces were connected at intervals by desmosomes (Fig. 1); some were unusually long (Fig. 4) with filaments parallel to their attachment plaque, while others were short with filaments perpendicular to the plaque. Coated and smooth-surfaced vesicles were seen adjacent to, or fused with the peritoneal, basal and lateral surfaces of the cell; many contained moderately dense material (Fig. 2).

The epithelial cell nuclei were large and irregular in outline, frequently with 2 or 3 lobes. In the squamous cells the nuclei were elongate and parallel to the surface of the ovary, while in the cuboidal and columnar cells they were more perpendicular to the surface and located in the coelomic two-thirds of the cell. Condensations of coarse, granular chromatin were present around the periphery of the nuclear membrane and scattered in clumps within the nucleoplasm (Fig. 1). There were one or two eccentrically placed nucleoli which were generally homogeneous and finely granular (Fig. 1).

The relatively dense cytoplasm contained abundant polysomes, free ribosomes and tonofilaments which were loosely arranged in bundles (Figs. 1, 6). Rough-surfaced endoplasmic reticulum, on the other hand, was relatively sparse. Occasionally it was associated with mitochondria, and some was dilated and contained material of low to moderate density (Fig. 6). A few vesicles or cisternae of smooth-surfaced endoplasmic reticulum were also present in the cytoplasm.

In columnar cells mitochondria tended to be more abundant in the basal third of the cells and their density varied from one ovary to another. The Golgi apparatus was usually to be found between the nucleus and the free surface of the cell. Lipid droplets were sometimes present in the basal cytoplasm (Figs. 2, 6). Membrane bound inclusion bodies similar to 'compound aggregates' (Hertig & Adams, 1967) were seen, which contained lipid droplets and dense, dark granules among a fine granular substance (Fig. 5).

Polymorphic cytoplasmic vacuoles were present in many cells (Figs. 3, 5 and 6); the large ones usually occurred in the basal cytoplasm, while the smaller were more often near the free surface. Many of the vacuoles contained a granular or finely stranded material of varying density, similar to that found in the intercellular channels (Fig. 3). It was noted that other cytoplasmic vacuoles in the fibroblast-like cells in the outer cortex also contained such materials (Fig. 7).

Degeneration

Focal areas of degeneration were present in all the epithelia studied. The cells in these areas showed graded changes ranging from loss of cytoplasmic density in the
L. Papadaki and J. O. W. Beilby

basal portions of the cell (Fig. 8), through degeneration affecting both the nucleus and cytoplasm (Fig. 9), to complete desquamation. The desmosomes and tight junctions of the degenerating cells remained intact and attached to one cell or the other. The flattened epithelial cells frequently fragmented before desquamation was complete (Fig. 10). In areas of complete cellular degeneration, the epithelium was entirely lost apart from a few membrane fragments which remained attached to a thickened basal lamina (Fig. 11).

A small area of inflammation was seen in one ovary in which there had been infiltration by polymorphonuclear leucocytes and plasma cells. Under the light microscope the area appeared as a small plaque with normal surface epithelial cells on either side. Some of the epithelial cells within the inflamed area contained many small, dense lysosomes, as well as large autophagic vacuoles containing the remnants of a variety of membranous cytoplasmic structures (Fig. 12).

Pregnancy

The surface epithelum on an ovarian biopsy obtained during the twelfth week of pregnancy had the same general appearance as that of the non-pregnant patient. The major difference was the deeply folded basal surface of the cells, penetrating deep into the tunica albuginea (Fig. 13). Beneath the basal lamina, which followed the irregularities of the plasma membrane, was another broad band of intermediate density which was continuous with the connective tissue matrix of the tunica albuginea. The epithelial cells were predominantly cuboidal in shape, there was little interdigitation of the lateral borders of adjacent cells and the number of intercellular channels was increased. A minor cytoplasmic difference was the more frequent occurrence of simple-structured compound aggregates and lipid, than in the ovaries from non-pregnant patients (Fig. 14).

Foetal ovary

The entire surface of the ovary of the 24-week foetus examined was covered with an epithelium. In most areas connective tissue elements of the developing tunica albuginea had separated the single surface layer of epithelial cells from the underlying cortex (Fig. 15). Even at this time there was the usual variety of cell shapes, with cuboidal cells predominating; all the cells rested on a thin basal lamina. Occasionally, the epithelial cells were several layers thick and flattened, still in continuity with the sex cords and in contact with morphologically similar cells surrounding the oogonia.

The single-layered epithelial cells were similar to those in the adult, but the cytoplasmic processes on the free surface were much fewer in number and simpler in form (Fig. 15). There was less interdigitation of adjacent cells. Tight junctions were present near the free surface and developing desmosomes were apparent along the lateral borders. There were very few large extracellular channels, but both coated and smooth vesicles were present in the peripheral cytoplasm. There were fewer intracellular vacuoles than in the adult, with little evidence of the moderately dense material seen in the cytoplasmic vacuoles and intercellular channels of the fully developed ovary.
DISCUSSION

Morphological observations of human ovaries, at the light-microscope level, have shown the patchy nature of the epithelium during the reproductive years and its relative absence after the menopause except as a lining to the walls of surface crypts (e.g. McKay, Pinkerton, Hertig & Danziger, 1961; Novak & Woodruff, 1967). In contrast, the entire surface of the ovary in many mammals, for example, the adult rat (Mandl & Zuckerman, 1951), is covered by epithelium, as also occurs in the human foetus.

The cause of the degeneration and desquamation of the ovarian surface epithelium in the human adult is not clear nor has its course been described. As is shown here, there may be simple degeneration ranging from loss of density in the basal cytoplasm to complete desquamation, or focal cytoplasmic degeneration (see autophagic vacuoles and lysosomes in Fig. 12) in areas of inflammation where damaged cells may be infiltrated by macrophages. The maintenance or degeneration of the remaining surface epithelium, between the menarche and the menopause, may depend on fluctuations in hormonal balance and may, therefore, be influenced by changes resulting from anovulatory cycles. Certainly there is evidence to suggest that the epithelium is sensitive to hormonal changes, particularly during pregnancy when decidual plaques, epithelial in nature, may form on the serosal surface of the ovary. Nelson & Greene (1958) have shown that in 74% of their patients there was a decidual reaction of considerable extent on the ovarian surface during the third trimester, which would then degenerate after the seventh day post partum. In the rat, proliferation of the epithelium occurs shortly after ovulation, presumably stimulated by oestrogens in the follicular fluid; proliferation may also be induced by the local injection of oestrone when ovulation is not occurring (Stein & Allen, 1942).

Variation in epithelial cell shape occurs in both human and animal ovaries, probably reflecting the expansion of the ovarian surface due to growth of underlying follicles (Wischnitzer, 1965). In general, the cellular morphology of the surface epithelial cells of the human ovary is similar to that of the mouse (Wischnitzer, 1965), hamster (Weakley, 1969) and rabbit (Gondos, 1969a). There is also a striking similarity between surface epithelial cells and the granulosa cells surrounding unilaminar primary follicles of human (to be published) and other mammalian ovaries (Björkman, 1962; Adams & Hertig, 1964; Odor, 1965; Gondos, 1969b).

The 2 types of desmosomes connecting the lateral borders of the human ovarian epithelium, which have not been described in animal studies, are presumably related to the mechanical requirements of the cells. Kelly (1966) believes that desmosome variations are related not only to the extent or strength of intercellular adhesion, but also to internal cell architecture and prevailing mechanical stresses.

The abundance of polysomes and ribosomes together with the occasional appearance of dilated cisternae of the endoplasmic reticulum containing electron-dense material suggest that some synthetic activity is occurring within the surface epithelial cells. It is known, for instance, that protein synthesis takes place on the ribosomes and does not require an extensive development of the cytoplasmic membranes (Fawcett, 1966).
The presence of lipid droplets in the surface epithelium has also been noted in the hamster, where it has been suggested that they might be related to steroid synthesis or metabolism (Weakley, 1969). Specific 17-\(\beta\)-hydroxysteroid dehydrogenase is present in ovarian epithelium in the mouse, rabbit and rat, and would seem to be concerned with the metabolism of oestrogenic steroids (Baillie, Ferguson & Hart, 1966). It is not unreasonable that this tissue should retain the potential for steroid metabolism, since it has been shown to contribute embryologically (Gillman, 1948) to the formation of steroidogenic cells. It may, therefore, be significant that there is an increase in the number of lipid droplets during pregnancy.

The presence of compound aggregates, of varying complexity, in the ovarian surface epithelial cells is unexpected, since they are a prominent feature of the oocyte cytoplasm, usually forming a major part of the vitelline body. However, they are also found in the primordial follicular cells and in many cells of the surrounding cortex, and it has been suggested that they represent nutritive material (Hertig & Adams, 1967). If this is so, it indicates that there must be a means of transporting this material between the oocyte and surface epithelium.

An adaptation of the epithelial cells for transport is suggested by cytoplasmic features which include the surface cytoplasmic projections and microvilli that may take up material from the coelomic cavity. Evidence of pinocytotic activity in these cells has been shown by their ability to take up colloidal gold within 24 h after intraperitoneal injection (Chiquoine, 1961). The presence of coated and smooth surfaced vesicles along and fused to the plasma membranes and the appearance of moderately dense materials in the extracellular channels and in cytoplasmic vacuoles of the fibroblast-like cells of the cortex, as well as in the epithelial cell vacuoles, provides further support for this concept. That the ovarian surface epithelium in animals also has features indicative of transport has been shown by Weakley (1969) and Gondos (1969a). It is impossible to say in which direction, however, the material contained in the vacuoles and extracellular channels of the ovarian surface is being transported.

That metabolites must be transported across the surface epithelium is indicated by the fact that follicular maturation in foetal ovarian transplants on the omentum of an adult host rat occurs only where the surface epithelium is present (Holyoke, 1949). In other epithelia also, e.g. gall bladder, ions in solution enter the cells across the luminal surface and are then pumped out into the intercellular channels across the lateral membrane (Tormey & Diamond, 1967). When the transport adenosine triphosphatase was inhibited by ouabain, the intercellular channels almost completely collapsed. More recently a similar phenomenon was observed with rumen epithelium (Harrison & Munn, 1970).

The marked irregularity of the basal surface of the epithelial cells and basal lamina in the ovary from the pregnant patient might be the result of luteal formation and previous ovulation which undoubtedly produces a continual change in the contour of the ovarian surface. Conversely, anovulatory cycles probably contributed to the smoothness of the surface observed in the non-pregnant patients.

At 24 weeks in the human foetal ovary much of the epithelium is separated into a
single layer from the underlying cortex by the developing tunica albuginea, although
the cellular morphology is still indicative of differentiating ovarian epithelial cells
(Weakley, 1969). The observation that at 24 weeks there are a few areas where the
epithelium is still multilayered and in continuity with the sex cords, supports the
previous conclusion that the follicular epithelium and ultimately the granulosa cells
are derived from the surface epithelium (Gillman, 1948; Franchi et al. 1962).
Similarly, the ultrastructural features of the ovarian surface epithelium in the newborn
rabbit are identical with the pregranulosa cells (Gondos, 1969a). Gondos has pointed
out that if the granulosa cells were to arise from the mesenchyme, this would have had
to take place at an earlier stage of development than sex cord formation, since there is
a basement membrane separating the sex cords from the surrounding stroma.

It would appear, therefore, that the prime function of the ovarian surface epithelium
is its contribution of pregranulosa cells which, in the human, terminates during early
foetal development. The epithelium may also influence follicular maturation up to the
resting meiotic prophase. In the adult, although the epithelium remains only in patches,
it still retains features that reflect its role in the transport of metabolites and its
potential for steroid metabolism. Degeneration of the epithelial cells and smoothness
of the ovarian surface are 2 features which may be related to fluctuating hormonal
balance.

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ABBREVIATIONS ON PLATES

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<thead>
<tr>
<th>Abbreviation</th>
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<tr>
<td>bl</td>
<td>basal lamina</td>
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<td>c</td>
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<td>ca</td>
<td>compound aggregate</td>
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<td>desmosome</td>
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<td>ec</td>
<td>extracellular channel</td>
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<td>Golgi complex</td>
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<td>lipid droplet</td>
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<td>p</td>
<td>polysomes and free ribosomes</td>
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<td>pm</td>
<td>plasma membrane</td>
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<td>rough-surfaced endoplasmic reticulum</td>
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<td>ser</td>
<td>smooth-surfaced endoplasmic reticulum</td>
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<td>t</td>
<td>tonofilaments</td>
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<td>tight junction</td>
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<td>tu</td>
<td>tunica albuginea</td>
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<td>v</td>
<td>smooth or coated vesicle</td>
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<td>tac</td>
<td>cytoplasmic vacuole</td>
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Fig. 1. A micrograph showing parts of 4 epithelial cells resting on a basal lamina (bl). The free surface exhibits a variety of cytoplasmic projections. Adjacent cells are joined by a tight junction (tj) near the free surface and a desmosome (d) on the lateral borders. The nucleus (n) contains peripheral and scattered condensations of chromatin, and an eccentric nucleolus (nuc). Abundant tonofilaments (i), polysomes and free ribosomes (p) can be seen, as well as scattered lamellae of rough endoplasmic reticulum (rer). The appearance of 2 cells in the centre is due to overlap of large cytoplasmic extensions; in the lower, a large cytoplasmic vacuole (vac) can be seen. Glutaraldehyde fixative, \( \times 18,400 \).
Fig. 2. A section of parts of 2 epithelial cells. A cilium (c) can be seen extending into the peritoneal cavity. Note the interdigitation of cytoplasmic processes and lateral plasma membranes (pm) of neighbouring cells. A lipid droplet (l) and a coated vesicle (v) fused to the plasma membrane can be seen. Glutaraldehyde fixative, $\times 22000$.

Fig. 3. A micrograph showing portions of 3 epithelial cells with large cytoplasmic vacuoles (vac) containing moderately dense material. Note the extracellular channel (ec) containing material similar in density to that seen in some of the smaller vacuoles (arrows). Adjacent cells are connected at their free surface by junctional complexes (tj) and a short desmosome (d) is seen above the extracellular channel. Note the somewhat dilated rough endoplasmic reticulum (rer). Karnovsky fixative, $\times 16000$. 
Surface epithelium of human ovary
Fig. 4. A section through a long desmosome (1.1 µm in length) showing the filaments parallel to the attachment plaque. Karnovsky fixative, × 40,000.

Fig. 5. A section of an epithelial cell showing mitochondria (m) above and below a compound aggregate (ca), composed of lipid and large dense granules surrounded by a finely granular substance. Slightly dilated rough endoplasmic reticulum (rer) is seen on either side. Small vacuoles (vac) occur near the surface of the cell and larger vacuoles more deeply in the cytoplasm. Karnovsky fixative, × 26,000.

Fig. 6. Parts of 2 overlapping surface epithelial cells. The dense cytoplasm contains many tonofilaments (t), polysomes and free ribosomes (p), as well as some vesicular smooth-surfaced endoplasmic reticulum (rer). Part of the rough-surfaced endoplasmic reticulum (rer), is associated with mitochondria (m) and part is dilated (arrows) and contains electron-dense material. A large, moderately dense cytoplasmic vacuole (vac) is also seen. Glutaraldehyde fixative, × 22,500.
Fig. 7. A section through a fibroblast-like cell in the tunica albuginea. Within the cytoplasm vacuoles (vac) can be seen which contain materials of varying density. Karnovsky fixative, × 18200.

Fig. 8. The basal portion of columnar epithelial cells where the first degenerative changes are seen. There is some loss of density but cytoplasmic organization remains unchanged except for the appearance of occasional membranous inclusions (arrows). Note the small vesicles (v) fused to the plasma membranes and the interdigitation of the lateral borders. Karnovsky fixative, × 20000.
Fig. 9. A section showing degenerative changes in a cuboidal epithelial cell. The nucleus (n), in which there has been loss of nucleoplasm and chromatin, appears to be fraying off into the peritoneal cavity together with the peripheral cytoplasm. Some mitochondria (m), rough-surfaced endoplasmic reticulum (rer), and disoriented tonofilaments (t) remain in the basal cytoplasm. The desmosome (d), remains attached to the cell on the right. Karnovsky fixative, × 13200.

Fig. 10. A section through a fragmented squamous epithelial cell. Some mitochondria (m), tonofilaments (t) and a few cisternae of rough endoplasmic reticulum remain on the basal plasma membrane. On the free surface the plasma membrane is fragmented, and the basal lamina (bl) is somewhat thickened. Glutaraldehyde fixative, × 24000.

Fig. 11. An area of complete epithelial desquamation. A few membrane fragments (arrows) remain on a thickened basal lamina (bl). Karnovsky fixative, × 24000.
Surface epithelium of human ovary
Fig. 12. Section of 2 epithelial cells from the small area of inflammation found on the surface of one ovary. A large autophagic vacuole (double arrows) can be seen containing membranous structures. There are also many small, dense lysosomes (ly). Glutaraldehyde fixative, × 22,400.

Fig. 13. The basal portion of an epithelial cell from the ovary of a pregnant patient. The cortical surface of the ovary is deeply infolded and the epithelial cell with its basal lamina (bl) has penetrated (arrows) deep into the tunica albuginea (tn). Glutaraldehyde fixative, × 11,400.
Surface epithelium of human ovary

[Image: Micrographs of surface epithelium of human ovary.]

12

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Fig. 14. A section of several epithelial cells from the ovary of the pregnant patient, cut tangentially to the ovarian surface. Cytoplasmic changes are minimal, but simple-structured compound aggregates (ca) and lipid droplets (l) occur more frequently during pregnancy. Glutaraldehyde fixative, \( \times 27200 \).

Fig. 15. Parts of two adjacent epithelial cells from a 24-week foetal ovary showing the epithelium already separated as a single layer by the underlying tunica albuginea (tu). The cellular morphology is essentially similar to that of the adult. Note the simple, slender form of the processes on the free surface, the thin basal lamina (bl) and the lack of cytoplasmic vacuoles. Karnovsky fixative, \( \times 17500 \).
Surface epithelium of human ovary

[Image 14: Detailed view of surface epithelium with labeled structures, such as m, ca, vac, ec, n, rer, l.]

[Image 15: High-magnification view of epithelial cells with labeled structures, such as m, n, rer, ec, tu, bl, v, tj.]

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