The histology and histochemistry of development and resorption in the terminal oocytes of the desert locust, *Schistocerca gregaria*

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With one plate (fig. 3)

**Summary**

During vitellogenesis the follicular cells play an active part in the synthesis of yolk. The term 'corpus luteum' as applied to the ovary of the locust is invalid and two terms 'white' and 'yellow' follicle have been introduced to describe the separate identities of the normal and pathological postovulatory follicle. The protein yolk is a protein-carbohydrate compound, presumably a glycoprotein. Three kinds of lipid bodies are present; the first is a phospholipid, the second a combined phospholipid and triglyceride, and the third triglyceride. Lipids are coloured by dissolved \( \beta \)-carotene. Concentration or absorption of the lipids causes the crystallization of carotene and the formation of the pigment body. During resorption the follicular cells act as lecitholytic cells, first breaking down the protein and then the lipid yolk, and finally degenerating themselves. It is suggested that the oocytes have an inherent potential for resorption, the realization of which depends on various factors within the body.

**Introduction**

Degeneration and resorption of the empty follicles and formation of a pigment body after ovulation in *Locusta migratoria* has been described by Singh (1958). He has also briefly dealt with these events in *Schistocerca gregaria* and other genera. Investigation in this Department (Highnam and Lüsis, 1962) on the possible causes of resorption and the correlation between neurosecretion and reproduction, clearly demanded more detailed knowledge of both the development and resorption of oocytes. For this reason the histological and histochemical studies described in this paper were carried out.

**Material and methods**

Female desert locusts (*S. gregaria* Forsk.) were reared with mature males from fledging as described previously (Highnam and Lüsis, 1962). Females were killed at various times during the development of the first batch of terminal oocytes, and their ovaries were fixed either in aqueous Bouin or Carnoy or cold acetone or Baker's formaldehyde-calcium with or without postchroming. Some ovaries were cleared in benzene, embedded in paraffin wax (m.p. 56° C), and sectioned parallel to the longitudinal axes of the ovarioles at a thickness of 6 or 7 \( \mu \). Others were embedded in gelatine, and frozen sections cut at 15 \( \mu \). For histological examination, sections were stained with Ehrlich's haematoxylin and alcoholic eosin, Azan, chrome-haematoxylin (Gomori, 1939b), paraldehyde-fuchsin (Gomori, 1950), or bromophenol blue (Mazia, Brewer, and Alfert, 1953).

For the histochemical determination of lipids, sections were coloured with Sudan black B, Sudan IV, Nile blue, performic acid / Schiff, or acid haematein (Baker, 1946). In addition Schultz's cholesterol test was used. Some frozen sections were treated with digitonin to precipitate sterols (Lison, 1936). The detection of polysaccharides and mucopolysaccharides was based on the periodic acid / Schiff reaction (PAS) (Hotchkiss's test, Pearse, 1953). Glycogen was identified by the saliva test, mucopolysaccharides by metachromatic stains, acid mucopolysaccharides by alcian blue, proteins by Millon's original method (Pearse, 1953), and also by the modification of Serra (1946), and by the ninhydrin reaction (Serra, 1946). RNA was stained by the pyronin in pyronine / methyl green; the control sections were treated with ribonuclease. Polarized light and ultra violet light were used for the study of crystalline inclusions.

**Gross anatomy of the ovaries**

The paired panoistic ovaries lie in the abdomen on each side of the midline. In general they resemble those of *L. migratoria*, as described by Albrecht (1953) and Singh (1958). Each ovary consists of about 50 ovarioles. The proximal ends of the ovarioles are thread-like, but thicken and become tubular distally. The tubular part is divided into follicles which carry oocytes at different stages of development. The terminal oocyte, that nearest the oviduct, is the most developed. Each ovariole is lined with a follicular epithelium and covered by two membranes: the tunica propria and the external ovariole sheath.

A short pedicel or ovariole neck connects each ovariole with the muscular oviduct. The successive follicles in one ovariole are separated from each other by thin layers of interfollicular tissue.

**Histology of the developing terminal oocyte**

The growth of the oocyte may be divided into a number of different stages according to its form and activity.

*Stage 1* is the earliest observed. The oocyte length increases from 0.5 to 1.4 mm. During this period an increasing number of mitoses occurs in the follicle cells and there is rapid growth. The follicular cells, which are originally flattened and about 0.5 μ high, increase in height perpendicular to the tunica propria and are packed closely together. Not all the follicle cells have the same appearance. At irregular intervals among the more typical cells, narrower, very basophil cells occur. These cells are clearly differentiated in sections stained with bromphenol blue, Millon, or Baker's acid haematein test after pyridine extraction. The cytoplasm of the terminal oocyte at this early stage of development is finely granulated and homogeneous. No perinuclear zone is present. The nucleus is oval with diameters of 4.5 and 8.0 μ; it is situated towards the distal end of the oocyte. The chromatin is amorphous, slightly basophil, and scattered in irregular clumps.

*Stage 2*. The length of the oocyte increases from 1.4 to 1.6 mm. Marked...
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changes occur in the histology and histochemistry both of the oocyte and of the surrounding follicle cells. The follicular cells become columnar, 8 to 12 μ high, with a conical process projecting into the cytoplasm of the oocyte. Mitosis ceases. In appearance the cytoplasm of the oocyte is still finely granulated, but at the periphery the granulation is denser and less homogeneous, and includes small less-stainable spheres. Cytoplasmic inclusions, staining with Gomori's haematoxylin, appear. At the same time a zone immediately surrounding the nucleus is differentiated by its denser granulation. The nucleus itself is now 60 to 70 μ in diameter.

Stage 3. The beginning of this stage is marked by the appearance of yolk in the cytoplasm of the oocyte, usually when the oocyte is about 1.6 mm long. Occasionally deposition of yolk begins in oocytes 1.4 mm long, or it may be delayed until a length of 1.8 mm has been reached. The peripheral zone of cytoplasm described above becomes reticulate and filled with droplets. Histochemical tests show these to be of two kinds, protein and lipid yolk (see below). The droplets increase both in number and size, progressively distending the cell until the cytoplasm remains merely as a framework. The terminal oocyte reaches its final length of about 8.0 mm about 14 days after fledging. As the oocyte enlarges the follicular epithelium becomes progressively flattened, its final thickness being about 8 μ (fig. 2, a, p. 63). The flattening of the epithelium is no index of its metabolic activity, since its cytological structure shows that it is very actively concerned in the transfer of yolk to the oocyte (see below). The tunica propria is also stretched and its thickness decreases from 2 μ to 1 μ. The distal ends of the follicular cells are extended and their cytoplasm shows slight basiphilia and is stained vividly red with pyronin. The extensions bear 'caps' of eosinophil material. In the cytoplasm of the oocyte immediately around these 'caps' are small newly-formed protein yolk droplets which stain blue with Azan. Later, when the protein yolk globules have increased in size, Azan stains them orange-red. Yolk deposition continues until the terminal oocyte reaches its final length of 7.5 to 8 mm.

Stage 4. In this stage the chorion is formed by the follicle cells. The cytoplasm of the latter is less basophil than in previous stages and becomes vacuolated. Fine, colourless secretory droplets appear above the brush-border. Only a few oocytes have been observed in this stage, possibly because the formation of the chorion is a rapid process. No detailed examination of the chorion has been made but it appears to agree with that of Schistocerca as described by Hartley (1961).

Histochemistry of the terminal oocyte

Stage 1. Tests for carbohydrate and proteins are negative or give a weak positive reaction. Sudan colouring agents for lipids show only a diffuse reaction in the cytoplasm of the oocyte or demonstrate only scattered granules. These, and similar granules observed in the follicular and pedicel cells, react positively to Baker's acid haematein test, are resistant to cold acetone extraction, but disappear when treated with pyridine.
Stage 2. When the terminal oocyte is 1.4 to 1.6 mm long, sudanophil material first appears in the cytoplasm as crescentic, kidney-shaped, or irregular bodies. After formaldehyde-calcium fixation and postchroming, sections stained with acid haematein show this material as crescentic or circular bodies around an unstained central region. It may be that part of the sudanophil material is a phospholipid. At this stage a definite, finely granulated, PAS-positive zone appears in the oocytic cytoplasm adjacent to the follicular epithelium.

Stage 3. The protein yolk which accumulates at this stage proves on histochemical analysis to be a combination of protein and polysaccharide. The protein fraction reacts positively to Millon's and the ninhydrine tests (which suggests the presence of tyrosine in the protein molecule).

The polysaccharide fraction is PAS-positive and \( \beta \)-metachromatic but resistant to saliva extraction. These tests indicate that it is a mucopolysaccharide and not glycogen. PAS-positive material appears also in the follicular epithelium and the cells of the extra-epithelial sheets during vitellogenesis. This too is mucopolysaccharide and not glycogen. The latter has been observed only in the fat-body and here only in the very early stages of oocyte development before vitellogenesis has begun.

Lipid yolk gradually spreads from the periphery towards the centre during the early part of this stage. Each globule is composed of two kinds of lipids. There is a central core of neutral lipid which is partially or completely enclosed by a shell of phospholipid. The neutral lipid stains pink with Nile blue, reacts negatively with acid haematein, and gives a positive PFAS reaction, which can be blocked by bromination. The latter test shows the lipid to be an unsaturated triglyceride. At a later stage in vitellogenesis the phospholipid disappears and the globules are composed entirely of neutral lipid. No positive evidence for cholesterol or its esters was obtained by Schultz's and the digitonin tests.

Normal oocytes are pale yellow owing to the presence of pigment, which is dissolved in the lipid material. If sections or whole oocytes are mounted in glycerol and left for several days, orange-red crystals of the pigment appear in the lipid globules in the form of needles, rods, rhomboids, or parallelograms. Concentrated sulphuric acid gives a green colour both with the crystals and with the lipid globules before crystallization, and this reaction, together with the shape and colour of the crystals, suggest that the pigment is carotene.

During vitellogenesis RNA is present in rather high concentration in the follicular cells, as shown by the vivid red staining with pyronin/methyl green, which was not obtained after prior treatment with ribonuclease.

Resorption of the terminal oocyte

For some reason, as yet unknown, not all the terminal oocytes develop into mature eggs. At any stage in its development an oocyte may cease to grow, lose its yolk, and become converted into a resorptive body (RB). Resorption may occur even before yolk has been deposited in oocytes about 1 mm in
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length. Resorption bodies may form anywhere in the ovary, but seem to occur most frequently at the anterior and posterior ends. The process of resorption may be divided into 6 stages according to the external appearance of the resorption bodies and their histological structure. The stages are numbered RB 1 to RB 6 for convenience. They are illustrated in fig. 1.

**RB 1.** This stage differs very little from a normal terminal oocyte but is identified by the presence of characteristic opaque patches on its surface.

**RB 2.** The opaque areas extend over most of the surface and the length of the oocyte is slightly reduced.

**RB 3.** The oocyte is still further reduced in length and is much attenuated and dark yellow.

**RB 4.** The length is reduced to half that of a normal oocyte, and the distal part is narrower. At the extreme distal end pigment has accumulated and behind it is an area from which yolk globules have disappeared.
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**RB 5.** The follicle is reduced to a short, rounded body containing some orange pigment.

**RB 6.** In this final stage the resorption body takes the form of a narrow pigment ring at the base of the penultimate oocyte in the ovariole. When the normal terminal oocytes reach a length of about 5 mm or more, all stages of resorption can be found in the same ovary.

**Histology**

For the study of the histological changes involved in oocyte resorption, comparable stages were collected from many animals with different terminal oocyte lengths.

In those cases where no yolk has been formed before resorption, the follicular epithelium shows symptoms of degeneration. The nuclei are irregular in shape and pycnotic, and each is surrounded by a condensed mass of uniform and intensely stained eosinophil cytoplasm. The nucleus of the oocyte is vacuolated peripherally. The beginning of the process of resorption, however, is more characteristic where yolk is present in the terminal oocyte.

**RB 1.** The cytoplasm of the oocyte is extensively vacuolated and some of the vacuoles are filled with eosinophil material. The protein yolk spheres are reduced in size, although the characteristic structure of the yolk is as yet still unaffected. The follicular epithelium is folded (fig. 3, A) and has increased in thickness from 8-0 to 25 μ; the nuclei, 20 μ in diameter, are surrounded by a thin layer of cytoplasm, which may be vacuolated. In parts the follicular epithelium is separated from the tunica propria and the space between them is usually filled with a structureless eosinophil material.

**RB 2.** The follicular epithelium is folded even more than in the previous stage, and the large folds, much thickened in some places, project deeply into the oocyte. The epithelium is no longer continuous around the oocyte, and isolated patches of cells remain attached to the tunica propria. In the central part of the oocyte the invading epithelium breaks down, and is seen in sections as large separate cells. These will be called lecitholytic cells, since their function appears to be similar to that of the vitellophages in embryonic development (Imms, 1957). The protein yolk loses its characteristic structure and breaks down into small spherules. The cytoplasm of the lecitholytic cells is vacuolated, and contains globular eosinophil inclusions of various sizes (fig. 2, B). The nuclei stain purple with toluidine blue. The cytoplasm stains pale blue with darker blue inclusions. Vacuolation of the periphery of the oocyte nucleus occurs at this stage and is a preliminary to its ultimate disappearance.

**RB 3.** Most of the shrunken oocyte is filled with lecitholytic cells, which are surrounded by the remains of yolk. No division of these cells has been observed. The nuclei of many of the lecitholytic cells become irregular and displaced to one side of the cell, while large lipid globules appear in the cytoplasm (figs. 2, C; 3, B). Later the nuclei fragment into small basiphil bodies which finally coalesce into large black globules (fig. 2, D). The tunica propria at this stage is thrown into folds at both ends of the follicle.
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RB 4. No traces remain of a compact follicular epithelium and the majority of the lecitholytic cells have pycnotic nuclei. The tunica propria thickens to $3 \mu$ and at the distal end the greatly folded membrane has an overall thickness of as much as $35 \mu$.

RB 5. Few active lecitholytic cells remain at this stage in the resorption body. Scattered among them are the remains of a degenerate oocyte (fig. 3, c).

RB 6. In this final stage two features alone indicate that absorption has occurred. One is the presence of a ring of orange-red crystals in the pedicel, the other is the shrunken remains of the folded tunica propria (figs. 1 (RB 6); 3, d). A normal plug of large nucleated cells guards the entrance into the oviduct.

Yolk formation does not usually begin in the penultimate oocyte until the

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**Fig. 2.** A, two follicular epithelial cells during late vitellogenesis. B, lecitholytic cell during the early stages of resorption. The vacuoles contain PAS-positive inclusions. C, lecitholytic cell at a later stage of resorption. Notice the stellate nucleus and large lipid globules. D, a degenerate lecitholytic cell with pycnotic nucleus. Camera lucida drawings.
normally developing eggs in other ovarioles are ejected and the next generation of oocytes begins its development.

Histochemistry of the resorptive bodies

The view that the lecitholytic cells are responsible for the breakdown of the yolk is supported by the histochemical observations at all stages of resorption. These cells contain in their large vacuoles PAS-positive, Millon-positive material similar to that of the protein yolk. Similar material is also present in the spaces between the cells. At stage RB 4 little of this material remains in the oocyte, and this indicates that protein yolk has been almost entirely resorbed.

The lipid distribution in stage RB 1 differs in no way from that of the normal oocyte, but as the lipid material becomes darker yellow in stage RB 2, an increase in the birefringent material can be observed. In fresh preparations a great number of smaller, darker bodies can be seen among the usual triglyceride globules. These bodies appear in polarized light as two kinds of multi-coloured crystals: one is a spherocrystal and the other is the orange-red rhomboid crystal described previously (p. 60). Transformation of the spherocrystals into needle-like or rhomboid forms has been observed in the resorptive bodies mounted in glycerine (fig. 3, F). This suggests that spherocrystals are a concentrated liquid precursor of the other, still dissolved in a droplet of lipid. The spherocrystals exhibit simple birefringence (4 positions of extinction) but not the Maltese cross birefringence which is characteristic of cholesterol esters and certain lipids (Pearse, 1953). The absence of cholesterol esters is further shown by the negative reaction to the digitonin test. The crystalline pigment is insoluble in water and pyridine but dissolves slowly in 70% alcohol and rapidly in absolute alcohol, acetone, and acids. The maximal absorption of light (tested spectrophotometrically) by the pigment dissolved in chloroform is at 460 mμ. All this evidence indicates the presence of a carotene and this is confirmed by the positive reactions to the iodine and antimony trichloride tests (Lison, 1936). Iodine gave a better reaction with the dissolved pigment and antimony trichloride gave the best result when used at 70° C. It remains to add that both types of crystal turned green when treated with Schultz's reagent or concentrated sulphuric acid. It is clear that

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**Fig. 3 (plate).**

A. Section of a resorption body at stage RB 1, showing the folded epithelium (Je) and vacuoles (V). Carnoy; haematoxylin and eosin.

B. Section of a resorption body at stage RB 3. Lecitholytic cells (lc), with irregularly shaped nuclei and vacuoles left by fat extracted in the staining process. Carnoy; haematoxylin and eosin.

C. Section of a resorption body at stage RB 5. Tunica propria (tp) folded at both ends of the contracted follicle. Some degenerate nuclei (dn) in the resorption body. Carnoy; haematoxylin and eosin.

D. Transverse section of an ovariole neck at stage RB 6 of resorption, showing the birefringent carotene crystal ring. Glycerine preparation. Polarized light.

E. Section of a yellow follicle, showing the accumulation of lipid globules (lg). Formaldehyde-calcium; Sudan black.

F. Glycerine preparation of a resorption body, showing the formation of a solid rod-like carotene crystal (x) from its liquid precursor—the spherocrystal (y). Polarized light.
FIG. 3

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this result is due to reaction between carotene and sulphuric acid and therefore Schultz's reagent cannot be used as specific for cholesterol (Kent, 1952).

Some sudanophil material is still present at stage RB 5 but it appears in an amorphous, granular form and not as droplets or globules. It stains in patches with aldehyde-fuchsin, which perhaps indicates the presence of oxidized lipid. At all stages of resorption, material is present which stains intensely with acid haematein and resists pyridine extraction. This is nucleoprotein, derived from the degenerate nuclei of the lecitholytic cells.

White and yellow follicles

An orange-red pigment ring is also formed during the resorption of the empty follicle after the egg has been ejected from the ovariole. In consequence a developing terminal oocyte of the second generation often has a pigment ring at its base. Singh (1958) has studied the resorption of the follicle and formation of the 'corpus luteum' in detail in Locusta. In Schistocerca the process is histologically very much the same, except that in this species some of the empty follicles, before being resorbed, resume lipid formation and become filled with lipid material, forming yellow follicles (fig. 3, E). Histochemically the lipid is a triglyceride, and orange pigment is present dissolved in the lipid material. The lipids are resorbed with the degenerating follicle but the pigment crystallizes. The total number of empty white and yellow follicles together represent the number of eggs produced and ejected.

Discussion

The development of the terminal oocyte in S. gregaria may be divided into 4 stages: an early growth period, characterized by rapid division of the surrounding follicle cells; a short preparatory period for yolk formation, with cytoplasmic differentiation; vitellogenesis; and finally chorion formation. This paper is concerned mainly with the process of yolk formation and resorption. The centripetal appearance of yolk in the oocyte suggests that the yolk-forming material is derived from the blood through the follicle cells. Telfer (1961) has shown that in saturniid moths, yolk proteins may be absorbed directly from the blood, reaching the oocyte surface by an intercellular route, but in S. gregaria the activity of the follicle cells during vitellogenesis indicates that the cells may be centres for the synthesis of protein and carbohydrate material. The varied staining reactions of different cells are perhaps due to different functional states. Further, the presence of RNA (either in the free form or as nucleoprotein) in rather high concentration in the follicle cells, particularly near the brush border, suggests that protein synthesis may occur here. The final disappearance of both RNA and the cellular basiphilia just before chorion-formation supports this view. Combination of the protein and carbohydrate components of the yolk is completed after passage into the oocyte, and is indicated by the change in reaction of the yolk globules to Azan stains in passing inwards from the epithelium. The nucleus of the oocyte shows little activity during vitellogenesis, and exchange of
material between it and the cytoplasm has not been observed. The only activity in the region of the nucleus occurs shortly before vitellogenesis, when a coarsely granulated zone of cytoplasm appears around the nucleus. This coincides with the differentiation of the rest of the cytoplasm and the appearance of cytoplasmic inclusions. There are 3 types of lipid bodies in a normal terminal oocyte: (1) phospholipid bodies, which appear abundantly before and during the early part of vitellogenesis; (2) compound bodies, consisting of a phospholipid cortex round a triglyceride medulla; these appear at the beginning of vitellogenesis; and (3) large triglyceride globules, which are present during all stages of yolk formation. These 3 types may be compared with the $L_1$, $L_2$, and $L_3$ bodies in the oocyte of the cockroach (Nath, Gupta, and Lal, 1958).

Resorption of the degenerating oocyte resembles in many way the resorption of the 'corpus luteum' (Ahrens, 1935; Singh, 1958). In both, tissue is resorbed and pigment deposited in the neck of the ovariole. However, in neither case should the term 'corpus luteum' be used in locusts. At no stage in resorption is there any progressive formation of new tissue, only degeneration and destruction. In oocyte resorption, the follicular cells before degenerating act as lecitholytic cells. By phagocytosis and enzyme production they break down and liquefy the yolk, making it suitable for resorption into the haemolymph. The release of enzymes is indicated by the vacuolization and disintegration of yolk in regions not yet reached by the invading lecitholytic cells. The invasion of the oocyte by the lecitholytic cells occurs by passive folding of the epithelium, when the volume of the oocyte is reduced and the expanded tunica propria contracts. The tunica propria is not a structureless membrane but contains fine fibres. These are revealed by the use of Gomori's modification of the Bielschowsky-Marsch method (Gomori, 1939a) for the demonstration of reticulin, and appear black after silver impregnation. The fibres are embedded in a neutral mucopolysaccharide substance and are stretched when the oocyte expands.

Protein yolk is dissolved and resorbed first. Lipid yolk absorption takes longer and continues up to stage RB 5. The lipids are resorbed but the pigment which is dissolved in them becomes more concentrated, crystallizes, and is deposited in the neck of the ovariole. Goodwin (1952) has suggested that this orange pigment is $\beta$-carotene, and the present results support this idea. The deposition of carotene seems merely to be the accumulation of a surplus material. It has been observed in the ovariolar necks and the walls of the oviducts in older females, 7 or 8 weeks old. In these cases the accumulation of lipid is the essential feature and the appearance of pigment is incidental. Similar lipid overproduction with a high concentration of carotene is the reason for the formation of yellow follicles. In normal white follicles metabolism ceases in the epithelial cells, but should the follicle cells continue or resume lipid metabolism after ovulation the yellow follicles result. The abnormality of this process is shown by the absorption of such yellow follicles in 2 or 3 days. A similar pigment ring, though with a much smaller amount of
pigment, is frequently produced by the white follicles in *Schistocerca*. It presumably has a similar origin. Singh's (1958) suggestion that in *Locusta*, pigment might arise in connexion with a resorption process in the *penultimate* oocyte, is certainly not true in *Schistocerca*. No reduction has been observed in the length of the penultimate oocyte above a resorption body or a yellow follicle, except when the penultimate oocyte itself becomes a resorption body. This, however, happens infrequently, though it may result from the delayed absorption of the terminal follicle.

The follicle cells and the oocyte co-operate in the orderly process of growth and yolk deposition characteristic of the normally developing egg. This process is controlled by factors produced by the neurosecretory system (Highnam, 1962). The process may be interrupted at any stage of oocyte development, short of full-grown. The number of resorptive bodies varies with the state of activity of the neurosecretory system (Highnam and Lüs, 1962). The deposition of yolk and its resorption are processes intimately associated with the protein turnover of the body, and there is now good evidence that neurosecretory factors control protein metabolism (Hill, 1962; Thomsen and Møller, 1959). But it is not thought that protein availability alone is responsible for variations in the proportions of the resorption bodies. In a normally developing ovary, certain oocytes seem to have an intrinsic potential for resorption. A larger number of oocytes are resorbed when other disabling factors are present and this may even result in complete resorption of all the terminal oocytes. The nature of the initial potential for resorption in some oocytes is now being investigated.

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**References**

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