dria is reduced, their ATP-synthetase function is known to be depressed, whereas increased permeability of the membrane promotes the passage of ATP through the mitochondrial membrane. Both these factors may thus participate in the increase in ATP-hydrolase activity of the mitochondria under the influence of chlorpromazine, for increasing membrane permeability alone (experiments with preliminary freezing and thawing of brain tissue) led to the deposition of only a small quantity of reaction product in the mitochondria. The heterogeneity of the reaction of the mitochondria can be explained by differences in the initial state of these organelles and also by differences in their "age."

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ULTRASTRUCTURE OF PARIETAL CELLS IN SUMMER AND DURING HIBERNATION

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The parietal cells of red-cheeked susliks were studied in summer and during hibernation. Electron-microscopic investigation and morphometric analysis revealed definite changes in ultrastructure during hibernation, reflecting the absence of secretory activity of the cells. No marked dystrophic changes were found in the parietal cells in this period. Structural differences determined by stages in the life cycle were preserved.

KEY WORDS: parietal cells; ultrastructure; hibernation; morphometry.

The state of hibernation in mammals is characterized, along with other features, by a fall in body temperature to 4-5°C and, in the species studied in this investigation (the red-cheeked suslik, Citellus erythrogenus Br.), by absence of exogenous feeding for a long period (up to 7-8 months). The study of the morphology of the stomach during hibernation, when specific secretory function is absent, is therefore of considerable interest, more especially because no research of this kind at the electron-microscopic level could be found in the accessible literature.

The object of this investigation was to compare the ultrastruture of parietal cells of the red-cheeked suslik killed in summer (i.e., in the active period) after starvation for 24 h, and during hibernation (December, January, or early February).

EXPERIMENTAL METHOD

The tissue was fixed with 4% paraformaldehyde solution, postfixed with 1% osmic acid solution, and embedded in a mixture of Epon and Araldite. Ultrathin sections were stained with uranyl acetate and lead citrate and examined in the JEM-100C electron microscope. Parietal cells along the whole length of the fundal glands in the region of the body of the stomach were studied. A comparative morphometric analysis was made

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TABLE 1. Morphometric Characteristics of Parietal Cells from Middle Portions of Neck of Fundal Glands (M ± m)

Index	Summer period (n = 70)	Hibernation (n = 50)
Area of cell, μ^2	110±3,77	55,6±2,1
Area of nucleus in cell, %	15±0,59	24,67±1,44
Area of mitochondria in cytoplasm, %	23,21±0,61	42,24±1,33
Area of tubulovesicles in cytoplasm, %	36,11±0,67	9,3±0,87
Area of nucleus in cytoplasm, %	0,91±0,15	0,84±0,22
Surface density of membranes on tubulovesicles, μ^2/μ^3	2,03±0,04	0,61±0,06
Surface density of secretory membranes,* μ^2/μ^3	2,71±0,06	2,33±0,11
Surface density of inner membranes,† μ^2/μ^3	0,62±0,02	1,44±0,10
Surface density of all cell membranes, μ^2/μ^3	3,35±0,06	3,78±0,15
No. of lysosomes per section through cell	1,17±0,20	1,36±0,24

*Secretory membranes include apical plasmalemma and membranes of tubulovesicles and intracellular tubules.

†Inner membranes include lateral and basal plasmalemma.

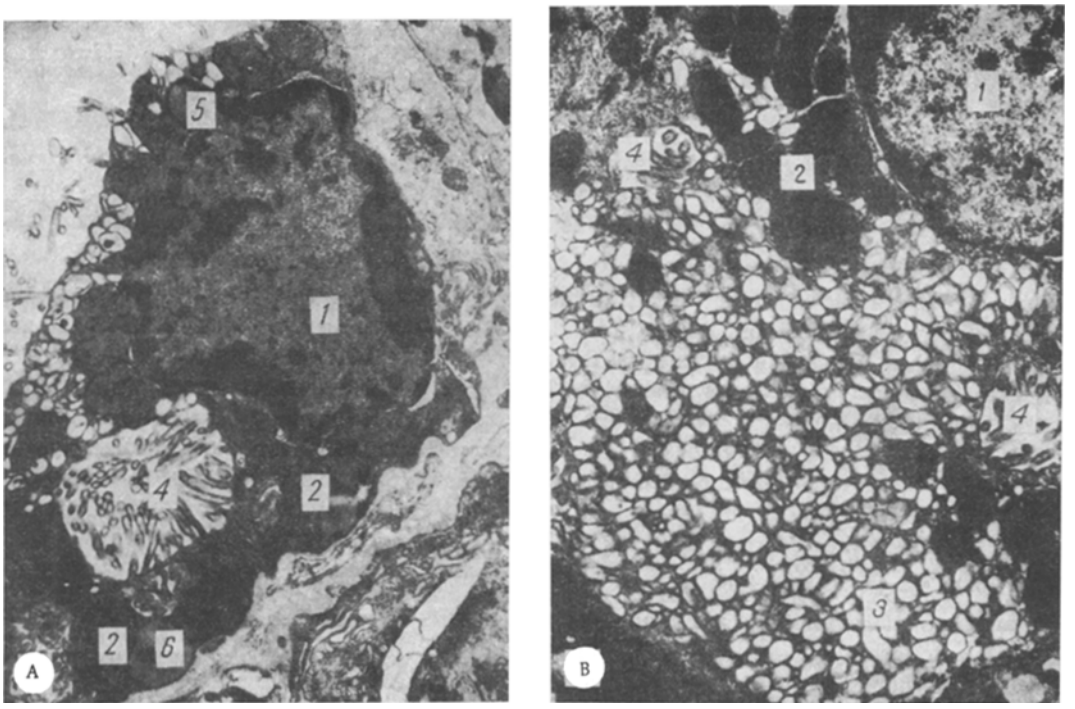

Fig. 1. Parietal cell from middle portion of neck of fundal gland (10,000×). A) Active state; B) state of deep hibernation. 1) Nucleus; 2) mitochondria; 3) tubulovesicles; 4) secretory tubules; 5) lysosome; 6) fat.

of parietal cells in the middle portions of the neck of the gland, for which purpose seven and five cells were selected at random from each of 10 grids with sections of tissue from active and hibernating animals respectively. Primary parameters were counted with a final magnification of the negatives of 20,000 times, with the aid of a square test grid with a step of 1 cm.

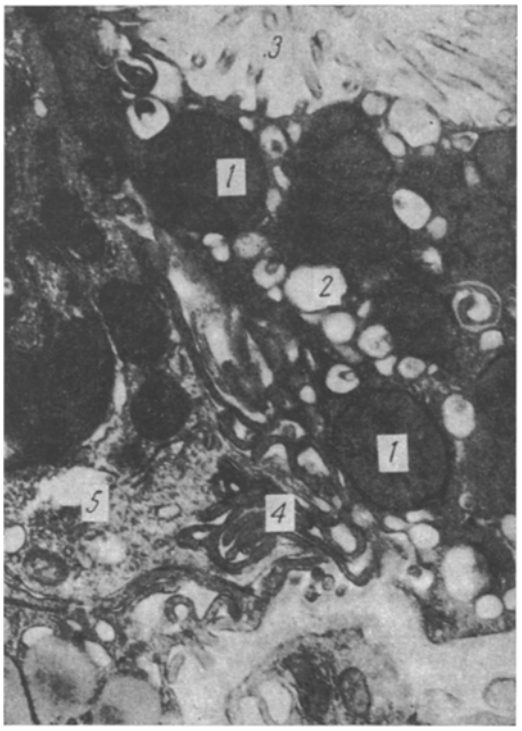

Fig. 2. Part of a parietal cell from middle portion of neck of fundal gland. Deep hibernation (17,000×). 1) Mitochondria; 2) tubulovesicles; 3) secretory tubule; 4) folds of lateral plasmalemma; 5) accessory cell.

EXPERIMENTAL RESULTS

Hibernation, as light microscopy shows, leads to marked changes in the whole of the digestive apparatus in mammals of various species [2, 3, 5, 8]. In the red-cheeked suslik, in particular, the glands are shortened, their mucous membrane becomes thinner, and changes in the gland cells and histochemical changes are observed [2].

Both in the active state and during hibernation the ultrastructure of the parietal cells is determined by the stage of the life cycle, which is connected with the location of the cells along the length of the gland. In the region of the isthmus and the upper portions of the neck of the glands, young parietal cells are found. In the course of maturation and migration downward the level of development of the secretory membranes increases progressively and the number of polysomes and cisterns of granular cytoplasmic reticulum (GCR) is reduced. In the middle portions of the neck of the gland the parietal cells show signs of maximal secretory activity. As they migrate further along the gland the level of development of the secretory membranes of the parietal cells gradually falls, whereas the number of lysosomes and the area of cytoplasm occupied by free ribosomes are increased. In the terminal portions of the gland the parietal cells come to the end of their existence.

For a comparative analysis of the parietal cells in different seasons of the year mature cells with maximal functional activity located in the middle portions of the neck of the gland were studied. The secretory apparatus (secretory membranes) of these cells in active animals consists of intracellular tubules, an apical plasmalemma, and numerous tubulovesicles formed by smooth membranes, occupying the main part of the cytoplasm and displacing the large mitochondria toward the nucleus and to the periphery of the cell (Fig. 1a). The membranes of the tubulovesicles account for about three-quarters of the total area of the secretory membranes (Table 1). The cytoplasm of the parietal cells also contains solitary cisterns of GCR and lysosomes, and the poorly developed Golgi complex consists of several flat cisterns and small vacuoles. Droplets of fat are frequently seen.

During the period of hibernation the parietal cells are greatly reduced in size (Table 1). Their cytoplasm becomes extremely dense and contains numerous free ribosomes. The most noteworthy features by

comparison with the active state are changes in the secretory membranes. The number of tubulovesicles varies in different cells: They are few in number and polymorphic and they often contain osmiophilic inclusions (Fig. 1B). The membranes of the tubulovesicles account for only one-quarter of the area of the secretory membranes, the greater part of which consists of numerous microvilli and secretory tubules. The secretory tubules of different cells differ in their degree of dilatation. Compared with the active state, the surface area of the inner membranes, including the lateral and basal plasmalemma (Table 1), is greatly increased. This increase takes place on account of the appearance of well-developed folding; the folds of plasmalemma, with dense cytoplasm contained between them, give the appearance of long microvilli (Fig. 2). The mitochondria of most parietal cells in the period of hibernation, just as in the active state also, have a dense matrix and numerous cristae. During hibernation, however, mitochondria with different degrees of dilatation of the intracristal space are often found. The number of lysosomes does not change significantly during hibernation (Table 1). The Golgi complex in the parietal cells of hibernating susliks consists of vacuoles of various sizes, but no flat cisterns are present. The ultrastructure of the parietal cells as described above does not change appreciably throughout the period of hibernation.

During hibernation not only were considerable changes found in the structure of the parietal cells, but cell forms not found in the active period also appeared. For instance, in the terminal portions of the glands parietal cells with grossly dilated tubules, resembling a hugh vacuole were found, together with cells resembling in their structure the young forms of parietal cells found in the upper regions of the neck of the glands.

Disappearance of the tubulovesicles from the parietal cells has been found in man after prolonged starvation, when, just as during hibernation, hydrochloric acid secretion is absent [1, 4]. However, as morphometric analysis showed, redistribution of the membranes takes place in the parietal cells of the suslik: The ratio of the surface area of the membranes of the tubulovesicles and of the secretory tubules is reversed during hibernation. Part of the membrane reserve is concentrated in the folds of the lateral and basal plasmalemma. It is interesting to note that the surface density (surface area of the membranes per unit volume of cytoplasm) of all cell membranes during hibernation was not reduced compared with the active state, possibly on account of a decrease in the volume of the cytoplasm.

The study of structural changes in the membranes of the parietal cells of mice and dogs in the course of secretion has also shown that not only membranes of the intracellular tubules and tubulovesicles, but also the basal and lateral plasmalemma take part in them. Budding of tubulovesicles from the folds of the basal plasmalemma, followed by their detachment, have also been observed [7, 9].

The redistribution of membranes in the parietal cells of the suslik during hibernation, as described above, is evidently an adaptation enabling the membrane reserves of the cell to be preserved for subsequent restoration on awakening.

Unlike prolonged starvation in man [1, 6, 10], during hibernation the number of lysosomes in the parietal cells does not increase and fatty infiltration is not observed. The absence of dystrophic changes in the parietal cells of the suslik is evidently due to some degree to the action of the temperature factor, and also to the presence of adaptive mechanisms aimed at preserving the cell population and the potential secretory powers during hibernation.

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