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Wacław WASILEWSKI, Maria PEDRYC-WRONA

Effect of Starvation and Resumption of Feeding on the Volume of the Liver Cell and of Its Nucleus and Nucleoli in the Golden Hamster

Wpływ głodu i powtórnego karmienia na objętość komórki, jądra i jąderek w komórkach wątroby chomika złocistego

Влияние голода и повторного кормления на объем клетки, ядра и ядрышек в клетках печени золотистого хомячка

INTRODUCTION

The effect of starvation on the morphology of the liver cells has been the subject of numerous studies, the liver being very sensitive to this kind of stress. Kosterlitz (14) demonstrated that the weight of the liver in rats which were starved for 24 hours was more markedly reduced than their body weight. Later on, this observation was confirmed by Hobik, Hobik and Grundmann (12, 13) who starved rats for 6 days, and by Tongiani (20) who subjected golden hamsters to 8-day fasting.

It was also noticed that the reduction of weight of the liver is mainly the consequence of changes which occur in the cytoplasm of the cell, such as increased cytoplasm volume (11), increased size of mitochondria with simultaneous reduction of their number (1), increased number of autophagic vacuoles (22), and drastic reduction of the surface of the smooth and granular endoplasmic reticulum (18). More controversial are the findings concerning the nuclei of the liver cells in animals subjected to starvation. Some workers find no changes in the size of the nucleus under these conditions (11, 1); others observe a distinct decrease (12, 13) or increase (20) of the nucleus. Studies on the nucleoli in the liver cells of some laboratory mammals (1, 6) suggest differences between the indivi-

dual animal species concerning changes in the size and number of nucleoli during fasting and resumed feeding.

So far, the effect of starvation on the liver cells has been studied mainly on rats, and few studies have been conducted on other species. For this reason, the present writers think it justified to undertake such investigations in the golden hamster.

MATERIAL AND METHOD

One hundred and forty golden hamsters (*Mesocricetus auratus* Waterhouse), obtained from 22 litters, were used for the investigations. The animals were given superabundant food every day at 9 a.m. The diet consisted of milk, oatflakes, wheat wafers and carrots. Moreover, in summer the hamsters were given green parts of various plants, and in winter germinating wheat. Water was supplied ad libitum. The experiment began when the hamsters reached the age of 2 months. One animal selected at random from each litter served as control. The remaining animals of the given litter were deprived of food at 11 a.m., water being left ad libitum. Part of the experimental animals received again normal food towards the end of the 7th day of fasting, at 8 a.m. Altogether, the study embraced 57 animals starved for 1 to 6 days, and 61 animals fed for 3 hours to 10 days after previous fasting continued for nearly 7 days. The control material consisted of 22 golden hamsters.

At 11 a.m., the hamsters were anaesthetized with ether and dissected. Portions of the liver were speedily removed and fixed in Carnoy's fluid at room temperature for 7 hours. The remaining manipulations, up to mounting the liver portions in paraffin blocks, always took 28 hours. Liver sections were cut at 8 μ. To obtain good visibility of the cell borders, the liver sections were stained with safranine 0 solution, water blue, orcein and eosin according to the method published by Romeis (19). To assure good visibility of the nucleoli, use was made of methyl green and pyronin Y staining at *pH* 5.2—5.3 according to the method given by Kurnick (16). Glycogen in the liver cells was detected by Best's method.

Morphometric measurements were carried out by means of a 15× micrometric eyepiece. The diameters of 25 mononucleate cells and of their nuclei, as well as the diameters of 5 binucleate cells, situated on the lines between the median and portal vein, were measured in the liver of each hamster, using a 40× objective. In preparations stained with methyl green and pyronin, the diameters of 25 nuclei in the liver cells of each animal, and the diameters of all nucleoli situated in these nuclei were measured with the use of a 90× objective. From the mean values thus obtained, the volumes of the cell, of the nucleus, or of both nuclei together in the case of binucleate cells, and the sum of the volumes of the nucleoli in each nucleus were calculated, using, as an approximation, the formula for the sphere. No allowance was made for the shrinking of the tissue during fixation and dehydration of the material. Glycogen concentration in the liver cells was estimated under the microscope using a 200-fold magnification. The mean percentage of the cross-section area of the cell filled with glycogen granules was determined for each animal (which, obviously, does not represent the percentage content of glycogen in the liver).

To verify the significance of differences, Student's t-test for non-matched pairs was used, and in the case of non-homogenous variances the approximte C test of Cochran and Cox (5) was applied.

RESULTS

1. Changes in the body and liver weight

In the starved hamsters, the body weight decreased by 35% in 6 days. Resumption of feeding resulted in a slow increase of the body weight in such animals, and it took 10 days before they reached the weight which averaged that found in the control animals at the beginning of the experiment. However, there were distinct differences in the rate of putting on weight by the individual animals, which found its expression in increased values of the standard deviation (Table 1).

The percentage ratio of liver weight : body weight, which in control animals was 5.49%, sank during fasting to 3.93%, which proved highly significant statistically ($P<0.001$). After 4 days of resumed feeding of the starved hamsters, this index obtained significantly higher values than in the controls ($P<0.01$), which was due to the fact that the liver weight grew faster than the weight of the body. After 10 days, the percentage ratio liver weight: body weight approached that observed in control animals (Table 1).

2. Changes in the cell size

After one or two days of fasting, the liver cells of the golden hamster reduced their volume by as much as 1/3 on the average, which was highly significant ($P<0.001$); after 5 or 6 days of fasting, the volume of the liver cell fell to 1/2 of that found in control animals. Changes in the cell volume in mononucleate cells (Table 2, Fig. 1) and in binucleate cells (Table 3) were very similar. Resumption of feeding after almost 7 days of fasting resulted in a rapid increase of the cell volume during the first days (Tables 2 and 3). Beginning with the 3rd day, the increase of the cell size proceeded very slowly. By the 10th day of resumed feeding, the cell volume had not yet reached the values observed in control hamsters, though the differences were not statistically significant.

3. Changes in the size of the nucleus

The volume of the nucleus decreased proportionately to the duration of fasting, and the total loss of the nucleus volume after 6 days of starvation were 32.5% for mononucleate cells, and 27.8% for binucleate cells ($P<0.001$), (Tables 2 and 3, Fig. 1). In the case of the preparations stained with methyl green and pyronin, the nucleus volume was reduced by 17%

Table 1. Changes in the body and liver weight under the influence of starvation and resumed feeding

		Number of animals studied (n)	Mean body weight ± standard deviation (g)	Mean liver weight ± standard deviation (g)	Mean liver weight : body weight index in % ± standard deviation
Control		22	88.05 ±13.75	4.79 ±0.75	5.49 ±0.75
Starvation	1—2 days	21	71.65 ±13.70****	3.24 ±0.66****	4.57 ±0.74****
	3—4 days	19	68.50 ±11.67****	2.65 ±0.40****	3.90 ±0.42****
	5—6 days	17	57.48 ±9.56****	2.25 ±0.43****	3.93 ±0.50****
Resumed feeding	3-hrs	9	54.78 ±8.54****	2.32 ±0.54****	4.25 ±0.70****
	1—2 days	20	66.58 ±14.95****	4.04 ±1.10*	6.09 ±1.12
	3—4 days	19	69.89 ±12.37****	4.33 ±1.13	6.15 ±0.90**
	10	13	90.14 ±19.46	5.14 ±1.08	5.72 ±0.60

* Explanation — statistical significance of differences in relation to the control is denoted by:
* $P<0.05$; ** $P<0.02$; *** $P<0.01$; **** $P<0.001$.

Table 2. Changes in cell and nucleus volume and in the volume nucleus: cell ratio in mononucleate liver cells

		Number of animals studied (n)	Mean volume of mononucleate cell in μ^3, ± standard deviation	Mean volume of nucleus in μ^3, ± standard deviation	Mean % index of the nucleus volume : cell volume ratio ± standard deviation
Control		22	3331.77 ±569.48	126.36 ±16.98	4.18 ±0.61
Starvation	1—2 days	21	2194.45 ±442.58****	109.55 ±16.32***	5.48 ±0.99****
	3—4 days	19	1856.45 ±288.38****	98.38 ±15.32****	5.70 ±0.88****
	5—6 days	17	1656.99 ±297.90****	86.59 ±9.95****	5.75 ±1.24****
Resumed feeding	3-hrs	9	1661.81 ±271.76****	95.31 ±7.63****	6.18 ±1.21****
	1—2 days	20	2752.79 ±402.16****	108.56 ±18.66***	4.35 ±1.00
	3—4 days	19	2864.65 ±568.09**	114.52 ±18.09*	4.34 ±1.34
	10	13	3056.42 ±509.76	106.28 ±13.08****	3.78 ±0.75

Explanation — see Table 1.

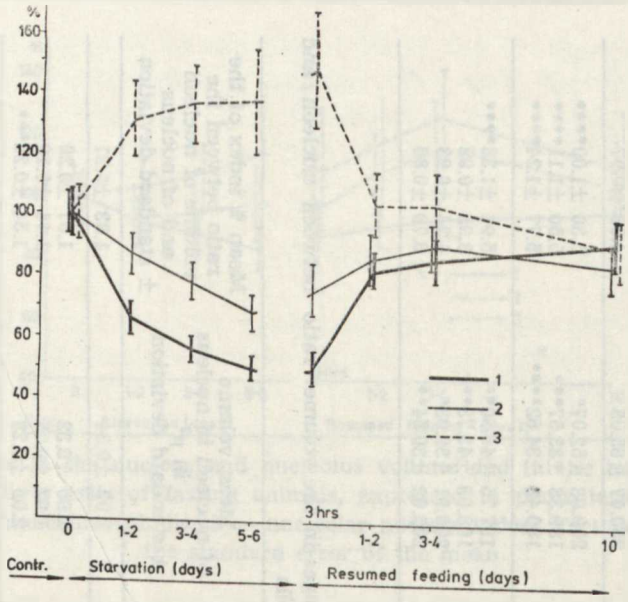

Fig. 1. Changes in the cell and nucleus volume and in the nuclear-cellular index in the liver of fasting animals, expressed in percentage; 1 — cell volume, 2 — nucleus volume, 3 — nuclear-cellular index. Vertical lines indicate the standard error of the mean

($P<0.01$), (Table 4, Fig. 2). Renewed administration of food to the starved hamsters resulted in an increase of the nucleus volume, which could be observed as early as 3 hours after feeding. During the further 4 days of feeding, the nucleus volume continued to grow slowly (Tables 2, 3 and 4), but the dimensions of the nucleus, observed during the whole period of resumed feeding, remained distinctly smaller than in the controls.

The percentage ratio of nucleus volume : cell volume was 4.18% in mononucleate cells. After 6 days of fasting it increased to 5.75%, which, in relation to the controls, was very significant ($P<0.001$). Resumed feeding of starved hamsters produced, as early as after one or two days, values of the percentage ratio nucleus : cell which approached those observed in control animals (Table 2, Fig. 1). Closely similar changes in this index were found in binucleate cells (Table 3).

4. Number of nucleoli

During starvation, as well as after resumption of feeding of golden hamsters, the number of nucleoli per one nucleus did not change and was the same as in the control group. The average number of nucleoli was 1.41 per one nucleus.

Table 3. Changes in the volume of binucleate cell and its both nuclei, and changes in the volume ratio between both nuclei and cell

		Number of animals studied (n)	Mean volume of binucleate cell in μ^3 ± standard deviation	Mean volume of both nuclei in μ^3 ± standard deviation	Mean % index of the both nuclei volume : cell volume ± standard deviation
Control		22	6732.72 ±2110.70	250.07 ±65.05	4.03 ±0.97
Starvation	1—2 days	21	4101.77 ±682.17****	209.88 ±52.07*	5.30 ±1.00****
	3—4 days	19	3616.78 ±461.60****	189.38 ±33.57***	5.50 ±1.11****
	5—6 days	17	3308.92 ±687.59****	180.43 ±34.62****	5.77 ±1.24****
Resumed feeding	3-hrs	9	3449.74 ±441.14****	197.75 ±46.50**	5.94 ±1.38****
	1—2 days	20	5341.15 ±950.40**	198.03 ±43.73***	3.95 ±0.92
	3—4 days	19	5452.19 ±1564.39*	209.91 ±39.93*	4.24 ±0.93
	10	13	5839.96 ±1410.74	205.02 ±30.54**	3.79 ±0.86

Explanation — see Table. 1.

Table 4. Changes in the volume of nucleus and nucleoli, and changes in the volume ratio between nucleoli and nucleus in liver cells

		Number of animals studied (n)	Mean nucleus volume in μ^3 ± standard deviation	Mean volume of nucleoli in nucleus in μ^3 ± standard deviation	Mean % index of the ratio between the volume of nucleoli and of nucleus ± standard deviation
Control		22	158.24 ±19.35	2.03 ±0.34	1.33 ±0.21
Starvation	1—2 days	21	145.95 ±15.12*	1.90 ±0.32	1.37 ±0.20
	3—4 days	19	139.68 ±21.29**	1.92 ±0.25	1.44 ±0.19
	5—6 days	17	131.07 ±20.65****	2.00 ±0.23	1.54 ±0.26***
Resumed feeding	3-hrs	9	139.86 ±7.88***	1.97 ±0.23	1.46 ±0.23
	1—2 days	20	143.67 ±17.65**	2.22 ±0.43	1.59 ±0.27***
	3—4 days	19	148.17 ±22.92	2.38 ±0.25****	1.70 ±0.26****
	10	13	152.12 ±20.90	2.11 ±0.33	1.48 ±0.35

Explanation — see Table 1.

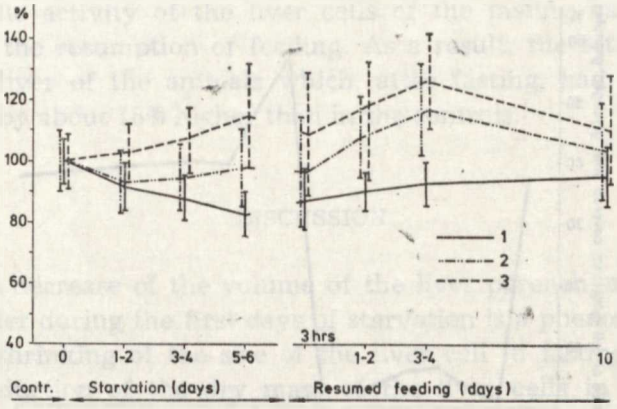

Fig. 2. Changes in the nucleus and nucleolus volume and in the nucleolar-nuclear index in the liver cells of fasting animals, expressed in percentage; 1 — nucleus volume, 2 — nucleolus volume, 3 — nucleolar-nuclear index. Vertical lines indicate the standard error of the mean

5. Changes in the size of nucleoli

During starvation of golden hamsters, the sum of the volumes of the nucleoli in the nucleus underwent only an insignificant decrease. On the other hand, renewed application of food to the starved hamsters produced a distinct increase of the volume of the nucleoli, which after 3 or 4 days became statistically significant ($P<0.001$). After 10 days of resumed feeding, the dimensions of the nucleoli again approached those observed in control animals (Table 4, Fig. 2).

The ratio of nucleolus volume sum : nucleus volume increased from 1.33% in the controls to 1.54% on the 5th or 6th day of fasting, and to the highest mean value of 1.70% on the 3rd or 4th day of resumed feeding of the experimental animals ($P<0.001$). After 10 days of resumed feeding of golden hamsters, the volume ratio of nucleoli : nucleus again approached that observed in control animals (Table 4, Fig. 2).

6. Changes in the cell morphology

In the liver cells of the control hamsters, 38% of the area of the cell cross-section was covered with glycogen granules of various size. After 24 hours of fasting, only an average of 1% of area of the cell cross-section was occupied by the glycogen granules. In the further course of starvation, a slight increase of the glycogen reserve in the cells was observed, with a maximum after 3 days (Fig. 3). Resumed feeding of the starved hamsters produced, as early as after 3 hours, an increase of the concen-

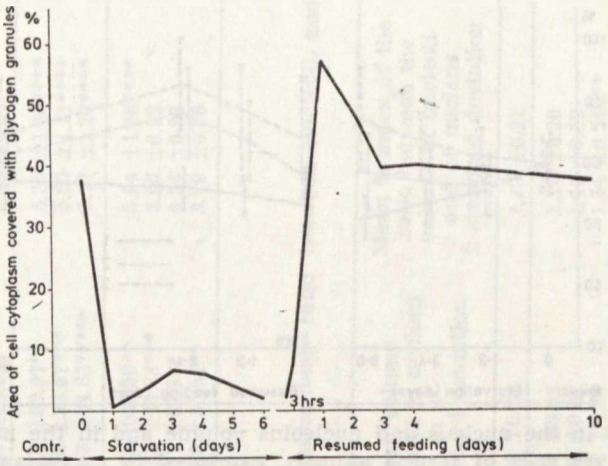

Fig. 3. Changes in the concentration of glycogen granules in the liver cells under the influence of starvation and resumed feeding

tration of glycogen granules in the cells which could be seen under microscope. After 24 hours, the concentration of this polysaccharide in the liver cells was much higher than in the control animals. Beginning with the 3rd day of resumed feeding, the accumulation of glycogen in the cells was similar to that in the controls.

During starvation, the border lines of the liver parenchyma cells of the experimental animals became blurred. After 4 days of fasting, in some individuals large vacuoles appeared in the cytoplasm of a few liver cells. The number of such vacuolized cells increased in proportion to the duration of fasting. Sometimes a desintegration of the nucleus was observed in the vacuolized cells, which pointed to the degeneration of a number of such cells. As it results from calculations made on the basis of comparing the size of the cell and the weight of the liver, but without taking into consideration the possible changes in the percentage participation of the intercellular spaces, the decrease of the total number of cells in the liver approximated as little as 5% after 6 days of starvation. The vacuolized cells were still seen after 24 hours since the resumption of feeding. These cells did not accumulate glycogen, or, if so, to a small extent only; the basophile character of their cytoplasm was distinctly reduced. After one day of resumed feeding, in spite of the increased area of the liver cell, the basophile cytoplasm, rich in RNA, was still present in the region near the nucleus, more or less the same as during starvation. After the second day, the areas of basophile cytoplasm were distributed almost regularly over the whole cell, similarly as in the cells of the control animals.

The mitotic activity of the liver cells of the fasting hamsters reappeared after the resumption of feeding. As a result, the total number of cells in the liver of the animals which, after fasting, had been fed for 10 days, was by about 18% higher than in the controls.

DISCUSSION

The rapid decrease of the volume of the liver parenchyma cell in the golden hamster during the first days of starvation is a phenomenon analogous to the shrinking of the size of the liver cell in fasting rats (3, 11), or to the reduction of the dry mass of the liver cells in the hamster during fasting (20). The decrease of the cell volume is above all the effect of the reduced volume of the cytoplasm, in which, under normal conditions, there occurs accumulation of various amounts of reserve materials, according to the quantity and quality of the food consumed by the animal (7). During the first 24 hours of fasting, an almost total depletion of the liver cell glycogen was observed in the golden hamster; similar observations, with reference to rats, were made by Harrison (11), Fišter, Lutkić and Roša (8), and Cardell, Larner and Babcock (4). The studies carried out by Harrison (11) also revealed that the decrease of the weight of the liver is accompanied by a decrease of the content of the cytoplasmatic components of the cell, first of all of the absolute content of water, protein and potassium, and, to a smaller extent, of RNA.

The high rate of disappearance of the cytoplasm components and of the liver weight observed by the present writers in hamsters during the first days of starvation is probably due to the high level of metabolic changes in the cells. Later on, with the progressing depletion of the substrates in the cytoplasm, the rate of these changes is slowed down, which is expressed, as in the present study, by a slower rate of the reduction of the cell size during the later days of fasting, or, as observed by Tongiani (20), by a reduced rate of the decrease of the dry mass of the cell. This opinion is confirmed by the studies of Freedland (9), who found that the activity of numerous enzymes in the liver cells of fasting rats is distinctly reduced during the first 24 hours of starvation. According to the same author, starvation brings about a concentration of the enzymatic systems which are indispensable for the cell's life, at the expense of other systems of less vital importance. This results in increased intracellular phagocytosis (22) and to changes, among others, in the volume ratios between the cell organellae, as it was observed by Rohr and Riede (18).

The increase of the liver cell volume in the golden hamster after the resumption of feeding was, with regard to its rate during the first two days, the reverse of the initial period of fasting. Afterwards, the liver cell seen under the light microscope differed from that of the control animals by slightly reduced dimensions only.

Opinions on the effect of starvation on the size of the liver cell nuclei are divided. Some investigators, such as Harrison (11), failed to notice any changes in the nuclei of the liver cells of fasting rats. Tongiani (20) observed an absolute increase of the dry mass of the nucleus in the liver cells of the golden hamster. Hobik and co-workers (12,13), using paraffin sections and a suspension of the nuclei in liquid paraffin, demonstrated an approximately 30% reduction of the nucleus volume in the liver cells of rats subjected to 7 days' starvation, as well as a decrease of the dry mass of the nucleus. The reduction of the nucleus volume in fasting rats has been confirmed by Krustev, Popov and Stefanova (15), and in fasting fish by Zaręba and Jasiński (23). The results of the present investigations demonstrate a decrease of the size of the liver cell nucleus in the golden hamster, which is in agreement with the observations of Hobik and co-workers (12, 13). However, the less distinct reduction of the nucleus volume observed by the present writers in preparations stained with methyl green and pyronin points to the need of assessing the results with caution.

The increase of the volume of the liver cell nuclei in the golden hamster proceeded rapidly during the first two days of resumed feeding, similarly as it was found by Hobik and co-workers (12, 13) in the rat. However, contrary to the observations of these authors, the dimensions of the nuclei of the animals whose feeding had been resumed did not reach those found in the control animals. This phenomenon, as it seems, was partly due to the increased number of mitotic divisions of the cells, and, in consequence, to the increased number of small post-mitotic nuclei, a fact noted by Gauthier (10).

The nucleolus, the main site of nuclear RNA, behaves during fasting differently in different species of mammals. An increase of the number of nucleoli, associated with a decrease of their volume, was observed in fasting rats (1, 6). A similar behaviour of the nucleoli was observed by David (6) in the guinea pig. On the other hand, the same author observed a distinct increase of the volume and number of nucleoli in fasting mice. As it results from the present studies, the number of nucleoli in fasting golden hamsters does not change, and their volume is only slightly decreased. When food was restored to the starved animals, there occurred an increase of the volume of the nucleoli, but only by 18% in relation to

that found in the control animals, which is obviously at variance with the observations of David (6), who found a 500—600% increase of the nucleolus volume in rats and guinea pigs after the resumption of feeding. The increase of the nucleolus volume after starvation can be partly explained by increased processes of synthesis in the cells, similarly as it was observed in the case of regeneration phenomena (17), or during intensive growth of the organism (2, 21).

To sum up, it can be said that starvation continued for many days does not produce lasting changes in the morphology of the liver parenchyma cells in the golden hamster, apart from the infrequent cases of cellular die-away. In a few days after the resumption of feeding, the liver cells resume their normal appearance, similarly as in the case of experimental rats. The interspecific differences in reacting to starvation and resumed feeding concern mainly the behaviour of the nucleolus.

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STRESZCZENIE

Do morfometrycznych badań wpływu głodu na morfologię komórek wątroby użyto 57 chomików złocistych (*Mesocricetus auratus* Waterhouse), głodzonych przez 1—6 dni oraz 61 chomików po uprzednim głodzeniu powtórnie karmionych przez 3 godz. do 10 dni. Jako materiał kontrolny służyły 22 zwierzęta.

W okresie 6 dni głodzenia straty ciężaru ciała wynosiły 35%, straty ciężaru wątroby 53%, straty objętości komórki miąższu wątroby 50%, a zmniejszenie objętości jądra ok. 30%. Objętość jąderek zmniejszyła się tylko nieznacznie, a ich liczba pozostała w czasie głodu nie zmieniona. Powtórne podawanie pożywienia spowodowało

wzrost ciężaru ciała, który powrócił do wartości wyjściowych (kontrolnych) dopiero po 10 dniach, a ciężar wątroby osiągnął wartości kontrolne już po 4 dniach. Objętość komórki i jądra szybko wzrosła w okresie pierwszych 2 dni powtórnego karmienia zwierząt, jednakże jeszcze po 10 dniach objętość ta była mniejsza niż u zwierząt kontrolnych. Objętość jąderek w okresie powtórnego karmienia chomików zwiększyła się ponad wartości kontrolne. Na skutek nierównomiernego tempa zmian wielkości uwzględnionych w pracy cech. tak podczas głodzenia, jak i podczas powtórnego karmienia zwierząt, stwierdzono istotne statystycznie zmiany wartości wskaźników: jądrowo-komórkowego, jąderkowo-jądrowego oraz stosunku ciężaru wątroby do ciężaru ciała.

Zapasy glikogenu w komórkach wątroby chomika złocistego po 24 godz. głodu zmniejszyły się do ilości śladowych. W następnych dniach głodzenia ilość glikogenu w komórkach przejściowo wyraźnie wzrosła z maksimum po 3 dobach. Po upływie 1 i 2 doby powtórnego karmienia zwierząt koncentracja glikogenu w komórkach wątroby znacznie przewyższała koncentrację tego polisacharydu w komórkach zwierząt kontrolnych, a od 3 doby była już normalna. Od 4 doby głodzenia pojawiły się komórki ze zwakuolizowaną cytoplazmą. Około 6 doby głodzenia spotykano komórki degenerujące. Komórki zwakuolizowane i degenerujące pozbawione były prawie całkowicie glikogenu i wykazywały bardzo zmniejszoną bazofilność cytoplazmy. Od 3 doby powtórnego karmienia wszystkie komórki wątroby w mikroskopie optycznym miały wygląd normalny.

РЕЗЮМЕ

Морфометрические исследования влияния голода на морфологию клеток печени проводились на 57 золотистых хомячках (*Mesocricetus auratus* Waterhouse), подвергнутых голоданию с 1 по 6 день, и на 61 хомячке, которые после предварительного голодания имели доступ *ad libitum* до корма в течение от 3 часов до 10 дней. В качестве контрольного материала употреблялись 22 хомячка.

В течение 6 дней голодания потери веса тела составляли 35%, печени — 53%, а потери объема клетки паренхима печени — 50%, объем ядра уменьшился почти на 30%. Объем ядрышек уменьшился незначительно, а их число в период голодания оставалось без изменения. Повторное кормление вызвало рост веса тела, который вернулся к исходным величинам (контрольным) лишь через 10 дней, а вес печени достиг контрольных значений уже через 4 дня. Объем клетки и ядра быстро возрастали в период первых 2-х дней кормления животных, однако даже через 10 дней они были меньше, чем у контрольных. Объем ядрышек в период повторного кормления хомячков увеличился и превысил контрольные величины. Вследствие неравномерного темпа изменения величины рассматриваемых в работе признаков, как во время голодания, так и повторного кормления животных, обнаружены статистически существенные изменения значений следующих индексов: ядерно-клеточного, ядрышково-ядерного и отношения веса печени к весу тела.

Запас гликогена в клетках печени золотистого хомячка через 24 часа голодания уменьшился до минимальных количеств. В последующие дни голодания количество гликогена в клетках временно отчетливо возросло (максимум на 3 сутки). После истечения 1 и 2 суток повторного кормления животных концентрация гликогена в клетках печени значительно превышала концентра-

цию этого полисахарида в клетках контрольных животных, а начиная с 3 суток достигла нормального уровня. На 4 сутки голодания появились клетки с вакуолизированной цитоплазмой, а на 6 сутки встречались дегенерирующиеся клетки. Вакуолизированные и дегенерирующиеся клетки были почти совсем лишены гликогена и проявляли сильно уменьшенную базофильность цитоплазмы. Через 3 дня повторного кормления все клетки печени под оптическим микроскопом выглядели нормально.