

## Changes in Thermogenesis and its Hormonal Regulators during the Postnatal Development of Rabbits and Guinea Pigs

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The studies carried out on 48 rabbits and 87 guinea pigs, during first weeks of their postembryonic life, were aimed to find the causes of the considerable differences in the capacity of the newborns of these two species to maintain thermal homeostasis. The poorer capacity of newborn rabbits to maintain thermal homeostasis is partly due to the lack of thermal insulation in the form of fur. Newborn rabbits are also characterized by lower heat production, which during the first week of life is 127.5 kcal/kg 24 h or 65.5 kcal/kg<sup>0.75</sup> 24 h, whereas in the case of guinea pigs these values are 137.6 kcal/kg 24 h or 73.3 kcal/kg<sup>0.75</sup>. Heat production rate during the initial period of young rabbits' life increases quite rapidly and in individuals 14-day-old is on an average 128.2 kcal/kg<sup>0.75</sup>, that is, about twice as much as in the newborn rabbits and the adult individuals of this species. In guinea pigs the changes in heat production rate during postembryonic development are far smaller. In both species ontogenic changes in heat production rate take place parallel to changes in thyroid activity. The differences found in morphological maturity and relative weight of the adrenal glands of these animals permit to assume that the adrenergic system plays a more important role in heat production in the newborn guinea pigs than in the newborn rabbits.

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### I. INTRODUCTION

Newborn mammals or newly-hatched birds usually possess a far weaker capacity for maintaining a constant body temperature than adult individuals of the same species. Physiology textbooks give the immaturity of thermoregulation mechanisms in newborn animals as the cause of this deficiency. Such immaturity, from the theoretical point of view, can be fully understandable, particularly in mammals, since throughout embryonic life the animals remain under thermostatic conditions ensured by the mother's organism, and do not, therefore, need their own thermoregulation mechanism. The moment of a mammal's birth, however, constitutes an abrupt change in environment from warm and wet to far colder and dryer. Rapid heat losses through radiation and convection

begin immediately, and during the first hours after birth also, through intensive evaporation of water from the moist body surface. Such losses usually lead to a quick drop in the body temperature of the newborn animals, this having been described in detail in piglets (Newland *et al.*, 1952) and young rabbits (Poczopko, 1969).

The various species differ, however, from each other very considerably in respect of their capacity for maintaining thermal homeostasis during the first few days after birth. For instance newborn calves (Obravec, 1954; Roy *et al.*, 1971) or lambs (Alexander & Brook, 1960; Simms, 1971) are capable of maintaining thermal homeostasis in only a slightly narrower range of variations in ambient temperature than adult cows and sheep, whereas newborn mice (Cassin & Otis, 1960; Lagerspetz, 1962) or the rat (Gulick, 1937; Buchanan & Hill, 1947; Poczopko, 1961) differ only slightly from poikilothermic animals. When comparing the capacity for maintaining thermal homeostasis in newborn rats and calves it is, however, difficult to understand clearly the causes of these differences, since they may to a considerable extent be due to the less favourable body surface to body mass ratio in the rat, and not only to the immaturity of thermoregulation mechanisms. Hull (1973) considers that even very limited capacity for maintaining a constant body temperature by newborn rabbits should be explained by the unfavourable body surface to body mass ratio and insufficient insulation, and not the immaturity of heat production mechanisms.

The purpose of the present studies was to trace the maturing process of the thermogenesis mechanism. They were carried out on animals with very similar relative body surface, but which even so differed considerably in their capacity for maintaining thermal homeostasis, *i.e.* rabbits and guinea pigs. Attention was paid to whether the animals chosen for the experiments differ in early stages of development in respect of rate of heat production in a way which would explain differences in capacity for thermoregulation. Examination was also made of thyroid gland activity and the weight and structure of the adrenal glands, since the hormones of these glands play an important part in regulation of thermogenesis and stimulation of heat production under the effect of cold.

## II. MATERIAL AND METHODS

### 2.1. Experimental Animals

The studies were carried out on 48 rabbits and 87 guinea pigs varying in age from several hours to about 4 weeks after birth, and also for purposes of comparison on adult individuals. Both rabbits and guinea pigs were unidentified

hybrids which were bred in the animal sheds of the Institute. The young animals remained with their mothers for 4 weeks after birth, except for the short intervals needed for measurements.

### 2.2. Heat Production

Heat production was evaluated on the basis of results of determinations of  $O_2$  and  $CO_2$  exchange made by means of a diaferometer (Kipp and Zonen, Delft, Holland). During measurements the animals were kept under resting metabolism conditions, that is, in a state of complete physical rest and at thermoneutrality but were not fasted before measuring. Choice of neutral ambient temperature for young rabbits of different age was made on the basis of the study by Hull (1965) and Poczopko (1969) and for guinea pigs on the study by Brück & Wünnenberg (1965a). The accepted temperatures were as follows:

Age, days	0—7	8—14	over 14	adult
Rabbits	35°C	30—31°C	27—29°C	24—26°C
Guinea pigs	32—34°C	30—31°C	25—28°C	24—25°C

The animals were taken out from their mothers and placed in a respiration chamber. After equilibrium had been established (20—30 minutes) measurements of  $O_2$  intake and  $CO_2$  emission were begun, which lasted about 40 minutes. The thermometer (Ellab, Copenhagen, Denmark) made it possible frequent temperature reading inside the respiration chamber. Heat production was calculated from the amount of oxygen consumed on the basis of the currently determined respiration quotient. The time between determination of the metabolic rate in the same individuals was not less than one day.

### 2.3. Development of Thyroid and its Activity

Radioactive iodine uptake was determined according to the method described by Barrington (1963). Before beginning the test the animals were weighed, then approximately  $1 \mu Ci Na^{131}J$  produced by the Nuclear Research Institute at Swierk was injected subcutaneously and the animals placed in cages (without the mother), ensuring neutral thermal conditions. After 3 hours the animals were killed with excess of ether, the thyroid dissected and immediately weighed on a torsion balance. The radioactivity of  $^{131}J$  dose given and radioactivity of the thyroid were measured in plastic test tubes in a well-type scintillation counter (type LL2—BUTJ, Poland). Uptake of  $^{131}J$  by the whole gland was expressed in percentages of the dose administered and after recalculation of the value per 1 mg of tissue.

Immediately after measuring radioactivity the thyroids were fixed in Bouin fixative, then embedded in paraffin, sectioned to  $7 \mu$  and stained with hematoxylin and eosine and by the PAS method.

### 2.4. Changes in Weight and Histological Picture of the Adrenals

The adrenals dissected from animal killed when investigating thyroid activity were weighed on a torsion balance, fixed in Bouin fixative, then embedded in paraffin, sectioned to  $7 \mu$  and stained with hematoxylin and eosine. During histological examination particular attention was paid to the blood supply to the gland and degree of formation of the medullar part.

## III. RESULTS

## 3.1. Changes in Resting Metabolic Rate

Comparison was made of the resting metabolic rate of animals of different age. This rate is expressed in two ways, namely as daily heat production per 1 kilogram of body weight and per metabolic unit of body weight ( $\text{kg}^{0.75}$ ).

Resting metabolic rate expressed per kilogram of body weight (Table 1) in newborn rabbits was about 127 kcal, and about 138 kcal/24 h in guinea pigs. In young rabbits significant reduction was observed in this rate on the second day, and later a gradual increase up to a maximum on the 14th day after birth. A certain increase in resting metabolic rate was also found in guinea pigs but the maximum was reached earlier, that is, as early as the 5th day after birth. On reaching the maximum metabolism rate in both species fell to the values characteristic of adult individuals. Maximum value of metabolic rate in rabbits was about 156, and in guinea pigs 116% of the rate observed on the first day after birth.

Changes in resting metabolic rate expressed per  $\text{kg}^{0.75}$  take a slightly different form to the rate calculated per kilogram of body weight. The results given in table 1 show that metabolic rate on the first day after birth, which is approximately 65 kcal/ $\text{kg}^{0.75}$  24 h in rabbits and approx. 73 kcal/ $\text{kg}^{0.75}$  24 h in guinea pigs, did not differ from the metabolic rate found in adult individuals of these species. During ontogenic development there were, however, fairly considerable changes. In young rabbits, after the initial decrease leading on the second day after birth to a value of about 46 kcal/ $\text{kg}^{0.75}$  24 h, there was a fairly rapid increase, so that at the age of 14 days rate was about 128 kcal/ $\text{kg}^{0.75}$  24 h. This high metabolic rate was maintained for about the 8th week of life, after which it gradually decreased to become equal at the age of 2.5 months in the case of rabbits with the level characteristic of adult individuals. The metabolic rate of guinea pigs also rose constantly during the initial period of postnatal development and reached a maximum of about 92 kcal/ $\text{kg}^{0.75}$  24 h at the age of 17 days. This increase was not as great as in the case of rabbits, but is highly significant statistically ( $P < 0.01$ ). After reaching the maximum there was a decrease in resting metabolic rate, which in guinea pigs was the same at the age of 3 weeks as that in adults, that is, about 80 kcal/ $\text{kg}^{0.75}$  24 h. Resting metabolic rate in adult guinea pigs is thus slightly higher than on the first day after birth, this difference being close to significance ( $P \approx 0.05$ ).

In order to analyze the relation between metabolic rate and body weight of the animals examined, calculation was made of the coefficient of regression for these variables.

Table 1

Age and heat production rate in rabbits and guinea pigs, means  $\pm$  S.E.

Age	Body weight, g	n	kcal/kg 24 h	kcal/kg <sup>0.75</sup> 24h
RABBITS				
12 h	71.0 $\pm$ 1.84	12	127.5 $\pm$ 7.99	65.5 $\pm$ 3.92
2 d	76.7 $\pm$ 1.99	6	87.3 $\pm$ 5.23	45.9 $\pm$ 2.86
4—5 d	85.1 $\pm$ 1.94	12	135.2 $\pm$ 8.03	72.9 $\pm$ 3.89
8 d	113.8 $\pm$ 6.00	12	165.9 $\pm$ 8.03	96.5 $\pm$ 5.21
10 d	133.0 $\pm$ 5.31	12	176.7 $\pm$ 7.35	106.8 $\pm$ 5.22
14 d	179.8 $\pm$ 8.25	12	198.1 $\pm$ 5.26	128.2 $\pm$ 2.36
18 d	226.6 $\pm$ 10.16	12	175.6 $\pm$ 5.32	120.6 $\pm$ 3.05
4 w	393.9 $\pm$ 26.02	12	140.4 $\pm$ 4.23	110.8 $\pm$ 4.27
6 w	576.9 $\pm$ 39.37	12	128.7 $\pm$ 5.49	111.3 $\pm$ 4.44
7—8 w	911.6 $\pm$ 70.28	6	129.5 $\pm$ 8.56	125.9 $\pm$ 7.88
2.5 m	2453.3 $\pm$ 28.12	6	52.6 $\pm$ 3.48	66.3 $\pm$ 3.79
Adult	3615.0 $\pm$ 299.46	6	48.3 $\pm$ 1.16	66.0 $\pm$ 1.81
GUINEA PIGS				
4—14 h	82.4 $\pm$ 3.92	31	137.6 $\pm$ 3.33	73.3 $\pm$ 1.46
1 d	75.0 $\pm$ 2.36	25	150.3 $\pm$ 3.66	78.2 $\pm$ 0.33
2 d	72.6 $\pm$ 2.34	24	156.6 $\pm$ 3.33	80.9 $\pm$ 1.56
3 d	77.2 $\pm$ 2.84	21	155.8 $\pm$ 4.04	81.6 $\pm$ 1.84
4—5 d	82.6 $\pm$ 3.22	39	161.1 $\pm$ 3.73	85.8 $\pm$ 1.58
6—7 d	95.9 $\pm$ 4.04	30	151.8 $\pm$ 3.74	85.2 $\pm$ 1.54
9—10 d	116.2 $\pm$ 5.71	17	150.0 $\pm$ 3.73	87.0 $\pm$ 1.62
14 d	142.1 $\pm$ 5.94	17	146.6 $\pm$ 5.30	89.5 $\pm$ 3.08
17 d	161.9 $\pm$ 6.81	11	145.9 $\pm$ 5.37	92.2 $\pm$ 3.20
21 d	173.9 $\pm$ 6.86	12	125.6 $\pm$ 8.36	80.6 $\pm$ 4.98
8 w	464.4 $\pm$ 20.70	8	99.5 $\pm$ 3.75	82.3 $\pm$ 3.77
3 m	633.0 $\pm$ 30.60	5	93.2 $\pm$ 3.46	83.0 $\pm$ 3.34
Adult	554.0 $\pm$ 50.31	6	93.2 $\pm$ 4.76	79.9 $\pm$ 2.96

Age: h=hours; d=days; w=weeks; m=months.

The relation between metabolic rate and body weight of adult homeotherms can be described by the equation:

$$\log M = \log a + b \log W$$

or

$$M = aW^b$$

where  $M$ =heat production under standard conditions,  $W$ =body weight in kg, and  $a$  and  $b$  are constants.

Value  $b$  (coefficient of regression) is 0.75 (that is,  $\frac{3}{4}$ ) (Kleiber, 1932; 1961; Poczkopko, 1971; Blaxter, 1972). The results given in Table 1, on the other hand, show that metabolic rate does not change during the

ontogenesis of rabbits and guinea pigs in proportion to  $3/4$  power of their body weight. Moreover, in rabbits during the period from birth up to about 2.5 months, the relation between metabolic rate and body weight is represented not by one but two straight lines (Fig. 1). Hence calculation was made of two coefficients of regression for this species, that is, one for rabbits aged from 1 to 10 days, which is 1.532, and the other for the period from the 10th day to 2.5 months of life, which is 0.712.

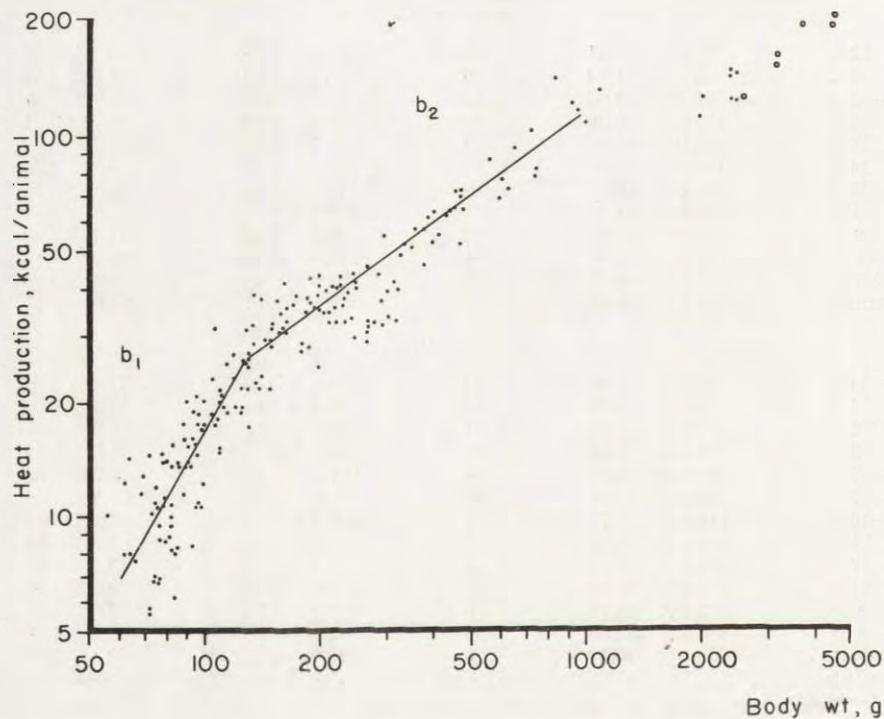


Fig. 1. The relationship between body weight and the resting metabolic rate in ontogeny of the rabbits.

The values of the exponent  $b$  in the equation:  $M = aW^b$  are:  $b_1 = 1.532$ ;  $b_2 = 0.712$ .

The relation expressed in the same way between metabolic rate and body weight during the development of guinea pigs (from birth up to the 12th week of life) is represented by one straight line only (Fig. 2). The coefficient of regression for this straight line is 0.843, and is thus greater than the coefficient 0.75 which, as already mentioned, is characteristic of the relation between metabolic rate and body weight of adult animals of different species.

### 3.2. Changes Taking Place in the Thyroid

#### A. Weight of the Gland

The weight of the thyroid in both the species examined during postnatal development increases linearly with increase in body weight, and the correlation between these variables is high. The coefficients of correlation are 0.844 for rabbits from 1 day to 1 month old, and 0.847 for guinea pigs from 1 day to 3 weeks old.

Increases in thyroid and body mass are not, however, strictly proportional. The data given in Table 2 show that the relative weight of the thyroid, which on the first day after birth was about 20 mg/100 g

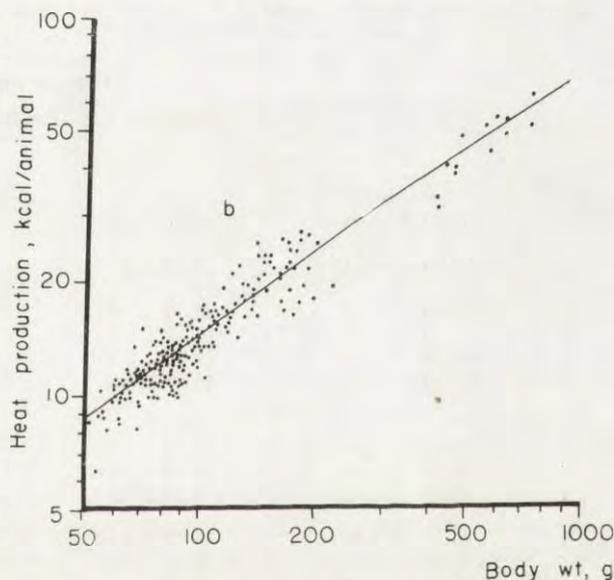


Fig. 2. The relationship between body weight and the resting metabolic rate in ontogeny of the guinea pig.  $b=0.843$ .

of body weight in both species, decreased significantly during the period of 3 weeks ( $P<0.01$ ), in rabbits to about 8 and in guinea pigs to about 15 mg/100 g. Since, however, the relative weight of the thyroid in guinea pigs decreased far more slowly than in rabbits after three weeks of postnatal life, it was significantly higher in the first of the species mentioned ( $P<0.01$ ).

#### B. Changes in the Histological Picture

The thyroid gland of a 12-hour old rabbit is morphologically very weakly formed (Photo 1, Plate VI). Only very few follicles filled with

unvacuolated colloid can be seen in histological slices. These generally small follicles are surrounded by cuboidal epithelium. Large round nuclei with deeply staining chromatine are situated in the centre of the cells and fill a considerable part of them. The major part of the gland is formed by undifferentiated tissue with deeply staining cell nuclei varying considerably in size. Mitotic figures can be observed in some of the cells. During the subsequent hours (from 12 to 36) the histological picture of the thyroid does not undergo any considerable change. The whole gland is richly supplied with blood capillaries. During the first week of the

Table 2

The change of total and relative thyroid weight in rabbits and guinea pigs during first 4 weeks of postembryonic life.

Age	n	Body weight, g	Thyroid weight	
			Absolute, mg	Relative, mg/100 g
RABBITS				
4-8 h	—	—	—	—
12 h	5	51.10 ± 2.41	9.80 ± 1.42	19.20 ± 1.42
24 h	—	—	—	—
36 h	5	76.00 ± 5.64	10.20 ± 2.10	13.98 ± 2.46
3 d	—	—	—	—
7 d	5	152.80 ± 4.92	21.80 ± 1.46	14.24 ± 1.44
14 d	5	192.40 ± 2.00	16.50 ± 2.00	9.10 ± 1.36
21 d	5	298.00 ± 12.78	24.00 ± 2.44	8.24 ± 1.17
28 d	5	526.00 ± 61.10	34.80 ± 5.58	6.64 ± 0.56
GUINEA PIGS				
4-8 h	13	76.83 ± 5.64	17.06 ± 0.82	22.92 ± 1.13
12 h	6	80.16 ± 3.98	16.83 ± 1.48	20.91 ± 1.22
24 h	11	81.95 ± 1.81	18.24 ± 0.99	22.26 ± 1.08
36 h	—	—	—	—
3 d	7	84.97 ± 3.64	19.37 ± 0.98	22.79 ± 0.66
7 d	6	79.52 ± 3.16	16.25 ± 0.42	20.55 ± 0.72
14 d	6	140.08 ± 10.38	22.22 ± 1.72	16.03 ± 1.18
21 d	6	184.50 ± 9.56	27.84 ± 1.44	14.92 ± 0.46
28 d	—	—	—	—

Mean ± S.E.; n = number of animals; age: h = in hours; d = in days.

- rabbit's life there is rapid differentiation of the thyroid tissue, although a considerable amount of undifferentiated tissue still occurs in a 7-day old rabbit (Photo 2, Plate VI). The existing and freshly formed follicles increase their dimensions chiefly as a result of increase in the amount of colloid they contain. The height of epithelial cells also increases. The thyroid of a 14-day old rabbit is fully formed morphologically (Photo 3, Plate VI). Small or medium-size follicles are surrounded by cuboidal epithelium and filled with unvacuolated or weakly vacuolated colloid. Large cell nuclei lie at the base or central part of the cell. During

further development of the rabbit (2.5 months) the dimensions of these follicles are observed to increase and also increasing secretion of hormones to the blood, as is shown by the appearance of a constantly increasing number of follicles filled with highly vacuolated colloid (Photo 4, Plate VI).

The thyroid in a guinea pig is morphologically well organized as early as 4—8 hours after birth (Photo 5, Plate VII). It is formed of round or oval follicles differing very slightly in respect of size and usually filled with generally unvacuolated colloid. Vacuolization of colloid is observed only in follicles situated along the course of blood vessels. Islands of undifferentiated tissue can be seen between the follicles. The cells surrounding the follicles are mainly tall-cuboidal, less often cylindrical. Oval nuclei with deeply staining chromatine lie at the base of the cells. Only a few mitotic figures are observed.

As early as the first day of life of guinea pigs considerable enlargement of follicles is observed, and also their differentiation in respect of size. In 12-hour old individuals medium and small size follicles occur in the peripheral part of the gland, and in the central part of the gland large follicles are encountered in addition to ones of medium size. Both in the central and peripheral part of the gland follicles are surrounded by cuboidal epithelium and filled with weakly vacuolated colloid. During the next 24 hours of life very considerable increase in the size of the follicles takes place, particularly in the central part of the gland. The colloid filling the follicles is generally vacuolated. The follicles are surrounded by cuboidal epithelium. In 3-day old guinea pigs the height of the epithelium has decreased in the majority of the follicles and there is further reduction in the amount of undifferentiated tissue. In certain individuals degeneration of some follicles takes place at the age of 7 days, their epithelium splitting and colloid spreading beyond the boundaries of the follicles. In older (2—3 weeks) guinea pigs the thyroid picture does not undergo any great changes (Photo 6, Plate VII), although degeneration of follicles is strongly marked (Photo 7, Plate VII). Large follicles, surrounded by epithelium varying in height even within the same follicle and filled with unvacuolated or weakly vacuolated colloid, are observed in the whole gland (Photo 8, Plate VII).

Data from histometrical measurements of the diameter of the follicles and height of epithelium cells of the animals examined are given in Table 3.

#### C. Radioactive Iodine Uptake

Changes in intake of  $^{131}\text{J}$  by the thyroid of young rabbits and guinea pigs taking place during the first weeks of postembryonic life are

illustrated in Table 4. In young rabbits about 12-hours old the uptake of  $^{131}\text{J}$  was considerable both when calculated for the whole gland (11.35%), and when calculated per milligram of thyroid tissue (1.18%). On the second day of the rabbits' life  $^{131}\text{J}$  uptake was almost twice greater, then decreased but remained on a high level up to the end of the second

Table 3

Epithelium height and colloid diameter in the thyroid follicles of baby rabbits and guinea pigs.

Means and standard errors are given.

Age	n	Rabbits		n	Guinea pigs	
		Epithelium height, $\mu$	Colloid diameter, $\mu$		Epithelium height, $\mu$	Colloid diameter, $\mu$
4—12 h	—	—	—	9	6.91 $\pm$ 0.19	52.41 $\pm$ 3.97
24 h	—	—	—	4	7.20 $\pm$ 0.29	62.44 $\pm$ 4.95
3 d	—	—	—	5	5.59 $\pm$ 0.45	58.57 $\pm$ 7.85
7 d	5	5.58 $\pm$ 0.30	10.58 $\pm$ 0.35	—	—	—
14 d	5	6.36 $\pm$ 0.58	6.54 $\pm$ 1.20	6	5.56 $\pm$ 0.33	58.55 $\pm$ 3.96
21 d	5	5.85 $\pm$ 0.41	13.05 $\pm$ 1.34	5	5.80 $\pm$ 0.56	57.28 $\pm$ 4.23
75 d	5	6.32 $\pm$ 0.34	20.69 $\pm$ 2.54	—	—	—

Age: h=hours; d=days; n=number of animals

No histometric measurements on the thyroid follicles of the rabbits less than 7 day-old were carried out, because majority of the gland tissue was not differentiated, and there were no colloid in some newly formed follicles.

Table 4

$^{131}\text{J}$  uptake by the thyroid gland of the rabbits and guinea pigs within 3 hours after injection.

Mean percent of the dose administered  $\pm$  standard error.

Age	n	Rabbit		n	Guinea pigs	
		Whole gland	1 mg tissue		Whole gland	1 mg tissue
4—8 h	—	—	—	13	17.71 $\pm$ 1.32	1.06 $\pm$ 0.08
12 h	5	11.35 $\pm$ 0.52	1.18 $\pm$ 0.01	6	12.07 $\pm$ 1.74	0.69 $\pm$ 0.05
24 h	—	—	—	11	11.38 $\pm$ 1.06	0.62 $\pm$ 0.04
36 h	5	23.56 $\pm$ 0.94	2.14 $\pm$ 0.29	—	—	—
7 d	5	25.61 $\pm$ 4.96	1.16 $\pm$ 0.56	6	8.56 $\pm$ 1.16	0.52 $\pm$ 0.07
14 d	5	21.39 $\pm$ 0.62	1.30 $\pm$ 0.21	6	2.96 $\pm$ 0.44	0.14 $\pm$ 0.02
21 d	5	7.91 $\pm$ 3.24	0.36 $\pm$ 0.13	6	3.32 $\pm$ 0.50	0.12 $\pm$ 0.02
28 d	5	13.01 $\pm$ 1.46	0.39 $\pm$ 0.04	—	—	—

Age: h=hours; d=days; n=number of animals.

week. During the third week it abruptly decreased, so that in rabbits 21 days old it was (when calculated per mg of tissue) only 0.36% of the amount given and then remained on a constant level. This decrease in iodine uptake was statistically highly significant ( $P < 0.01$ ).

The first measurements of iodine uptake by the thyroid in guinea pigs was made on individuals 4—8 hours old, that is, at least 4 hours

younger than the youngest of the rabbits examined. The average value of iodine uptake by the thyroid in guinea pigs was 17.17% when calculated for the whole gland, and 1.06% when calculated per 1 mg of thyroid tissue, that is, was close to the iodine uptake by the thyroid of rabbits 12 hours old. In 12 hour-old guinea pigs, however, iodine uptake calculated per 1 mg of tissue fell to 0.69%, that is, was significantly lower than uptake by the thyroids of rabbits of the same age ( $P < 0.01$ ). During further development of guinea pigs iodine uptake continued to decrease and at the age of 3 weeks reached a value of 0.12% (calculated per mg of tissue), *i.e.* significantly lower ( $P < 0.01$ ) than in 12 hour old individuals. The iodine uptake by the thyroids of 3 weeks old guinea pigs did not, however, differ significantly from the uptake of this element by the thyroid of rabbits of the same age ( $P = 0.2$ ).

### 3. Changes in Weight and Histological Picture of the Adrenals

The relative weight of the adrenal glands in young rabbits from the age of 12 hours to 4 weeks *post natum* and guinea pigs from 4 hours to 3 weeks old varied considerably, but did not exhibit changes in any particular direction (Table 5). The relative weight of adrenals in guinea pigs, expressed in mg per 100 g of body weight, is far higher than in young rabbits. In cases in which it was possible to compare animals of the same age of the two species studied (Table 5) the differences were statistically highly significant ( $P < 0.001$ ).

Considerable differences were also found in the histological picture of the adrenals taken from newborn individuals of these species of animals. In newborn rabbits no distinct boundary is observed between the medullary and cortical layers of the adrenals (Photo 9, Plate VIII). The medullary layer of the gland has a poor blood supply. As development continues, however, the boundary between the medullary and cortical layers becomes increasingly distinct, the medullary part gradually increases in size and the number of blood vessels in it increases. Between the first and seventh day of life of young rabbits the shape of the adrenal medulla cells becomes more regular (Photo 10, Plate VIII) and their nuclei, with clearly visible chromatine, increase in size. By the fourteenth day the adrenals of young rabbits have a completely typical structure (Photo 11, Plate VIII), their cells are regular in shape and the boundary between the medullary and cortical layers is as distinct as in adrenals of rabbits 2.5 months old (Photo 12, Plate VIII).

A distinct boundary between the medullary and cortical layers can be seen in histological slices of the adrenals of guinea pigs from 4 to 8

hours old (Photo 13, Plate IX). Unlike the adrenals of young rabbits, numerous blood vessels can be seen between the different, cell groups of the medulla on the first day after birth. The cells occurring within this layer have regular shapes. The large cell nuclei, with clearly visible chromatine, are mainly localized in the centre of the cells of the medulla, and less often at the base. The histological picture of the adrenals of newborn guinea pigs above described does not differ from the picture of this gland in adult guinea pigs (Photo 14, Plate IX).

Table 5

The changes of the absolute and relative weight of adrenal glands in rabbits and guinea pigs during first 4 weeks of postembryonic life.

Age	n	Body weight g	Adrenal weight	
			Absolute mg	Relative mg/100 g
RABBITS				
4—8 h	—	—	—	—
12 h	5	51.10 ± 4.20	4.20 ± 0.80	8.28 ± 1.67
24 h	—	—	—	—
36 h	5	76.00 ± 5.64	4.40 ± 0.98	5.62 ± 0.96
3 d	—	—	—	—
7 d	5	152.80 ± 4.92	15.20 ± 0.98	9.96 ± 0.68
14 d	5	192.40 ± 12.94	15.60 ± 1.72	8.44 ± 0.82
21 d	5	298.00 ± 12.78	40.20 ± 1.50	13.66 ± 1.08
28 d	5	526.60 ± 61.10	47.00 ± 3.66	8.81 ± 3.46
GUINEA PIGS				
4—8 h	13	76.83 ± 5.64	19.65 ± 0.82	25.21 ± 1.96
12 h	6	80.16 ± 3.98	24.95 ± 2.04	32.03 ± 3.33
24 h	11	81.95 ± 1.81	23.50 ± 2.02	28.58 ± 2.16
36 h	—	—	—	—
3 d	7	84.97 ± 3.62	33.60 ± 2.14	39.80 ± 2.59
7 d	6	79.52 ± 3.16	29.96 ± 2.12	38.38 ± 4.08
14 d	6	140.08 ± 10.38	60.82 ± 3.48	44.92 ± 5.11
21 d	6	184.50 ± 9.56	60.65 ± 2.91	33.16 ± 1.80
28 d	—	—	—	—

Means ± S. E.; Age: h = hours; d — days; n = number of animals.

#### IV. DISCUSSION

Under neutral and physiologically low temperature conditions loss of heat from the organism takes place chiefly on the external surface. The animal's surface area can be calculated from the equation:

$$S = kW^{0.67}$$

in which  $S$  = surface in  $\text{cm}^2$ ,  $k$  = coefficient of proportionality established empirically for the given species,  $W$  = body weight in grammes. Accepting for purposes of simplification that the coefficient of proportionality  $k$  for the two species examined is 10, it can be calculated that with average

weight for a newborn rabbit of 71 g, and for a guinea pig 75 g, their relative surface is respectively 2.45 and 2.40 cm<sup>2</sup>/g. The average body weight of 18-day old rabbits was however 220 g, and relative surface 1.66 cm<sup>2</sup>/g, whereas 17-day old guinea pigs weighing on an average 160 g have a relative surface of 1.86 cm<sup>2</sup>/g. The rapid reduction of the ratio of surface area to body mass in young rabbits undoubtedly contributes to the improvement with age of the capacity for thermoregulation, which in 18-day old individuals of this species is already fairly efficient (Poczopko, 1969). This is not, however, the only factor involved, for if this were so newborn rabbits and guinea pigs would have to have uniform thermoregulation capacity.

The second important factor on which capacity for thermoregulation depends is the insulating value of the surface. Newborn rabbits, which are practically devoid of fur, do not obviously have the same insulation as that provided for guinea pigs by their hair covering. The fur of rabbits does not begin to be of importance as a barrier to heat loss until the 8th day after birth (Poczopko, 1969).

It follows from the above discussion that under the same ambient temperature conditions newborn rabbits must lose more heat from their bodies than newborn guinea pigs, despite the fact that they have similar ratios of surface areas to body mass. Hence the body temperature of newborn rabbits decreases rapidly even at relatively high ambient temperatures, e.g. at 20 or even 30°C (Daves & Mestyán, 1963; Hull, 1965; Poczopko, 1969), whereas in newborn guinea pigs hypothermy is not observed even after the animals have remained an hour in a temperature of 8°C (Barič, 1953; Daves & Mestyán, 1963; Brück & Wünnenberg, 1965a).

We have so far discussed the factors on which the rate of heat loss from the organism of the animals examined depends. In order to maintain a constant body temperature heat losses must be balanced by heat production. The most intensive metabolic rate is exhibited not by newborn animals, but by those slightly older, that is, in young rabbits at the age of 14 days and guinea pigs at the age of 5 days. It may therefore be considered that the metabolic activity of tissues of the animals examined directly after birth is relatively low, and only increases with time in order, after attaining a certain maximum, to decrease again.

Increase in intensity of metabolic rate during the first days of postnatal life has been described in many species of mammals, for instance intensity of metabolic rate increases by 75% in newborn humans during the first 2 days of life (Hill & Rahitnulla, 1965), in puppies by three times as much during the 3—4 days of life (Gelineo, 1954;

McIntyre & Enderstrom, 1958), in the rat by 50% during the first 2 days (Taylor, 1960), in domestic pigs it doubles during two days (Mount & Stephens, 1970; Studziński, 1972) and in calves doubles during the three days after birth (Roy *et al.*, 1957).

The significance and mechanism of the phenomenon of increase in intensity of metabolic rate have not as yet been explained, although it has been discussed by many authors (Brück *et al.*, 1958; Daves & Mott, 1959; Daves *et al.*, 1960; Levison & Swyer, 1964).

The smaller the animal, the greater the intensity of metabolic rate measured by the amount of heat produced (or oxygen intake) in a unit of time and per unit of body weight. Calculation of this same amount of heat per  $\text{kg}^{0.75}$  results in metabolic rate being uniform in large and small animals (Kleiber, 1932; 1961), at least when the metabolic rate of adult animals is compared. According to Kleiber (1961) average heat production of all homeothermic animals under standard conditions is  $70 \text{ kcal/kg}^{0.75} 24 \text{ h}$ . It may be expected that basal metabolic rate in young rabbits and guinea pigs will be similar to the Kleiber interspecies mean. The resting metabolic rate determined in this study for adult guinea pigs was about  $80 \text{ kcal/kg}^{0.75} 24 \text{ h}$ , but was raised by the calorogenic effect of food, since the animals were not kept fasted before making measurements. The basal metabolic rate of these animals is thus very close to the interspecies mean, but basal metabolic rate of adult rabbits must be far lower than this mean, since even resting metabolic rate, in which it is also included the calorogenic effect of food, is lower. The fact that basal metabolic rate in adult rabbits is relatively low has been known for a long time (Voit, 1901; Lee, 1939).

Several hypotheses have been put forward in explanation of the fact that metabolic rate varies with  $3/4$  power of the body weight (Kleiber, 1961), but none of these hypotheses is fully satisfactory. It must, however, be assumed that in adult animals with normally formed hair covering heat production rate similar to the Kleiber's interspecies mean must, in general, be in a state of balance with the losses taking place under thermally neutral conditions. In the case of adult rabbits and guinea pigs heat losses should be balanced by production, which is respectively about 66 and  $70 \text{ kcal/kg}^{0.75} 24 \text{ h}$ . It cannot therefore be considered surprising that heat production rate of  $66 \text{ kcal/kg}^{0.75} 24 \text{ h}$  balancing heat losses from the body of adult rabbits is not capable of balancing losses from the body of newborn rabbits, almost completely devoid of thermal insulation on account of the absence of fur.

The capacity of young rabbits to withstand hypothermy develops, however, far more rapidly than is the case with reduction of surface to body mass ratio and development of fur (Poczopko, 1969). This

is fully understandable in the light of the present studies, which show that heat production rate in young rabbits rises abruptly, resulting in its being twice greater in individuals two weeks old (128 kcal/kg<sup>0.75</sup> 24 h) than in newborn and adult animals. The insufficient thermal insulation in rabbits from 10 to 14 days old is therefore balanced by their high heat production rate.

Increase in the metabolic rate of young rabbits during the first 10—14 days of postnatal life must be considered as very rapid, since the relation between changes in this rate and changes in body weight is characterized by a coefficient of regression of 1.532. At a later period of growth increase in heat production rate is lower than increases in body weight, and the coefficient of regression takes on a value of 0.712, that is, is close to the value 0.75 (or  $\frac{3}{4}$ ) characteristic of the relation between basic metabolic rate and the body weight of adult homeothermic animals.

A similar rapid increase in metabolic rate in the early stages of postnatal life has been described for certain other species of animals, *e.g.* young pigs (Mount & Stephens, 1970), chickens (Freeman, 1964) and Japanese quails (Freeman, 1967).

Taking the ratio of weight of the thyroid gland to body weight as a criterion of thyroid activity, it could be concluded that this activity is identical in newborn rabbits and guinea pigs. The relative weight of the thyroid gland in both species is about 20 mg/100 mg of body weight at birth. It would then be possible to conclude that in both species thyroid activity decreases with age, this process taking place more quickly in young rabbits. Histological examination of the thyroid shows, however, that conclusions as to the states of thyroid activity drawn on the basis of changes in the relative weight of this gland may only be correct in the case of guinea pigs, but would be incorrect in the case of young rabbits. At birth the thyroid of guinea pigs is morphologically well developed (as has been described earlier by Sugiyama & Sato, 1954a, b), and the small follicles with high epithelium and structure of colloid provides evidences of the fairly high degree of activity of this gland. There are, however, islets of undifferentiated tissue in the thyroid of newborn guinea pigs which disappear during the first few days of postnatal life. Transformation of undifferentiated tissue into regular follicles undoubtedly brings about increase in the gland's activity. During the later part of life in guinea pigs changes in thyroid structure show that there is gradual reduction in the gland's activity, taking place parallel to changes in its relative weight. Changes in <sup>131</sup>I uptake by the thyroid of guinea pigs also take place in approximately parallel fashion. Changes in thyroid activity during the development of guinea pigs are not,

however, very great, which corresponds to the changes, also not very great but tending in the same direction, of the resting metabolic rate of these animals.

The considerable relative weight of the thyroid in newborn rabbits is not accompanied by high activity of this gland, since only a few primordial follicles occur at this time in the thyroid. It would therefore seem unlikely that such a morphologically undeveloped gland could synthesize and liberate thyroxine and tri-iodotyronine into the blood in amounts sufficient to play a part in control of metabolism. It must therefore be assumed that the intensive of  $^{131}\text{J}$  uptake by the thyroid of newborn rabbits also is not indicative of the currently high activity of the gland, but serves only to accumulate iodine for later synthesis of the hormones of the thyroid gland. The results of studies by Ślebodziński & Srebro (1968) also point to the correctness of this assumption, since these authors found that the level of protein bound iodine (PBI) in the blood of newborn rabbits is low, but rises rapidly to attain a maximum in two-week old rabbits. It may thus be concluded that the thyroid gland of newborn rabbits is morphologically and functionally undeveloped and cannot therefore play a significant part in regulation of thermogenesis. The development of the thyroid in young rabbits however takes place quickly and the thyroid of two-week old rabbits must be considered as very active. The gradual increase in resting metabolic rate in rabbits discussed above, leading to maximum values in individuals two weeks old, can therefore (at least partly) explain the gradual increase in the role of the thyroid gland in thermogenesis.

In summing up the above discussion it may be concluded that the species examined differ considerably in respect of the degree of morphological and functional maturity of the thyroid gland in the earliest stages of postnatal development, which provides a partial explanation of the differences in their capacities for maintaining thermal homeostasis in a cool environment.

Other species of animals possessing a well formed thyroid at birth (or on hatching) like the guinea pig, are characterized by a relatively considerable capacity for thermoregulation from the earliest stages of postembryonic life, *e.g.* young pigs (Kaciuba-Uściłko, 1971; 1972), lambs (Gerneke, 1963), calves (Abbot & Prendergast, 1962), goslings (Kaciuba-Uściłko & Piekarzewska, 1973) and ducklings (Kamar & Yamani, 1972). On the other hand species with poor thermoregulation capacity in the early stages of postembryonic development are born, like young rabbits, with an undeveloped thyroid gland, *e.g.* rats (Carpenter & Randon-Tarchetti, 1957; Homma *et al.*, 1969; Nataf, 1968; Samel, 1968; Samel & Ca-

puta, 1962), mice (Tarkkonen & Tirri, 1964) and hamsters (Seibel, 1972).

The animals' capacity for self-defence against hypothermy is ensured by two mechanisms, shivering and nonshivering thermogenesis. In nonshivering thermogenesis, the chief role is played by catecholamines (Moore & Underwood, 1960; Janský, 1973), and in order that they can carry out the function of thermogenic mediators the following conditions must be met: there must be an appropriate »stock« of them in the organism, the organism must be susceptible to their action and the mechanism stimulating release of catecholamines must function with the increased demand for them (Lagerspetz & Hissa, 1968).

The chief site of adrenaline production is the adrenal medulla (Himmis-Hagen, 1967; Malinoff & Axelrod, 1971; Janský, 1973) and therefore supplies of this hormone in the organism must depend, to a great extent, on the size and degree of development of the adrenals. The structure and size of this gland may also, although in a lesser degree, be an indicator of the supplies of noradrenaline in the organism. The results of studies discussed in the earlier part of the present paper may suggest that the adrenals of guinea pigs are capable of producing more adrenaline than those of young rabbits, since their relative weight is far greater. In addition the histological picture suggests that the adrenals of guinea pigs directly after birth have the morphological structure typical of this gland, while those of newborn rabbits can be considered as morphologically, and probably also functionally, undeveloped. Maturation of these glands in the rabbit takes place gradually and ends (in the same way as maturation of the thyroid) towards the end of the second week after birth. Similar gradual morphological maturation of the adrenals has been described in mice (Moog *et al.*, 1954; Lagerspetz & Hissa, 1968). The fact that this gradual maturation of the adrenals in mice is accompanied by parallel increase in the contents of adrenaline in them, this content being very small during the first days after birth and gradually increasing, is of very great importance to the present discussion. The conclusion that the adrenals of newborn guinea pigs can produce more adrenaline than that of newborn rabbits has been confirmed in the results of studies (unfortunately not very thorough) by Shepard & West (1951).

When the above data, although not very complete, are considered it may be provisionally concluded that in respect of »stocks« of adrenaline and noradrenaline in the organism newborn rabbits are »handicapped« in comparison with newborn guinea pigs.

On account of the differences in thermal insulation referred to and in

the thermogenetic mechanism, reaction to cold in newborn rabbits and guinea pigs takes a different course.

Day-old rabbits increase heat production to the greatest possible extent, even with relatively slight decrease of ambient temperature namely from 35° to 27.5°—22.5°C. This maximum heat production, which is three times higher than that found at thermoneutrality, is maintained unchanged despite further reduction in ambient temperature to 15°C (Hull, 1965). Since with such cooling of the environment the demand for heat essential to maintain a constant body temperature systematically increases (in accordance with Newton's law of cooling) it may be concluded that the capacity of thermogenesis mechanisms in newborn rabbits is completely exhausted even at ambient temperatures of about 22 to 27°C. When ambient temperature falls below the values given, hypothermy is inevitable.

In day-old guinea pigs increase in heat production due to the effect of cooling is far slower than in rabbits, since this production does not reach a value about three times higher than that noted at thermally neutral conditions until ambient temperature drops to 8°C. This threefold increase in heat production does not, however, exhaust the capacity of the thermogenesis mechanism of newborn guinea pigs, and they are consequently able to maintain a constant body temperature even with an ambient temperature slightly below 8°C.

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#### ZMIANY TERMOGENEZY I JEJ HORMONALNYCH REGULATORÓW W ROZWOJU POSTNATALNYM KRÓLIKÓW I ŚWINEK MORSKICH

##### Streszczenie

W badaniach przeprowadzonych na 48 królikach i 87 świnkach morskich poszukiwano przyczyn różnej zdolności do utrzymania homeostazy termicznej przez noworodki tych gatunków. Jedną z przyczyn gorszej zdolności noworodków królika do utrzymania homeostazy termicznej jest brak u nich izolacji, którą świnkom morskim zapewnia uwłosienie. Noworodki królików mają też mniejszą produkcję ciepła (Tabela 1), która w pierwszym dniu po urodzeniu wynosi 127,5 kcal/kg 24 h, lub 65,6 kcal/kg<sup>0.75</sup> 24 h, podczas gdy u świnek morskich 137,6 kcal/kg 24 h, lub 73,3 kcal/kg<sup>0.75</sup> 24 h. Tempo produkcji ciepła w początkowym okresie życia postembrionalnego wzrasta bardzo szybko i u królicząt 14-dniowych sięga średnio 128,2 kcal/kg<sup>0.75</sup> 24 h tj. niemal dwukrotnie więcej niż w pierwszym dniu po urodzeniu. Zmiany tempa produkcji ciepła w ontogenezie świnek morskich przebiegają podobnie lecz są znacznie mniejsze. U obu gatunków ontogenetyczne zmiany produkcji ciepła przebiegają równolegle do zmian w morfologicznej i funkcjonalnej dojrzałości gruczołu tarczowego (Tabele 1—4 i zdjęcia 1—8). Stwierdzone różnice w ciężarze i dojrzałości morfologicznej nadnerczy (Tabela 5 i zdjęcia 9—14) pozwalają również przypuszczać, że układ adrenergiczny odgrywa poważniejszą rolę w produkcji ciepła u noworodków świnek morskich niż u noworodków królików.

## EXPLANATION OF PLATES VI—IX

## Plate VI.

- Phot. 1. Thyroid gland of a rabbit 12-hours-old. Considerable majority of the thyroid tissue is not organised into follicles. Scarce follicles contain unvacuolated colloid. (272×).
- Phot. 2. Thyroid gland of rabbit 7-day-old. The follicles definitely more numerous than in the new born specimens, but the amount of the tissue not organized into follicles is still large. (272×).
- Phot. 3. Fully developed thyroid gland of a rabbit 14-day-old. The follicles of intermediate size contains colloid with little or no vacuolization, and are lined with cuboidal epithelium. (274×).
- Phot. 4. Thyroid gland of a rabbit 2.5-month-old. Average size of the follicles is much larger than in previously presented photograph. The proportion of the follicles with vacuolated colloid is also much larger. (272×).

## Plate VII.

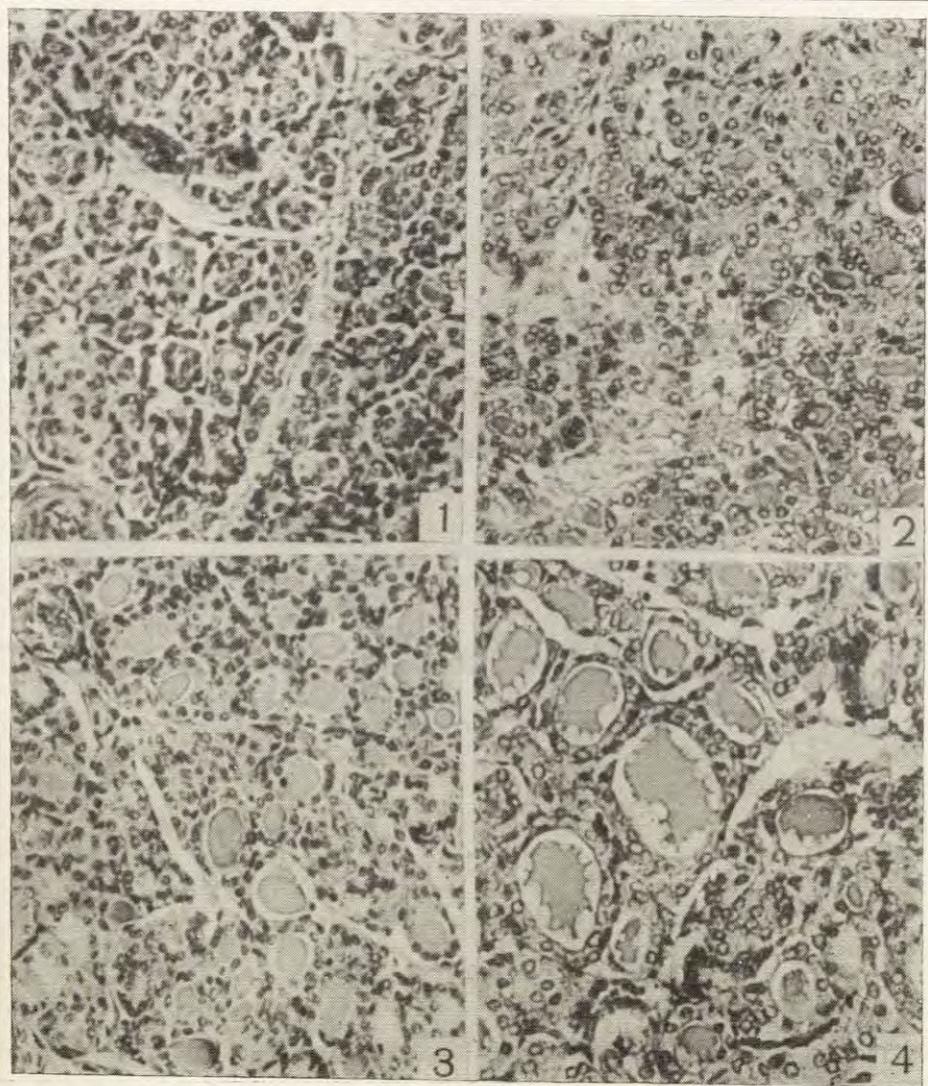
- Phot. 5. Thyroid gland of a guinea pig 8-hour-old. The follicles contain unvacuolated colloid. The little islands of the tissue not organised into follicles are quite numerous. (272×).
- Phot. 6. Thyroid gland of a guinea pig 14-day-old. A fragment of the gland not much different from that in new-born specimen. (272×).
- Phot. 7. Thyroid gland of a guinea pig 14-day-old. A fragment of the gland with the follicles undergoing destruction. (272×).
- Phot. 8. Thyroid gland of adult guinea pig. The follicles in total gland are very large. Epitelium height is differentiated even within the same follicles. (272×).

## Plate VIII.

- Phot. 9. Adrenal gland of a rabbit 12-hour-old. The borderline between the medulla and the cortex is very unclear. (174×).
- Phot. 10. Adrenal gland of a rabbit 7-day-old. On the left side of the photograph the islands of the cells characteristic for developing medullary layer are visible. (174×).
- Phot. 11. Adrenal gland of a rabbit 14-day-old. The picture remains fully developed gland and the borderline between the cortex and the medulla is easy to distinguish. (174×).
- Phot. 12. Completely developed adrenals of a rabbit 2.5-month-old. (174×).

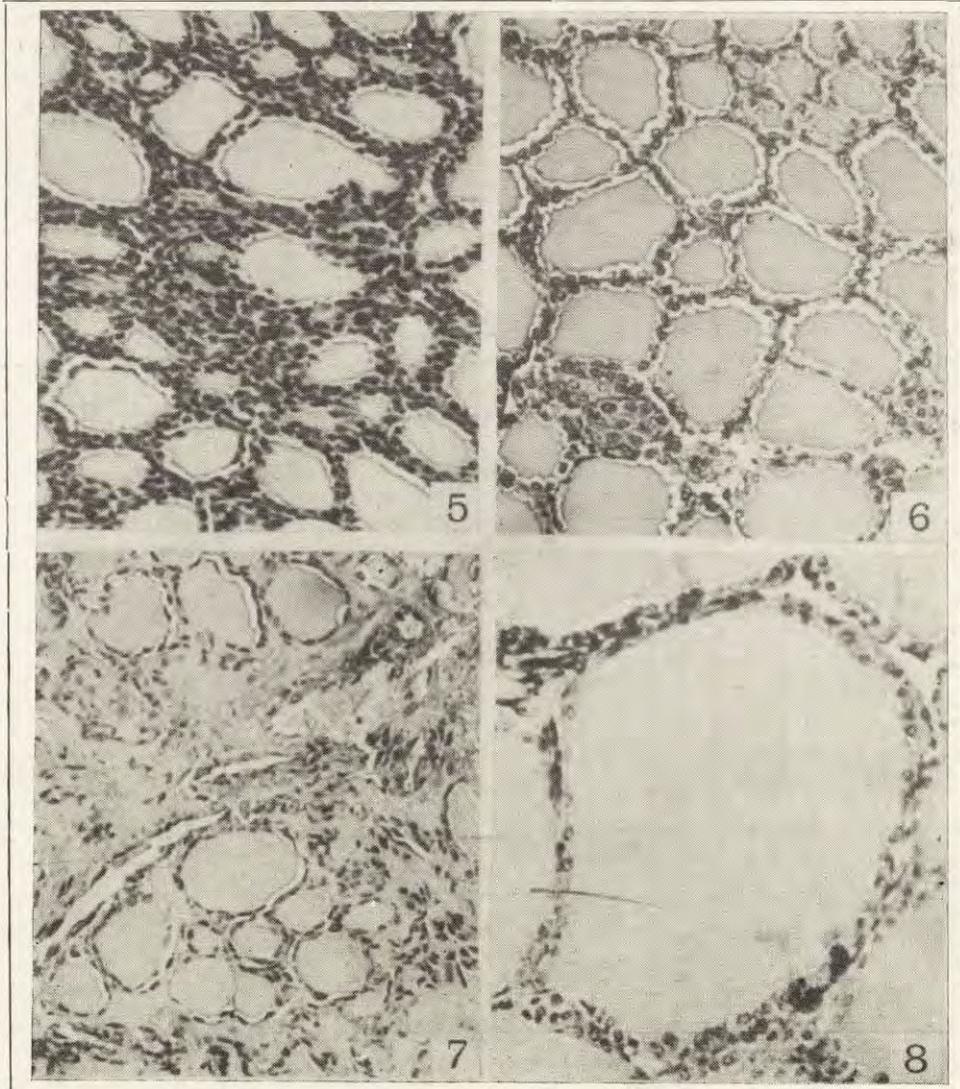
## Plate IX.

- Phot. 13. Adrenal gland of a guinea pig approximately 8-hour-old. The histological structure of the gland is fully formed. (174×).
- Phot. 14. Adrenal gland of the adult guinea pig. The difference between the histological structure of the gland and the structure of the gland in the new-born specimens (previous photograph) is difficult to notice. (174×).



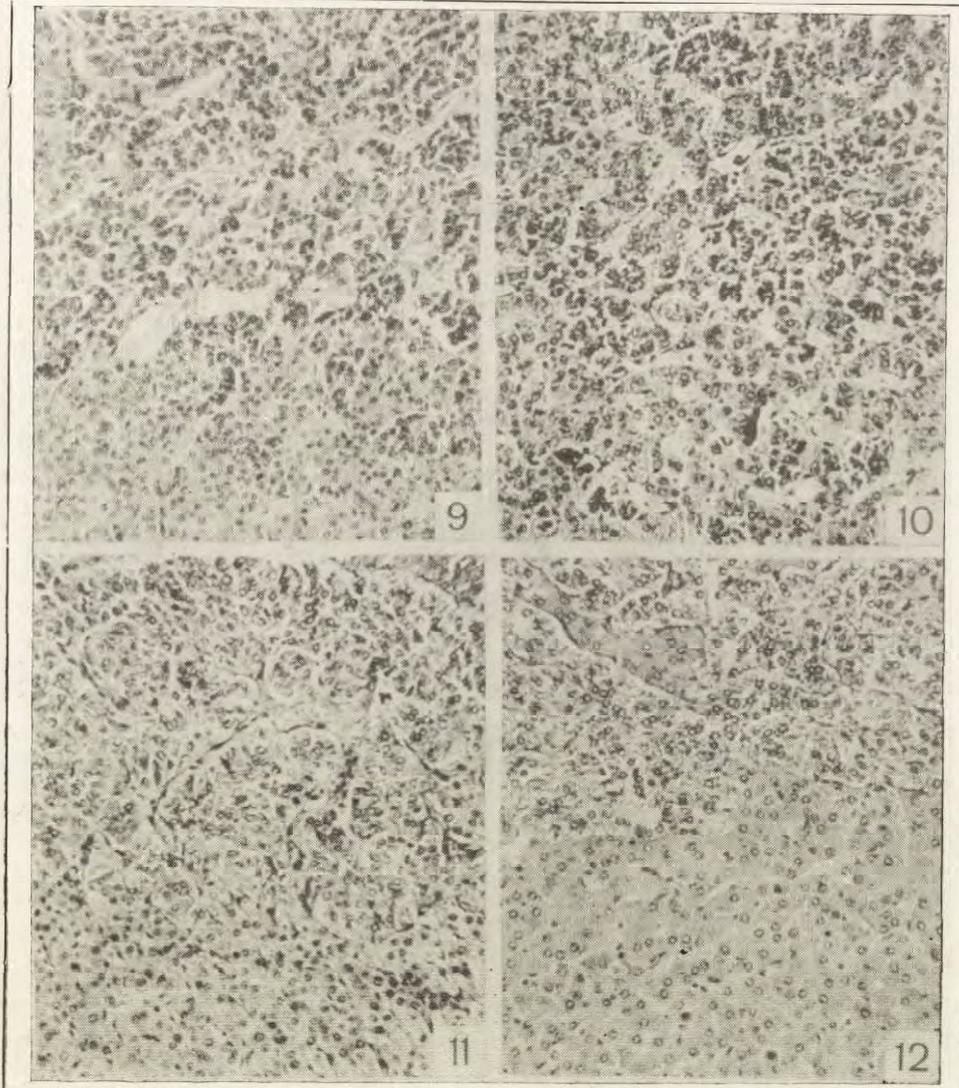
A. B. Piekarżewska

B. Gałka phot.



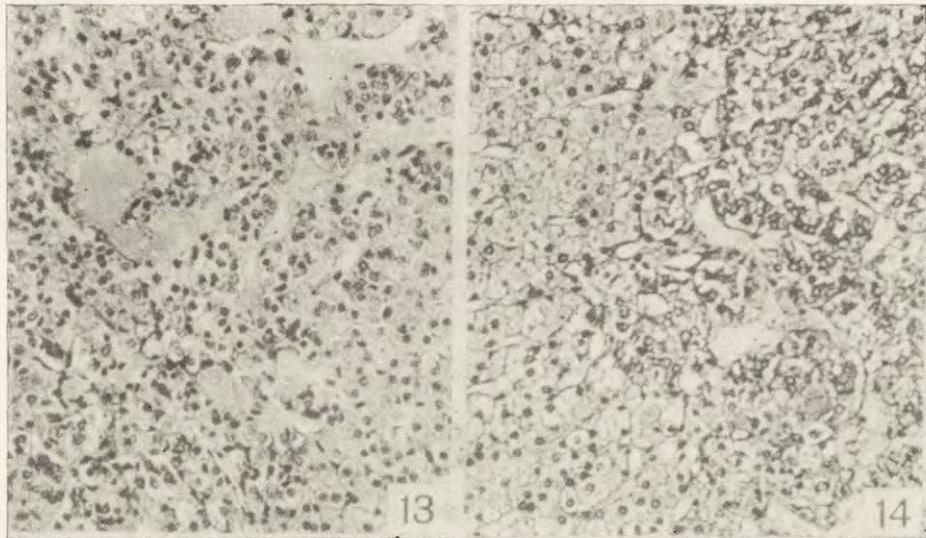
A. B. Piekarzewska

B. Gałka phot.



A. B. Piekarzewska

B. Gałka phot.



A. B. Piekarzewska

B. Gałka *phot.*