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**Regularities of Variations of the Haematological Values  
Characterizing the Respiratory Function of Blood in Mammals \***

[With 8 Tables &amp; 21 Figs.]

Analysis was made of mutual relations between blood values of 1072 individuals belonging to 6 species of *Microtidae* in various biological situations. These relations were statistically analysed, calculating the correlations, regression equations and confidence and tolerance limits of these equations. Examination was also made of the vertical cross-section of the groups of data examined, representing a variety of relations. This analysis was a starting point for examination of general variations of blood values in mammals. The author's own studies were taken as a basis for this part of the work, as they had been carried out on *Microtidae*, and also on two species of *Soricidae* and on *Sus scrofa*, and also use was made of data in literature referring to the haematological values of other mammals. Data were available referring to 126 species belonging to 10 orders. Relations were examined between the particular blood values and the body weight of mammals. The term of haemoglobinous level was introduced which made possible a more exact and dynamic analysis of all these relations. The way in which the blood values vary with the body weight of mammals in ranges of different haemoglobinous levels was traced, and also the way in which they are distributed in animals with similar body weight, but representing different haemoglobinous levels. All these considerations led to setting forth of an equation expressing the possibility of a unit of blood volume for transporting oxygen. They also made a critical examination possible of some of the views formulated on mutual relations between blood values, which were prematurely accepted as regularities consistently occurring in mammals. In the light of the studies presented it is clear that they are only a part of more general regularities and some of them would even appear to be completely without foundation.

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\* This study is dedicated to the memory of my Teacher, the late Professor Zdzisław Raabe.

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## I. INTRODUCTION

One of the basic functions of blood, termed the respiratory function, is to supply all cells with oxygen and carry carbon dioxide away from them. In homoiotherms, in which the metabolic rate even under basal conditions is nearly ten times greater than the average metabolic rate of poikilotherms (Hemmingsen, 1960), the mechanism ensuring that the organism is supplied with oxygen must be particularly efficient.

Respiratory pigments, have the function of the oxygen carriers in many invertebrates they are dissolved in plasma. In all vertebrates, on the other hand, the respiratory pigment is haemoglobin, which is present in erythrocytes. In this case not only the amount of haemoglobin determines the possibility for oxygen transport, but also the number and size of red blood cells, since they define the pigment concentration in a cell and also the total volume and surface area of these cells on which this amount of haemoglobin functions.

Evaluation of the respiratory function of blood obviously necessitates a knowledge of a large number of parameters which describe it from the morphological and physiological aspects. It is undoubtedly essential to ascertain the oxygen capacity of a unit of blood volume and minute volume of the circulation in order to assess the amount of oxygen carried



by blood in a unit of time. A far more exact and more dynamic description would be obtained by defining the possibility of one unit of blood volume for oxygen transport on the basis of its morphological parameters, than by a static measurement of oxygen capacity, since it would simultaneously explain the mechanism causing variations in the capacity of a unit of blood volume to carry oxygen and, in addition, would be more convenient on account of the widely used methods of morphological studies.

Attempts have been made long since at defining the interrelations between blood values, but as such studies were made chiefly for diagnostic purposes, research on this question was confined to man and a small number of domestic and laboratory animals. It is on this account that formulation of more general regularities was usually based on material relating to a small number of species. It is probable that a number of such generalizations have been prematurely considered as regularities occurring in mammals. An example of this is the view, until recently widely held, that blood values increase in mountains (Folk, 1966) but which is not the case with all animals (Kostelecka-Myrcha, 1967, 1969). A completely different standpoint is represented by Morrison *et al.* (1963a, 1963b, 1964) who, after examining the blood picture in certain species of rodents living in lowlands and in the Andes, found that there are no differences in the blood values between these two groups of animals. The results obtained for *Clethrionomys glareolus* (Schreber, 1780) living in lowland areas and in mountains and for *Microtus nivalis* (Martins, 1842), occurring only in mountain regions, show, however, that it is insufficient to take Hb and Hct values only into consideration, as animals having similar Hb contents and similar haematocrit can have a very different number and very different size of red blood cells and consequently their total surface area different (Kostelecka-Myrcha, 1966c).

Further examples of views too hastily considered to be general regularities are the »law of constant haemoglobin concentration«, formulated by Drastich (1928) and Bürker's view (1922) that the amount of haemoglobin per unit of surface area of red blood cells is constant. The results of studies made by Emmons (1927), who calculated that the total surface area of these cells in 1 mm<sup>3</sup> of blood is the same in man and in several species of domestic animals, refute Bürker's opinion.

The indexes introduced by Wintrobe (1963) make it possible, to estimate the amount of haemoglobin in one blood cell and the mean corpuscular haemoglobin concentration of this pigment, thus making it possible to trace more accurately the interrelations between the blood values.

The examples given above form evidence that a search has been made long since for general relations between the blood values and the regularities in their variations. The existence of these relations is obvious even during fragmentary haematological observations, but it is not easy to establish any general rules for them. There are only a few known attempts at searching for such generalizations which would provide an explanation of all facts often only apparently contradictory. An example of this is to be found in the concept introduced by Götze (1923 cited after Koržuev, 1964), accepted by Nikitin (1956) and developed by Monastyrskij & Polovinkina (1966) of the »haemoglobinous area«. These authors, however, based their findings on a small amount of material only, relating to a few species of domestic animals and on theoretical reasoning, and therefore the model they give is not fully justified.

A large amount of very varied material was obtained during the long-term haematological studies (Kostelecka-Myrcha, 1966a, b, c, 1967; Kostelecka-Myrcha *et al.*, 1970) made for the purpose of describing the blood picture in *Microtidae* under different physiological and ecological conditions. It was decided to make an accurate statistical analysis of the material and to define exactly the interrelations occurring between all the blood values examined in these rodents. It was likewise decided to check whether the regularities examined in this group of animals also apply to other mammals. If regularities governing variations in blood values in mammals were found, it would make it possible to formulate an equation expressing the capacity of a unit of blood volume to transport oxygen.

## II. MATERIAL AND METHODS

Analysis of the relations between blood values were based on the values of these indexes examined in 1072 individuals belonging to 6 species of *Microtidae*. Data were available referring to 670 bank voles *Clethrionomys glareolus* (Schreber, 1780), 250 of which were obtained from long-term breeding in the Mammals Research Institute of the Polish Academy of Sciences at Białowieża, 405 were caught in the Białowieża National Park and 42 in the Tatra Mountains at a height of about 1850 m above sea level (Kostelecka-Myrcha, 1967; Kostelecka-Myrcha *et al.*, 1970). Among the captive bank voles there were 198 young individuals, from 1 to 72 days old, 32 adult individuals (5–6 months old), 10 pregnant females and 10 lactating females. A total of 315 voles were caught over the course of a year (the blood picture was defined every month) and in addition 90 individuals were caught in autumn, divided into three groups and kept in different temperatures and length of daylight period.

Other species of *Microtidae* were represented by 255 individuals of the European pine vole *Pitymys subterraneus* (de Selys-Longchamps, 1835), 42 individuals of *Lagurus lagurus* (Pallas, 1773), 30 field voles *Microtus agrestis* (Linnaeus, 1761), 28 common voles *Microtus arvalis* (Pallas, 1779) and 20 snow voles *Micro-*



*tus nivalis* (Martins, 1842). All, except *M. nivalis*, originated from the breeding centre in the Mammals Research Institute, Polish Academy of Sciences. Representatives of *P. subterraneus* included 208 young individuals, from 1 to 90 days old, 30 animals 5—6 months old and 17 very old animals (2—3 years old) Kostelecka-Myrcha, 1966a, 1966b). The other captive *Microtidae* examined were 5—6 months old (Kostelecka-Myrcha, 1966a). *M. nivalis* was caught in the Tatra mountains at a height of about 1850 m above sea level (Kostelecka-Myrcha, 1966c).

The blood picture was always examined in the same way in all these animals. Blood was taken from the jugular vein between 9.00—11.00 a.m. Haemoglobin content (Hb%) was defined with a Zeiss haemometer with artificial lighting (about 1000 luxes). In those cases in which it was necessary for all parameters to describe the same unit of blood volume, haemoglobin content was expressed in mg/mm<sup>3</sup>. Haematocrit value (Hct %) was determined by the micromethod, centrifuging blood in heparinized capillary tubes for 10 minutes at 6500 rev/min. Mean corpuscular haemoglobin concentration (MCHC %) was calculated on the basis of haemoglobin content in 100 ml of blood and Hct value. Red blood cells (RBC mln/mm<sup>3</sup>) were counted in counting chamber with a Thom ruling, and their diameter measured with a Zeiss micrometric eye-piece on dry preparations stained by the Pappenheim method. Reticulocytes and erythrocytes were treated jointly, assuming that the number of young red blood cells is small in comparison with the number of their mature forms, and their mutual ratio is normal and constant in the various groups of animals examined.

The anisocytosis was defined in all these groups and proved to be small, and therefore it was possible on the basis of 50 measurements of the diameters of red blood cells to obtain an average figure repeatable for each of the other 50 measurements made in the same individual. Poikilocytosis was not found in the animals examined. More detailed observations to establish if the blood picture is normal were not made, as a statistically sufficiently large number of individuals was available for the results obtained to be treated as representative of the groups of animals examined.

Variation of particular blood values was slight in these groups. This is shown by the fact that confidence intervals for averages calculated from only 20—30 observations were not usually greater than the errors of the methods used for these measurements (Kostelecka-Myrcha, 1966a, 1966c, 1967).

This is undoubtedly a proof that the animals examined formed physiologically uniform material and that no deviations occurred in them from the standards characteristic of the various groups.

Owing to the uniform study methods and the considerable differences in the values considered, found after taking the different biological situations of the animals into consideration, this material could form a basis for accurate analysis of the interrelations between blood values. The following relations were considered: between the number of red blood cells in 1 mm<sup>3</sup> of blood and their size, the number of these cells and Hb content in 1 mm<sup>3</sup> of blood, size of red blood cells and Hb content in a unit of blood volume, haematocrit value and number of red blood cells in 1 mm<sup>3</sup> of blood, haematocrit value and size of red blood cells, haematocrit value and total red blood cells surface in a unit of blood volume, haematocrit value and Hb content in 1 mm<sup>3</sup> of blood and between amount of Hb and total red blood cells surface in 1 mm<sup>3</sup> of blood.

These relations were defined by calculating correlation coefficients and the regression equations. In the case of the relation between the number and size of red blood cells calculation was also made of the exponential equation and a non-linear



correlation coefficient. The two blood values under investigation, the mutual relations of which are to be defined, may of course depend on other blood values. For this reason when examining particular relations, they were considered in different intervals of the value, which might possibly modify them. In this way a number of regression equations were obtained, the values  $a$  and  $b$  of which, describing the position of straight lines in relation to the co-ordinates, were presented on axis  $y$  and their relations with this third value examined. When it was not found to exert any significant effect on the relation examined, calculation was made of the total correlation for the whole material. In addition, confidence limits and tolerance limits (Elandt, 1964) were defined for those relations which are probably of greater physiological significance. In order to ascertain what the decisive factor is determining the considerable size of the tolerance range, analysis was made of the vertical cross-sections at these points of certain of the relations. Unit data were plotted at these points in order to determine which biological factors determine the order in which they are stratified. For the same purpose, a different method was used in the analysis of the wide tolerance limits of other relations, consisting in calculating regression equations for physiologically different groups of animals examined and plotting straight lines on the diagram representing the relation common to *Microtidae*.

Variation in the blood values of mammals was considered in relation to their body weight. For this purpose use was made of data from the author's own studies on *Microtidae* and also on *Sorex araneus* Linnaeus, 1758, *Sorex minutus* Linnaeus, 1766 and *Sus scrofa* Linnaeus, 1758. Animals belonging to the last three species were obtained from the Kampinos National Park near Warsaw. 19 individuals of *S. araneus* and 5 of *S. minutus* were caught during the autumn-winter season. Results for 15 3-month old individuals of *S. scrofa* formed part of the data obtained in studies on changes in the blood picture during the postnatal development of these animals (Kostelecka-Myrcha, 1973).

The blood values of other species of mammals were obtained from literature. In all, data for 126 species belonging to 10 orders of mammals were available. When different data for the same species were given by different authors the average values were not calculated, but the data were used independently.

The average value  $F$  ( $F = f/\text{Hb}$ ,  $\text{RBC}$ ,  $4r^2$ ) describing the capacity of a unit of blood volume to transport oxygen in different groups of the *Microtidae* examined, were compared by means of the  $t$ -Student test for two independent groups. Variations in this value during postnatal development were assessed by the regression method. Comparison of value  $F$ , calculated from a simplified equation, with results obtained for the same animals but using the complete equation, was made by means of the difference test (Perkal, 1963).

### III. INTERRELATIONS BETWEEN BLOOD VALUES OF *MICROTIDAE*

#### 1. Size vs. Number of Red Blood Cells

From the physiological point of view the most interesting characteristic of the size of a red blood cell is the measure of its surface area. This problem repeatedly appears in comparative haematology and attempts have been made at formulating equations expressing this value. All of them required the acceptance of certain assumptions as to the shape of the blood cell, the introduction of constant corrections for their biconcave



shape and taking into consideration the thickness of the cells. Certain authors assumed that the thickness of cells of different mammals is approximately similar (E m m o n s, 1927), while others calculated it on the basis of a knowledge of surface area and volume of these cells, establishing these values from equations based on the diameter or radius of red blood cells (Bürker, 1922; Monastyrskij & Polovinkina, 1966). Monastyrskij & Polovinkina (1966) found that the thickness of these cells calculated on the basis of diameter corresponds reasonably accurately with the results of measurements made in a suspended drop.

Table 1

Relation between value  $4r^2$  and number of RBC for different classes of Hb content in the blood of *Microtidae*.

No. of straight line	n	Class of Hb content mg/mm <sup>3</sup>	Range of RBC mln/mm <sup>3</sup>	r	Equation
1	14	0.125 — 0.129	3.88 — 10.70	—0.831	$y = 96.26x^{-0.564}$
2	20	0.130 — 0.134	3.18 — 11.28	—0.937	$y = 128.64x^{-0.727}$
3	26	0.135 — 0.139	4.08 — 12.08	—0.836	$y = 123.83x^{-0.657}$
4	32	0.140 — 0.144	4.70 — 13.78	—0.787	$y = 93.16x^{-0.536}$
5	58	0.145 — 0.149	4.65 — 13.52	—0.772	$y = 132.66x^{-0.685}$
6	74	0.150 — 0.154	3.97 — 13.29	—0.821	$y = 120.20x^{-0.623}$
7	91	0.155 — 0.159	4.58 — 13.30	—0.806	$y = 139.85x^{-0.701}$
8	111	0.160 — 0.164	3.73 — 15.32	—0.708	$y = 96.73x^{-0.528}$
9	82	0.165 — 0.169	6.32 — 16.48	—0.561	$y = 82.06x^{-0.463}$
10	99	0.170 — 0.174	5.67 — 16.78	—0.725	$y = 129.57x^{-0.640}$
11	87	0.175 — 0.179	4.80 — 15.93	—0.660	$y = 95.09x^{-0.510}$
12	59	0.180 — 0.184	5.20 — 15.72	—0.664	$y = 98.93x^{-0.524}$
13	45	0.185 — 0.189	5.00 — 16.00	—0.766	$y = 110.05x^{-0.561}$
14	43	0.190 — 0.194	5.00 — 17.45	—0.697	$y = 81.13x^{-0.438}$
15	45	0.195 — 0.199	5.32 — 18.05	—0.672	$y = 70.87x^{-0.374}$
16	27	0.200 — 0.204	5.43 — 15.90	—0.802	$y = 116.31x^{-0.559}$
17	10	0.215 — 0.219	5.22 — 15.43	—0.978	$y = 181.65x^{-0.716}$
18	17	0.220 — 0.224	8.22 — 16.45	—0.533	$y = 47.90x^{-0.229}$

On the other hand calculation of the correction for the biconcave shape of blood cells in wide-scale comparative studies would appear too laborious in view of the very slight error involved this is not taken into consideration. G ö t z e (1923; cited after K o r ž u j e v, 1964) calculated for several species of domestic animals, having considerable differences in the diameter of red blood cells, that this error is from 12% to 17% depending on the size of these cells. Thus the error in the comparative studies would be only a few percent. Under these circumstances it would appear fully sufficient to accept, for comparative purposes, the second power of the diameter of the blood cell as the measure of its surface area [ $d^2 = (2r)^2 = 4r^2$ ], since the only real and easy available size for measurements is the diameter of the blood cell.

The relation between the measure of surface area of a red blood cell and the number of these cells was examined in different classes of haemoglobin content. The purpose of this analysis was to check whether Hb content in blood exerts a modifying influence on the course of this relation. The range of variations in Hb level found in *Microtidae* is fairly large, from 12.5 g<sup>0</sup>/<sub>0</sub> to 22.5 g<sup>0</sup>/<sub>0</sub>. The relations between  $4r^2$  and RBC for different classes of Hb content are expressed by exponential equations and are characterized by straight lines on a logarithmic scale (Table 1).

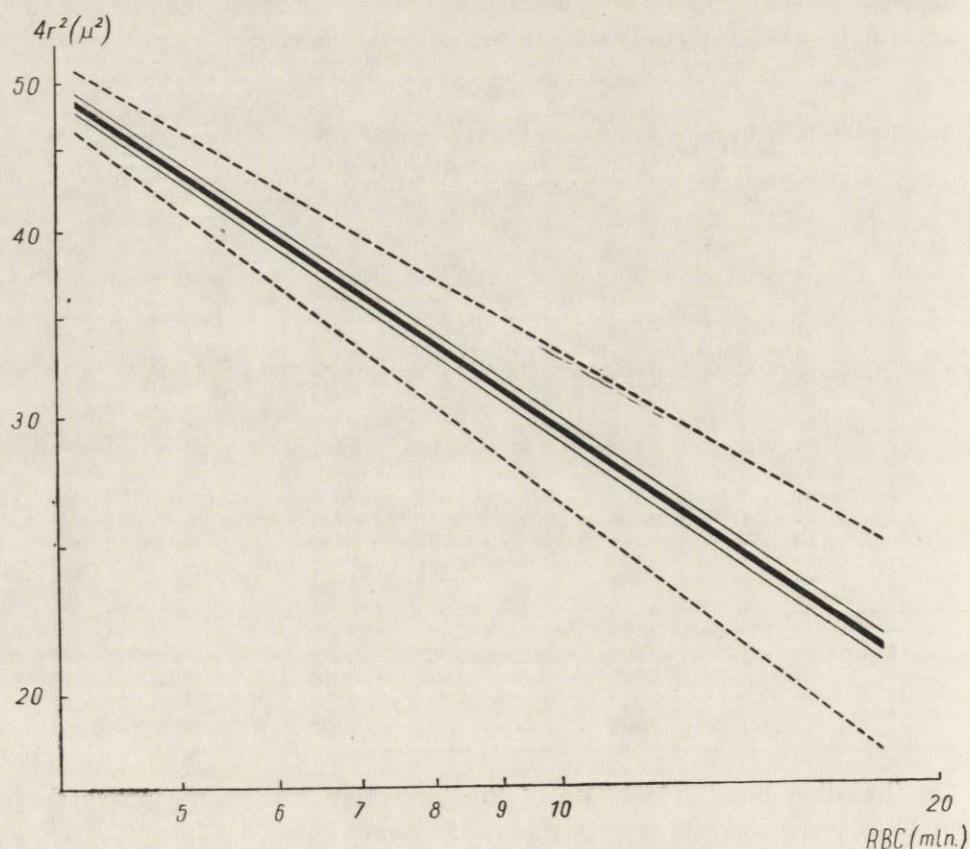


Fig. 1. Relation between size and number of RBC in *Microtidae*.

$$y = 105.9x^{-0.561} \pm 3.29; r = -0.888; n = 1014$$

$$G_x = Y_x \pm 3.28 \sqrt{0.000986 + \frac{(\lg x - 1.041)^2}{13.30}}$$

Examination was next made of the relations between  $a$  coefficients of these equations and Hb content. The equation  $y = 2.251 - 1.375x$  was obtained, and the statistically non-significant correlation coefficient  $r = 0.304$ , which shows that Hb content does not modify the course of straight lines expressing the relation between size and number of red blood cells.



This finding forms grounds for calculating the general relation between  $4r^2$  and RBC for *Microtidae*, irrespective of Hb content (Fig. 1). The small confidence area is a proof that a sufficiently large number of observations have been taken into consideration, but tolerance limits are fairly wide, and therefore the vertical cross-section of the given sample was analysed. It was found that the considerable width of tolerance limits is determined by the stratification of successive data for different groups of *Microtidae* examined (Fig. 2). Thus a given number of red blood cells corresponds,

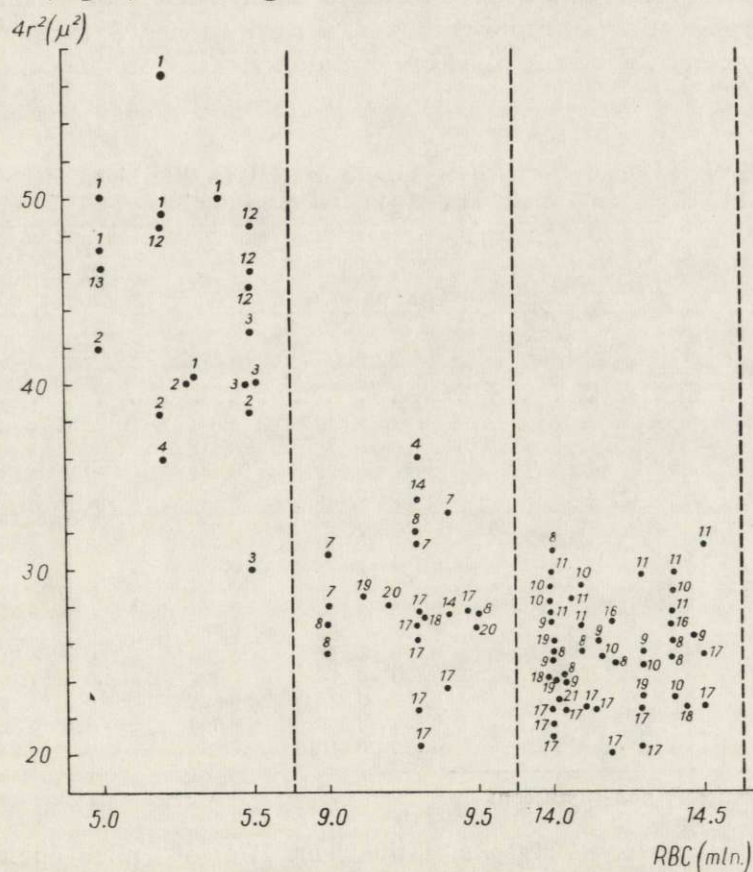


Fig. 2. Vertical cross-section made in three points of relation  $4r^2$  and number of RBC in *Microtidae*.

1 — *C. glareolus*, 0—3 days old; 2 — *C. glareolus*, 6—9 days old; 3 — *C. glareolus*, 10—12 days old; 4 — *C. glareolus*, 13—15 days old; 5 — *C. glareolus*, 16—18 days old; 6 — *C. glareolus*, 27—29 days old; 7 — *C. glareolus*, 21—25 days old; 8 — *C. glareolus* VII, VIII, IX; 9 — *C. glareolus* X, XI; 10 — *C. glareolus* XII, I, II; 11 — *C. glareolus* III, IV, V; (Roman numerals indicate different months of the year) 12 — *P. subterraneus*, 1—7 days old; 13 — *P. subterraneus*, 8—11 days old; 14 — *P. subterraneus*, 12—17 days old; 15 — *P. subterraneus*, 18—21 days old; 16 — *C. glareolus* (captive); 17 — *P. subterraneus* (captive); 18 — *L. lagurus* (captive); 19 — *M. arvalis* (captive); 20 — *M. nivalis*; 21 — *M. agrestis* (captive).

e.g., to: their greater sizes in *C. glareolus* caught in spring, their smaller sizes in voles caught in winter and even smaller in *P. subterraneus* kept in captivity. This analysis also showed that particular groups of the animals examined fill successive sections of the whole straight line representing the relation between the number and the size of red blood cells in *Microtidae*. Thus large blood cells and their simultaneous small number are found in young developing individuals, smaller blood cells and their simultaneous larger number are found in slightly older individuals of the same species and adult representatives of other species. A further section of this general relation is filled by yet other species, or the same species

Table 2

Relation between number of *RBC* and Hb content in the blood for different values  $4r^2$  in *Microtidae*.

No. of straight line	n	Value $4r^2$ , $\mu^2$	Class of Hb content, mg/mm <sup>3</sup>	r	Equation
1	12	21.16	0.138—0.194	0.572*	$y = 2.89 + 58.78x$
2	12	21.81	0.146—0.182	0.626	$y = 1.09 + 68.19x$
3	30	22.37	0.108—0.206	0.499	$y = 3.71 + 53.92x$
4	43	23.04	0.128—0.235	0.524	$y = 4.89 + 45.62x$
5	50	23.72	0.125—0.230	0.515	$y = 4.40 + 48.34x$
6	63	24.30	0.146—0.228	0.542	$y = 5.64 + 40.07x$
7	82	25.00	0.110—0.222	0.714	$y = 2.60 + 55.79x$
8	102	25.70	0.117—0.232	0.673	$y = 1.94 + 57.92x$
9	90	26.32	0.130—0.246	0.531	$y = 4.96 + 40.98x$
10	85	27.04	0.133—0.227	0.573	$y = 3.02 + 51.29x$
11	26	27.77	0.134—0.250	0.624	$y = 3.28 + 46.28x$
12	66	28.51	0.128—0.255	0.711	$y = 0.55 + 62.14x$
13	52	29.16	0.140—0.244	0.597	$y = 3.52 + 45.01x$
14	43	29.92	0.128—0.250	0.563	$y = 4.51 + 38.41x$
15	41	30.69	0.130—0.216	0.674	$y = 1.35 + 56.49x$
16	27	31.36	0.108—0.234	0.864	$y = 1.25 + 68.92x$
17	14	32.15	0.130—0.200	0.698	$y = 0.52 + 53.52x$
18	18	32.95	0.132—0.210	0.650	$y = 0.93 + 50.53x$

\* Statistically non-significant

examined at different seasons of the year. It is of course obvious that such falling out and the filling of their places by other groups of *Microtidae* takes place gradually, but completely distinctly. It is not therefore strange that examination of the relations between blood values (also between any other indexes) with relatively small range of variation, for a small amount of material, may lead to incorrect conclusions, as only a small fragment of the whole is then obtained, which will most often be represented as a straight line. In the case of the relation discussed here there is a danger that it may even be found to be non-significant, when the red blood cells in the material available are large in number but small



in size, since in the arithmetic rectangular co-ordinates this relation is hyperbolic. The equation expressing the relation between  $4r^2$  and RBC in the *Microtidae* examined is probably also correct for other rodents with similar body weight, since the available data given by various authors for some species of these animals come within tolerance limits of this equation (Moore, 1966; Sealander, 1962, 1965). It may also be

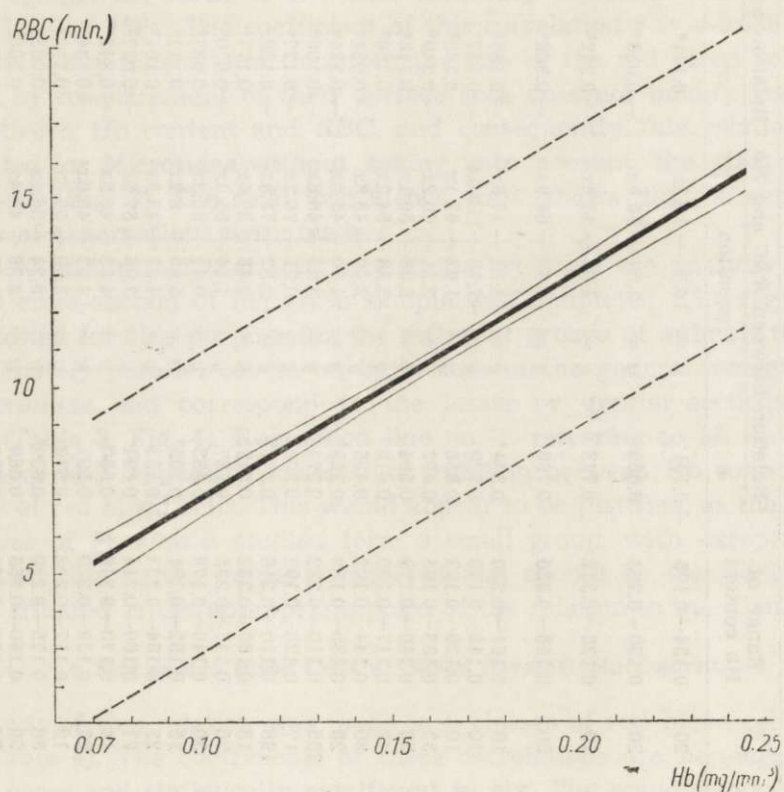


Fig. 3. Relation between number of RBC and Hb content in the blood of *Microtidae*.  
 $y = 1.10 + 60x \pm 4.04$ ;  $r = 0.561$ ;  $n = 1000$ ;

$$G_x = Y_x \pm 4.042 \sqrt{0.001 + \frac{(x - 0.1705)^2}{0.5477}}$$

assumed that for other groups of mammals the type of this relation will be the same, although its coefficients may be different. It might prove interesting to ascertain, using a large amount of material, what causes determine the differentiation of the coefficients of this relation and whether this differentiation takes place continuously, by stratification, or in jumps.

Table 3  
Relation between RBC (mln/mm<sup>3</sup>) and value  $4r^2$  ( $\mu^2$ ) and Hb content (mg/mm<sup>3</sup>) in different groups of *Microtidae* examined.

Groups	n	Range of Hb content	Relation between RBC and Hb		Relation between $4r^2$ and Hb	
			r	equation	r	equation
1. <i>M. nivalis</i> , adult	20	0.134-0.175	-0.131*	$y = 10.8 - 12.3x$	0.171*	$y = 24.4 + 21.6x$
2. <i>C. glareolus</i> from Białowieża acclimated in Tatra Mts.	20	0.130-0.203	0.669	$y = 2.69 + 55.5x$	-0.038*	$y = 26.5 - 2.99x$
3. <i>C. glareolus</i> from Tatra Mts. acclimated at Białowieża	19	0.128-0.222	0.723	$y = 4.09 + 46.3x$	-0.242*	$y = 31.4 - 28.5x$
4. <i>C. glareolus</i> , Tatra Mts., June	20	0.158-0.230	0.796	$y = -0.63 + 64.8x$	-0.368*	$y = 35.3 - 26.5x$
5. <i>C. glareolus</i> , Tatra Mts., Sept., 65	15	0.161-0.220	0.334*	$y = 3.69 + 47.8x$	-0.165*	$y = 31.4 - 23.2x$
6. <i>C. glareolus</i> , pregnant females	10	0.145-0.179	0.729	$y = -7.78 - 115.0x$	-0.127*	$y = 32.1 - 30.5x$
7. <i>C. glareolus</i> , lactating females	10	0.129-0.193	0.656	$y = 1.62 + 52.1x$	-0.280*	$y = 33.3 - 30.4x$
8. <i>C. glareolus</i> , adult	32	0.153-0.196	0.492	$y = 2.21 + 60.2x$	-0.249*	$y = 31.7 - 33.2x$
9. <i>P. subterraneus</i> , adult	30	0.140-0.179	0.594	$y = 5.03 + 50.1x$	0.118*	$y = 21.9 + 11.6x$
10. <i>L. lagurus</i> , adult	42	0.117-0.180	0.615	$y = 3.58 + 54.2x$	0.156*	$y = 20.9 + 33.3x$
11. <i>M. agrestis</i> , adult	30	0.144-0.192	0.435	$y = 3.49 + 46.8x$	-0.054*	$y = 27.3 - 11.5x$
12. <i>M. arvalis</i> , adult	28	0.135-0.188	0.323*	$y = 4.50 + 45.2x$	-0.294*	$y = 34.7 - 53.0x$
13. <i>P. subterraneus</i> , growing	208	0.110-0.222	0.274	$y = 3.06 + 46.6x$	-0.108*	$y = 38.2 - 55.7x$
14. <i>P. subterraneus</i> , 2-3 years old	17	0.128-0.192	0.808	$y = 0.91 + 76.7x$	-0.177*	$y = 25.7 - 21.0x$
15. <i>C. glareolus</i> , growing	198	0.110-0.216	0.546	$y = -2.82 + 78.8x$	-0.198	$y = 42.2 - 74.9x$
16a. <i>C. glareolus</i> , June '64	19	0.160-0.232	0.517	$y = 2.48 + 39.4x$	0.177*	$y = 22.9 + 27.0x$
16b. <i>C. glareolus</i> , July '64	26	0.147-0.235	0.737	$y = 1.14 + 55.3x$	-0.010*	$y = 28.1 - 1.35x$
16c. <i>C. glareolus</i> , Aug '64	30	0.140-0.178	0.463	$y = 0.44 + 66.3x$	0.037*	$y = 25.2 + 8.99x$
16d. <i>C. glareolus</i> , Sept '64	25	0.152-0.191	0.295*	$y = 5.56 + 8.2x$	0.111*	$y = 23.9 + 27.1x$
16e. <i>C. glareolus</i> , Oct '64	25	0.154-0.223	0.533	$y = 4.82 + 43.3x$	-0.101*	$y = 27.3 - 7.49x$
16f. <i>C. glareolus</i> , Nov '64	21	0.160-0.214	0.694	$y = 2.96 + 57.3x$	-0.027*	$y = 28.9 - 3.23x$
16g. <i>C. glareolus</i> , Dec '64	14	0.170-0.240	0.660	$y = 4.83 + 46.5x$	-0.343*	$y = 30.3 - 33.3x$
16h. <i>C. glareolus</i> , Jan '65	27	0.159-0.220	0.597	$y = 4.22 + 48.6x$	-0.154*	$y = 29.9 - 17.3x$
16i. <i>C. glareolus</i> , Febr. '65	19	0.117-0.228	0.676	$y = 3.09 + 57.3x$	0.112*	$y = 24.7 + 7.33x$
16j. <i>C. glareolus</i> , March '65	30	0.175-0.238	0.339*	$y = 6.24 + 36.4x$	-0.063*	$y = 27.8 - 6.54x$
16k. <i>C. glareolus</i> , April '65	29	0.160-0.255	0.669	$y = 2.38 + 49.4x$	0.288*	$y = 23.6 + 19.6x$
16l. <i>C. glareolus</i> , May '65	26	0.162-0.222	0.759	$y = -4.18 + 86.1x$	-0.474	$y = 40.6 - 61.3x$
16l. <i>C. glareolus</i> , June '65	24	0.139-0.198	0.791	$y = -0.70 + 65.2x$	-0.602	$y = 47.1 - 93.8x$

\* Statistically non-significant



## 2. Number of Red Blood Cells vs. Blood Haemoglobin Content

In order to determine the type of relation between the number of red blood cells and Hb content in 1 mm<sup>3</sup> of blood in *Microtidae*, 18 classes of surface area of blood cells were distinguished for which this relation was examined (Table 2). Coefficients  $b$  for the equations obtained, were next plotted against the value of  $4r^2$ . The following equation was obtained  $y = 57.128 - 0.186x$ . The coefficient of this correlation  $r = -0.068$  is not statistically significant, and therefore the size of the red blood cells expressed by measurement of their surface area does not modify the relation between Hb content and RBC, and consequently this relation was elaborated for *Microtidae* without taking into account the size of red blood cells (Fig. 3). The small confidence area shows that a sufficient number of observations were made.

In view of the fact that tolerance limits are wide the analysis of the vertical cross-section of the given sample was completed. The regression lines plotted for this purpose for the different groups of animals take an approximately parallel course on both sides of the general straight line for *Microtidae* and correspond to the lesser or greater sections of its length (Table 3, Fig. 4). Regression line no. 1, referring to *M. nivalis*, is very short and expresses absence of relation between Hb content and number of red blood cells. This would appear to be justified, as the representatives of *M. nivalis* studied form a small group, with exceptionally slight variation in the values considered and should be treated only as a point situated in the appropriate place of the relation in question.

## 3. Size of Red Blood Cells vs. Blood Haemoglobin Content

Analysis of this relation was made in 8 classes of red blood cell numbers (Table 4). The coefficients of these correlations are non-significant in two cases and statistically significant in six. The equation expressing the dependence of the value of coefficients  $b$  on RBC takes the form of  $y = 104.62 - 4.57x$ , while the correlation coefficient is  $r = -0.613$  and comes close to the limit of significance. As, however, it is statistically non-significant it formally provides grounds for calculating the general regression equation characterizing the relation between size of red blood cells and Hb content in the blood of *Microtidae*. After plotting this straight line (Fig. 5) it was found that it exhibits a tendency to decline, despite the fact that the various straight lines for different classes of RBC rise, usually in a statistically significant way. The correlation coefficient of this general relation for *Microtidae* is statistically non-significant. In other words this relation is so small that it is visible only when a number of RBC is constant.

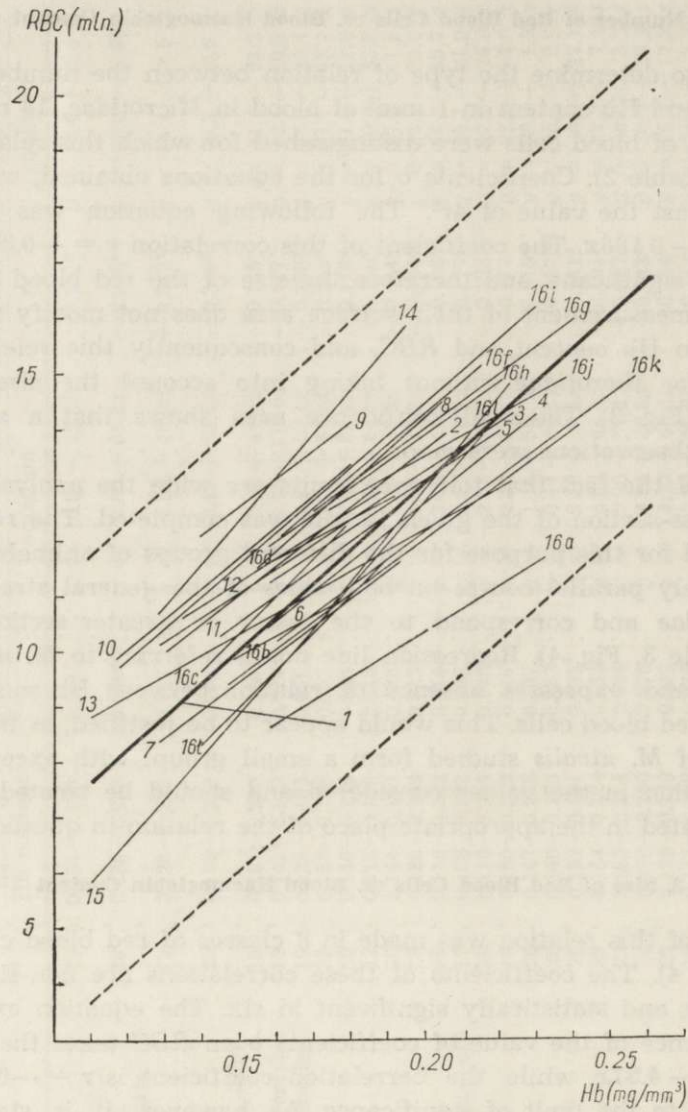


Fig. 4 Analysis of the cross-section of relation between number of RBC and Hb content in the blood of *Microtidae* (Symbols and equations in Table 3).

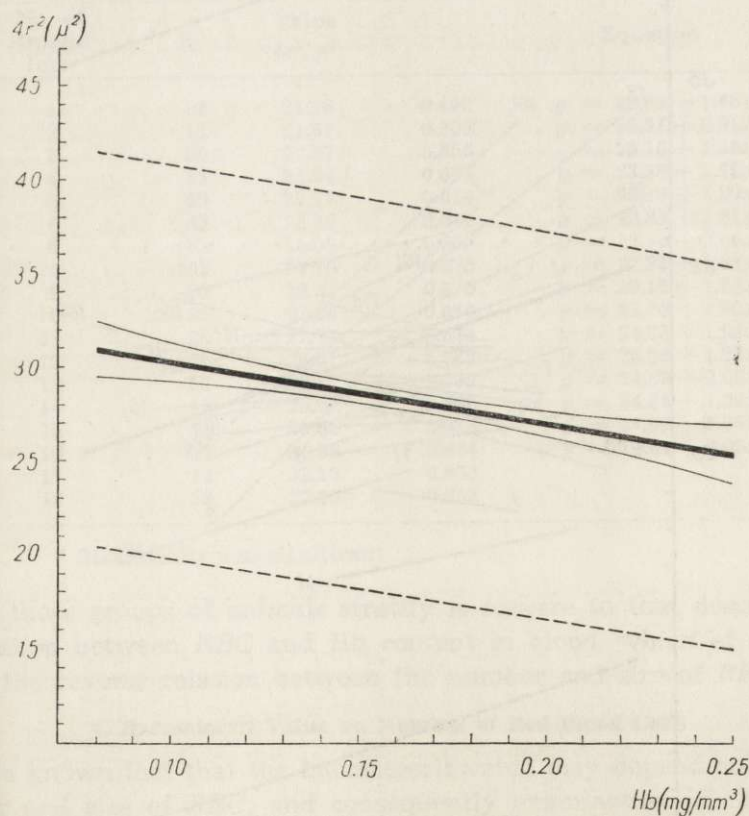
The tendency of this straight line to decline is due to a certain order in the mutual positions of straight lines obtained for 8 classes of RBC, since these straight lines are distributed increasingly close to the abscissa, the higher the number of RBC for which they were plotted, and in addition simultaneously shift in the direction of larger amounts of Hb. The absence of a relation between size of RBC and amount of Hb is thus in



Table 4  
Relation between value  $4r^2$  and Hb content in the blood for different classes of number of RBC in *Microtidae*.

No. of straight line	n	Range of RBC, mln/mm <sup>3</sup>	Class of Hb content, mg/mm <sup>3</sup>	r	Equation
1	57	8.00—8.99	0.117—0.181	0.352	$y = 17.42 + 84.58x$
2	87	9.00—9.99	0.108—0.214	0.273	$y = 19.56 + 55.87x$
3	160	10.00—10.99	0.117—0.232	0.177*	$y = 22.23 + 32.57x$
4	208	11.00—11.99	0.133—0.216	0.375	$y = 16.03 + 61.38x$
5	161	12.00—12.99	0.140—0.232	0.358	$y = 18.69 + 41.26x$
6	117	13.00—13.99	0.144—0.50	0.260	$y = 19.55 + 35.25x$
7	76	14.00—14.99	0.151—0.250	0.480	$y = 15.24 + 55.80x$
8	41	15.00—15.99	0.160—0.255	0.291*	$y = 18.88 + 31.50x$

\* Statistically non-significant



$$G_x = Y_x \pm 10.438 \sqrt{0.001 + \frac{(x - 0.1705)^2}{0.5477}}$$

Fig. 5. Relation between size of RBC and Hb content in the blood of *Microtidae*.  
 $y = 33.5 - 32.2x \pm 10.45$ ;  $r = -0.138$ ;  $n = 1000$ ;

*Microtidae* the result of the influence of two strong relations on the  $4r^2$  — Hb system: between *RBC* and blood haemoglobin content and between the number and size of *RBC*. The first of these causes straight lines plotted for higher values of *RBC* to be located in the part of the diagram corresponding to higher Hb contents, while the second determines the increasing close position of these straight lines in relation to the abscissa, since the greater the number of *RBC*, the smaller they are. In general,

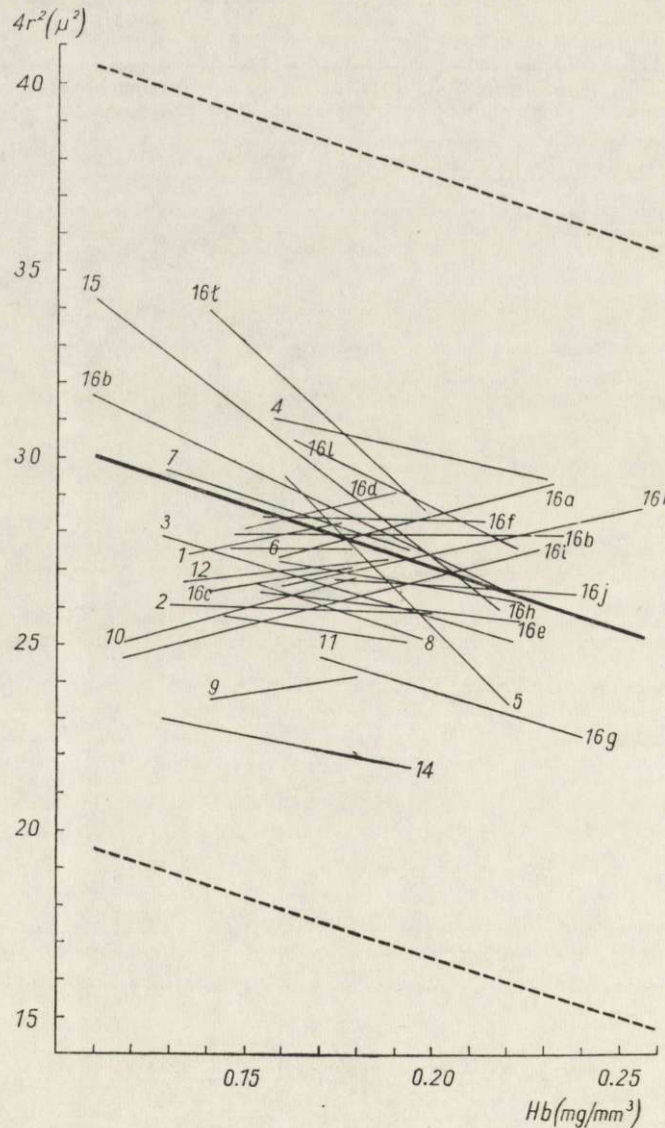


Fig. 6. Analysis of the cross-section of the relation between  $4r^2$  and Hb content in the blood of *Microtidae* (Symbols and equations in Table 3).



however, it may be said that the relation between size of *RBC* and haemoglobin level does not however affect the amount of Hb in blood. It is only in cases in which the number of *RBC* does not alter that an increase in their size may slightly increase the amount of Hb, but practically speaking this mechanism is not of any significance, as shown by the discussion given in the following parts of this section.

Analysis of the vertical cross-section of this group of data shows that its variation is determined by stratification of data for different groups of *Microtidae* (Table 3, Fig. 6). The direction in which straight lines plot-

Table 5  
Relation between Hct (%) and number of *RBC* (mln/mm<sup>3</sup>) for different values  $4r^2$  in *Microtidae*.

No. of straight line	n	Value $4r^2, \mu^2$	r	Equation
1	12	21.16	0.492*	$y = 26.62 + 1.46x$
2	12	21.81	0.308*	$y = 32.51 + 0.91x$
3	30	22.37	0.556	$y = 25.16 + 1.50x$
4	43	23.04	0.691	$y = 23.38 + 1.75x$
5	50	23.72	0.619	$y = 22.15 + 1.89x$
6	63	24.30	0.588	$y = 23.83 + 1.81x$
7	82	25.00	0.659	$y = 22.12 + 2.00x$
8	102	25.70	0.633	$y = 27.85 + 1.64x$
9	90	26.32	0.576	$y = 29.16 + 1.53x$
10	85	27.04	0.670	$y = 23.70 + 1.92x$
11	26	27.77	0.674	$y = 24.73 + 1.99x$
12	66	28.51	0.749	$y = 25.69 + 1.93x$
13	52	29.16	0.730	$y = 24.59 + 2.00x$
14	43	29.92	0.320	$y = 34.64 + 1.29x$
15	41	30.69	0.616	$y = 27.09 + 1.85x$
16	27	31.36	0.864	$y = 14.08 + 3.03x$
17	14	32.15	0.835	
18	18	32.95	0.653	

\* Statistically non-significant

ted for these groups of animals stratify is reverse to that described for the relation between *RBC* and Hb content in blood, which of course is due to the reverse relation between the number and size of *RBC*.

#### 4. Haematocrit Value vs. Number of Red Blood Cells

It is a known fact that the haematocrit value may depend only on the number and size of *RBC*, and consequently examination of the dependence of Hct on the number of these cells was carried out in different classes of  $4r^2$  values (Table 5). Among the 18 correlations obtained only two, for classes containing the smallest number of observations, are statistically non-significant. Coefficients  $b$  of these equations exhibit a significant dependence on the size of blood cells:  $y = -0.2453 + 0.0765x$ ,  $r =$

0.617. This shows that the larger are the blood cells for which examination of the relation between their number and Hct value is made, the higher the straight line expressing it, is situated in relation to abscissa. This appears understandable, since with the given number of *RBC* the haematocrit will be greater, when the blood cells are larger and the same increase in the number of cells causes a smaller increase in Hct value if these cells are smaller.

It would be incorrect to accept an equation common to all *Microtidae* expressing the relation between Hct value and *RBC*, because the course taken by straight lines within its tolerance limits is not random in character, but exhibits a close dependence on the size of *RBC*. In other mammals with similar size but varying numbers of blood cells, this rela-

Table 6  
Relation between Hct (%) and value  $4r^2$  ( $\mu^2$ ) for different classes of number of *RBC* in *Microtidae*.

No. of straight line	n	Range of <i>RBC</i> mln/mm <sup>3</sup>	r	Equation
1	57	8.00— 8.99	0.449	$y = 26.67 + 0.48 x$
2	87	9.00— 9.99	0.418	$y = 29.60 + 0.51 x$
3	160	10.00—10.99	0.315	$y = 33.60 + 0.41 x$
4	208	11.00—11.99	0.428	$y = 26.94 + 0.72 x$
5	161	12.00—12.99	0.375	$y = 29.86 + 0.70 x$
6	117	13.00—13.99	0.367	$y = 32.77 + 0.63 x$
7	76	14.00—14.99	0.471	$y = 32.14 + 0.74 x$
8	41	15.00—15.99	0.192*	$y = 44.43 + 0.34 x$

\* Statistically non-significant

tion should take a similar course with the appropriate coefficient *b*. Confirmation of this assumption is provided by the course of this relation in laboratory mice presented by *Russell et al.* (1951).

##### 5. Haematocrit Values vs. Size of Red Blood Cells

In order to examine this relation in *Microtidae* regression equations were calculated for different classes of *RBC* (Table 6). The general range of variation in the number of *RBC* in 1 mm<sup>3</sup> of blood is fairly large and in the 8 classes chosen varies from 8 to 16 mln. The coefficients of these correlations are statistically significant, except for that obtained for the least numerous class, and thus Hct value significantly depends on the size of the blood cells, if the number of these cells remains constant.

Examination was next made of the dependence of coefficients *b* of these eight equations on *RBC* and the following equation obtained:  $y =$



$0.470 + 0.008x$ . The statistically non-significant correlation coefficient  $r = 0.146$  permits to introduce a general relation between Hct value and size of the red blood cells for all *Microtidae*. It must, however, be remembered that Hct also increase as the result of increase in *RBC*. It is also known that increase in number is accompanied by decrease in the size of red blood cells. This latter relation will thus to a certain extent modify the dependence of Hct on  $4r^2$ , reducing its significance. At the same time as increase in *RBC* increases Hct value, the decreasing size of the blood cells tends to lower this value and therefore the effect of the number of *RBC* on Hct value can be most accurately expressed only if  $4r^2$  is constant and *vice versa*, the influence of the size of these cells on Hct value is expressed most exactly if number of *RBC* is constant. A more detailed analysis of these relations was not made since Hct value, which is the result of the reciprocal action of the number and size of *RBC*, would not appear to be of essential importance in characteristic of the respiratory function of a unit of blood volume.

#### 6. Haematocrit Values vs. Total Surface Area of Red Blood Cells

The value  $4r^2$  was taken as a measure of the surface area of one red blood cell, and thus correspondingly the measure of the total surface area of *RBC* will be the product of  $RBC \times 4r^2$ . It therefore follows from this that an increase in this value may be achieved either by increasing the number of these cells, or by increasing their size. A case in which both these parameters increase simultaneously cannot of course be taken into consideration, as there is a reverse relation between them (Fig. 1).

A discussion is given in sections 4 and 5 of this chapter of the effect of the number and size of *RBC* on Hct value. Increase in the number or in the size of these cells consequently causes increase in Hct value and also increase in total surface area. Therefore it is not surprising that the correlation obtained for *Microtidae* between Hct value and total surface area of *RBC* is statistically significant:  $r = 0.660$ ;  $y = 25.304 + 0.068x$ . The simplest mechanism leading to increase in the total surface area of *RBC* is a rise in their number in  $1 \text{ mm}^3$  of blood, which usually causes an increase in Hct value. Increase in the total volume of the cells in the blood can, however, take place only up to certain limits, after which there is a possibility of their total surface area increasing without variations in Hct value accompanying it. This mechanism consists in the increase in number of *RBC* closely limited by their decreasing size. The ratio of volume of *RBC* to the total volume of the blood does not undergo change, Hct value remains the same, while the total surface area of *RBC* increases. Therefore when considering regression expressing dependence of

Hct on  $RBC \times 4r^2$ , this mechanism should be located in the vertical cross-section of the range of variations in the group of data analysed. It seems that this way of increasing the total surface area of *RBC* occurs primarily in small mammals, and mention will be made of this in the further part of this study.

#### 7. Haematocrit Values vs. Blood Haemoglobin Content

A further consequence of the relations already discussed is the correlation between Hct value and Hb content in the blood of *Microtidae*:  $y = 8.68 + 220.5x$ . The coefficient of this correlation is very high ( $r = 0.853$ ),

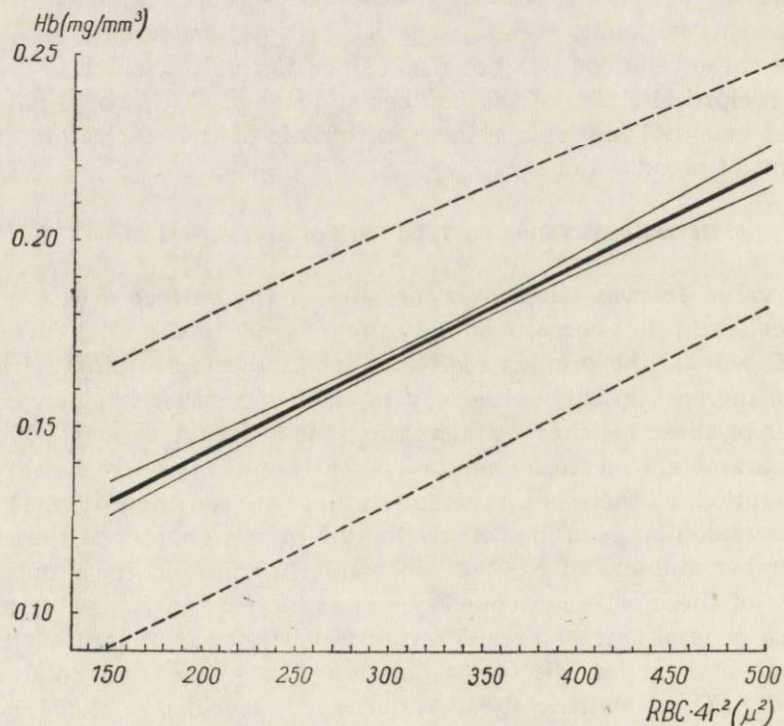


Fig. 7. Relation between Hb content and total surface area of *RBC* in  $1 \text{ mm}^3$  of the blood of *Microtidae*.

$$y = 0.0909 + 0.00026x \pm 0.037; r = 0.621; n = 1000;$$

$$G_x = Y_x \pm 0.0367 \sqrt{0.001001 + \frac{(x - 309.04)^2}{2979400.7}}$$

which explains the small degree of variation in *MCHC* in these animals, since a strictly defined increase in Hb content corresponds to each increase in Hct value. In view of the fact that the basic mechanism leading to increase in Hb content in blood is, in the case of *Microtidae*, increase



in the number of red blood cells, it is not difficult to understand that in simultaneously causes the corresponding rise in Hct value. The relation between Hct and Hb content in blood is thus in this case a reflection of the correlation between the number of RBC and the amount of Hb in a unit of blood volume. The modifying significance of changes in the size of blood cells comes within the tolerance limits of this relation and thus a slightly smaller or larger Hct value may correspond to the same Hb level in this range.

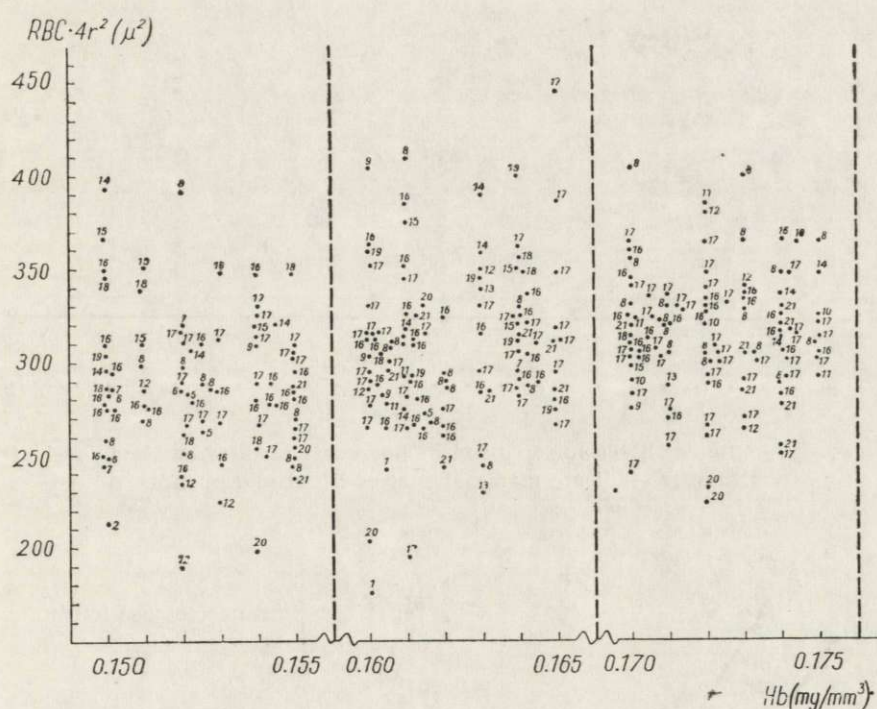


Fig. 8. Vertical cross-section made in three points of the relation between  $RBC \times 4r^2$  and Hb content in the blood of *Microtidae* (Symbols as for Fig. 2).

**8. Haemoglobin Content vs. Total Surface Area of Red Blood Cells**

On the basis of the discussion given up to the present it might be expected that the relation between Hb content and total surface area of RBC will be very close, and in fact the correlation coefficient obtained for this relation is high, and the confidence area small (Fig. 7). Tolerance limits, on the other hand, are unexpectedly great, and they show that with the same Hb level the total surface area of blood cells varies fairly considerably. The explanation of this fact can be found in the mechanism specific to small mammals, increasing the total surface area of RBC in

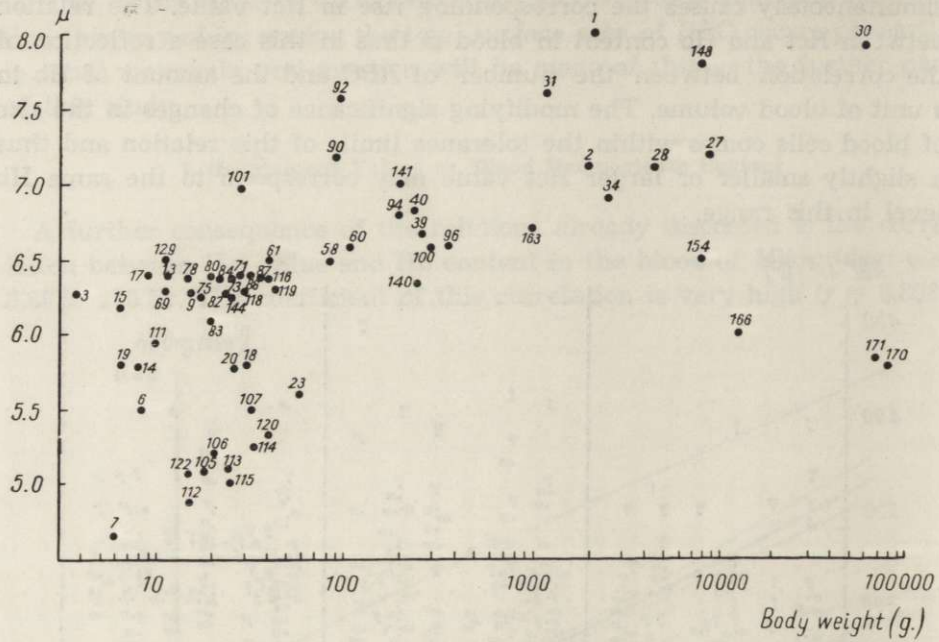


Fig. 9. Hb contents in 100 ml of blood of mammals of different body weights (Numbers indicate mammal species listed in Appendix).

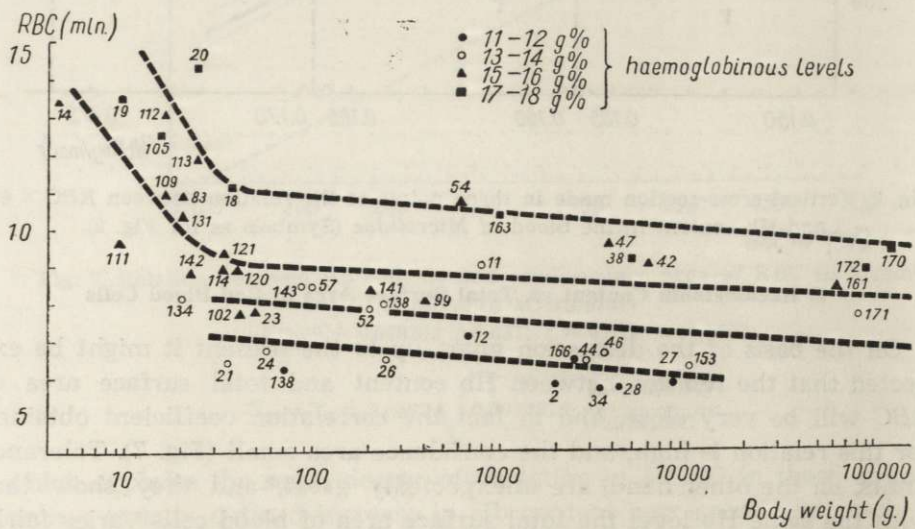


Fig. 10. Relation between number of RBC in 1 mm<sup>3</sup> of blood and body weight of mammals (Numbers indicate mammal species listed in Appendix).



a unit of blood volume. Increase in number with simultaneous decrease in the size of these cells may probably lead, in the case of animals with greater oxygen requirements, to increase in the total surface area of cells with unchanging Hb content in the unit of blood volume (Fig. 8). Only any considerable change in the size of the total surface area is probably connected with a change in Hb content. Acceptance of this interpretation involves the necessity for recognizing the fact that the same amount of Hb functioning in *Microtidae* over a greater area should be more efficient than when functioning over a smaller area.

#### IV. RELATION BETWEEN THE BLOOD VALUES AND BODY WEIGHT OF MAMMALS

##### 1. The Concept of the Haemoglobinous Level

Examination of the relation between Hb content in the unit of blood volume and the particular blood values in *Microtidae* permits of observing that the breadth of the vertical cross-section of the analysed groups of data is determined by stratification of data obtained for physiologically different groups of these animals. Stratification is probably governed by differences in the metabolic level of *Microtidae* depending on their ecological and physiological situation (Gębczyński, 1964; Górecki, 1968; Grodziński & Górecki, 1967). It was therefore postulated that when analysing the dependence of blood values on Hb level in mammals, the variation in given value at a constant Hb content should result from the different metabolic requirements of these animals and thus should be defined by their different body weight, since it is known that the metabolic rate of mammals is the function of their body weight (Kleiber, 1961; Poczopko, 1971).

As all blood values in *Microtidae* depend on Hb content, it was decided first of all to establish its connection with the body weight of mammals (Fig. 9). It was found that the Hb content in a unit of blood volume does not depend on the size of the animals, but that animals of a given body weight are characterized by fairly considerable differences in the Hb content in their blood. The conclusion then becomes obvious that the best form of examining variations in blood values in mammals will be to analyse their dependence on the animals' body weight and simultaneously, on Hb content. For this reason data from the author's own studies and those from literature were plotted against the body weight on a semilogarithmic scale. In this arrangement of co-ordinates the variation in particular blood values were traced in different haemoglobinous levels. Par-

tical haemoglobinous levels represent animals (both individuals of the same species and representatives of different species) possessing the same Hb content in 100 ml of blood. In distinguishing these levels it was accepted as a principle that the difference between them will always be 1 g<sup>0</sup>/<sub>0</sub> of Hb.

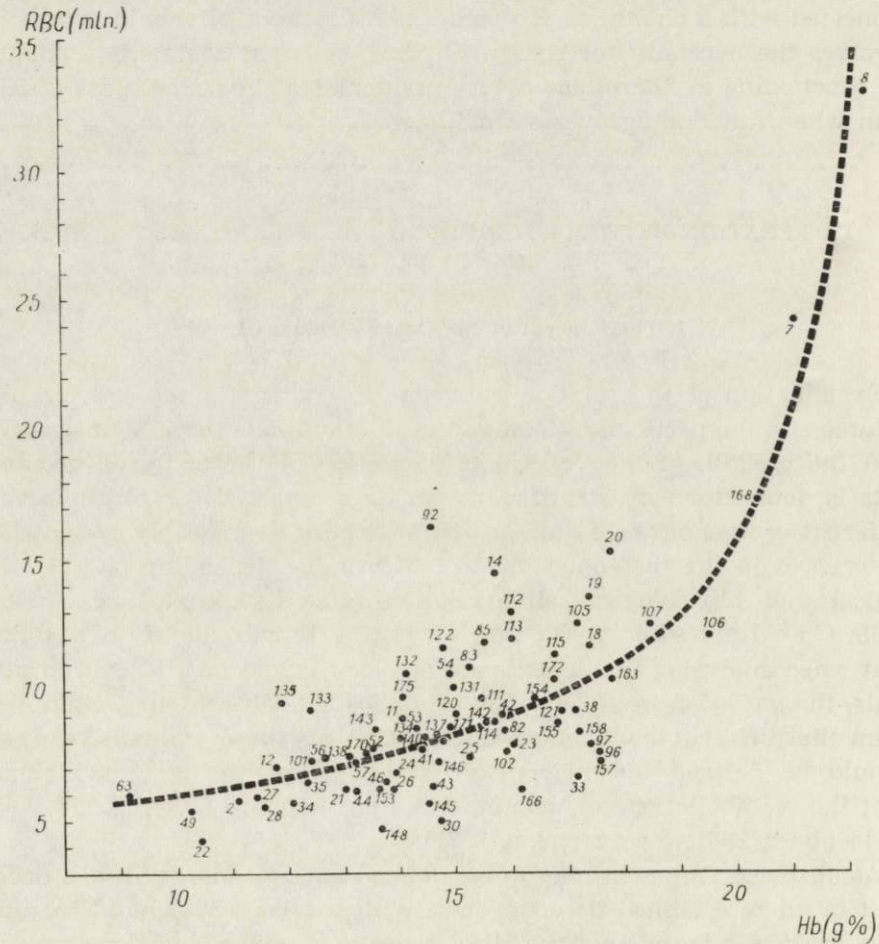


Fig. 11. Relation between number of RBC and Hb content (g%) in mammals. (Numbers indicate mammal species listed in Appendix).

## 2. Number of Red Blood Cells

Speaking in the most general way it may be said that the number of RBC decreases with increase in mammals' body weight (Fig. 10), although this statement is not entirely accurate. If we consider the occurrence of some given RBC value it will be found that it may be encountered in mammals differing in body weight. An example of this is the straight



line corresponding to 10 mln. *RBC* in 1 mm<sup>3</sup> of blood plotted parallel to the abscissa. It is not, however, difficult to see that it intersects the curves illustrating different haemoglobinous levels at points corresponding to different body weights of mammals. The same number of *RBC* may thus be found in animals of different body weight, but only when they have different haemoglobin content in a unit of blood volume. To put it more exactly, larger animals may have the same number of *RBC* as smaller animals, if the former have an correspondingly larger amount of Hb in the blood.

There is always the same difference in the Hb content between the adjacent haemoglobinous levels as shown in Fig. 10. It is noticeable that the increase in the number of *RBC* is greater when it is associated with the rise in Hb content taking place in the range of its higher levels, than the increase in the number of *RBC* when it is associated with the same rise in Hb content taking place in the range of its lower levels. This is fully confirmed by the nonlinear character of the relation between *RBC* value and Hb content in the blood of mammals (Fig. 11). The straight line obtained illustrating this correlation in *Microtidae* thus proves to be only part of this general relation. While the general statement that the number of *RBC* decreases with increase in the body weight of mammals was inaccurate, it is completely accurate in relation to each of the haemoglobinous levels separately. Attention must, however, be paid to the fact that decrease in the number of *RBC* together with increase in body weight in small animals (up to 50 g) takes place very intensively, and that in animals with greater body weight this decrease is very slow. Therefore when examining small animals it would be easy to reach an incorrect conclusion as to the decisive influence of body weight on the number of *RBC* in 1 mm<sup>3</sup> of blood, and when examining larger or in the case of large animals to state that the Hb content in a unit of blood volume defines the number of these cells.

Analysis of the relation between *RBC* and body weight of mammals made in the range of different haemoglobinous levels would thus appear to be a good method for ascertaining regularities in differences in the number of *RBC* in mammals. It also permits of interpreting fragmentary observations on the relation of *RBC* to animals' body weight given by other authors (Dunaway & Lewis, 1965).

### 3. Size of Red Blood Cells

The size of *RBC* increases with increase in the body weight of mammals (Fig. 12). These changes thus take place in reverse to the course of changes in the number of these cells. It is on the other hand more difficult

to estimate differences in the size of these cells in animals with similar body weight but representing different haemoglobinous levels. In *Microtidae* the correlation between  $4r^2$  and Hb content is not statistically significant, exhibiting a tendency to decrease, and thus smaller red blood cells correspond to a larger amount of Hb in the blood (Fig. 5). It would seem that this relation reflects the highly statistically significant relation between size and number of *RBC* (Fig. 1). As larger numbers of *RBC* are connected with greater amounts of Hb in a unit of blood volume and simultaneously higher values of *RBC* correspond to smaller cells, then a greater amount of Hb in the blood is accompanied by smaller cells. This

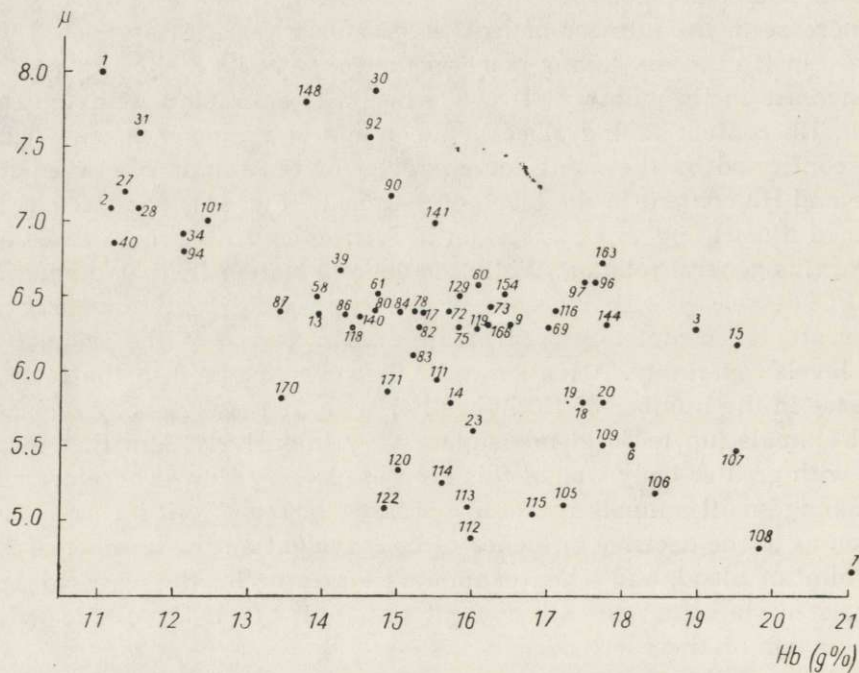


Fig. 12. Relation between diameter size of *RBC* and boody weight of mammals (Numbers indicate mammal species given in Appendix)

latter relation is, as already mentioned, only faintly marked in *Microtidae*. When a larger number of different species of mammals are taken into consideration it becomes more distinct (Fig. 13), but even so it is difficult to distinguish the various haemoglobinous levels.

It can, however, be said on the basis of the above analysis that higher haemoglobinous levels are characterized by the occurrence of smaller cells. The fact that this connection is less distinctly marked than the connection between the corresponding number of *RBC* and given haemoglobinous level can be explained as follows. Measurement of the diameter



of these cells may be not exact enough in relation to the slight changes in it which may, however, be of considerable significance to a change in their total volume. Evidence of this is provided by situations, frequently encountered, in which Hct value does not change with the intensive increase in number of RBC and simultaneously only with slight decrease in their diameter. The examined change in diameter referring to one cell, multiplied by their number present in a unit of blood volume, consequently gives considerable differences in the total volume of blood cells. Therefore, although changes in the size of these cells are not very

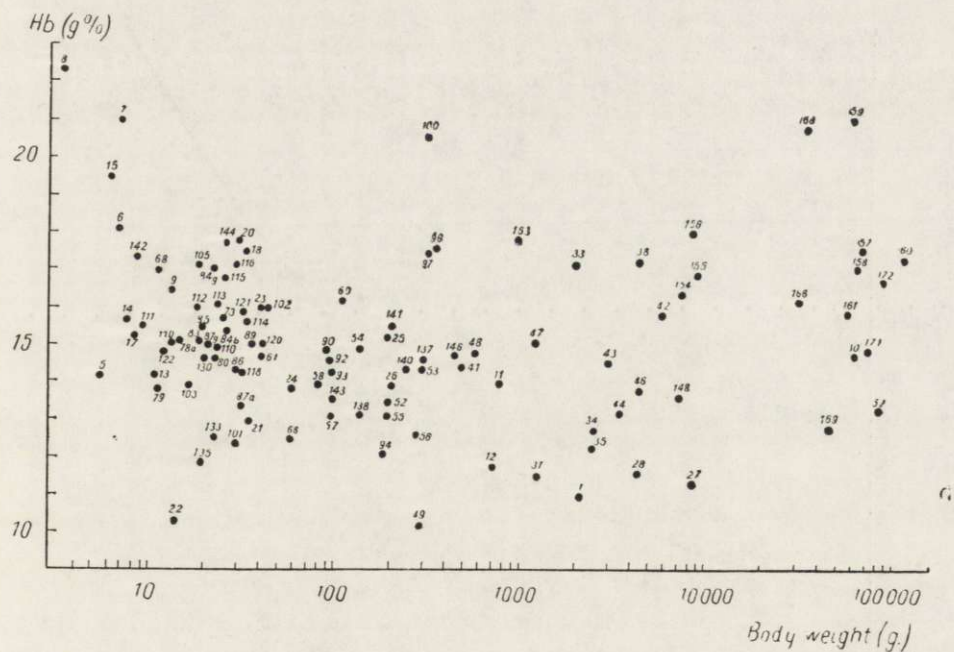


Fig. 13. Relation between diameter size of RBC and Hb content (g%) in mammals. (Numbers indicate mammals species listed in Appendix).

distinctly marked, their physiological importance is very great, consisting in creating possibilities for further increase in the number of RBC and consequently increase in their total surface area, with a minimum change in Hct value.

To sum up the above discussion it may be said that in the range of the same haemoglobinous level blood cells increase in size together with the rise in the animals' body weight, and mammals with the same body weight have smaller blood cells when the haemoglobinous level represented by them is higher.

## 4. Haematocrit Value

The relation between Hct and Hb content in blood was examined in fairly great detail by Sealander (1965), who had a considerable amount of material at his disposal, consisting of data for 34 species, all of which were, however, small mammals. The same relation in *Microtidae* has the same pattern and is illustrated by a straight line. Using Sea-

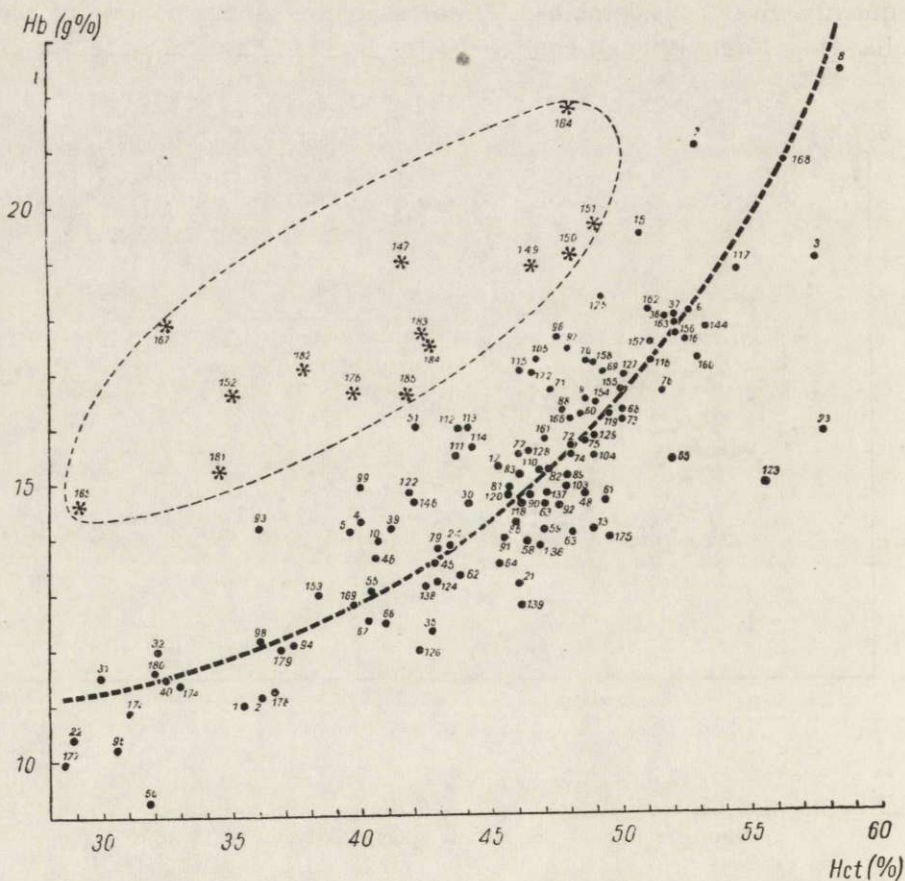


Fig. 14. Relation between Hb content in 100 ml of blood and Hct value in mammals. (Numbers indicate mammals species given in Appendix: mountain and diving mammals marked with an asterisk).

lander's results (1965), together with a large number of data taken from literature referring to animals of different body weights, the relation between Hct value and Hb content in the blood of mammals has been presented (Fig. 14).

The pattern of this relation is not unequivocal if all the data used are taken into consideration. Allowing for the fact that points lying above



their maximum density refer to large mountain animals and diving animals, it becomes clear that this relation is not of a linear character. At the same time this leads to the assumption that in animals breathing air with lower partial pressure of oxygen and periodically interrupting respiration, relations between blood values are shifted to a higher level, but probably their general type is the same as in other mammals, and therefore when considering variations in blood values in mammals the mountain and diving animals have been excluded.

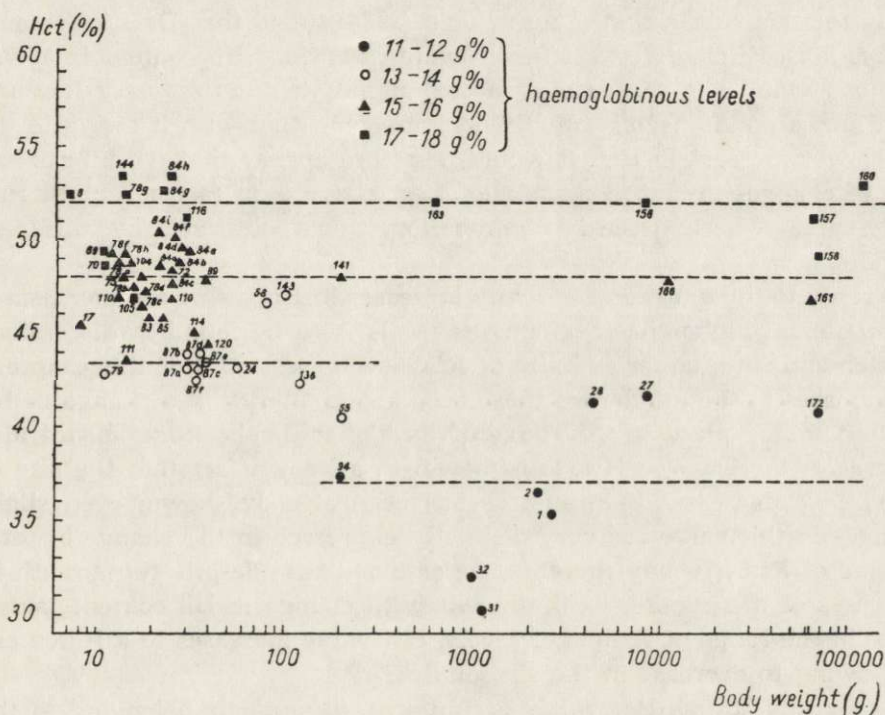


Fig. 15. Relation between Hct value and body weight of mammals (Numbers indicate mammal species given in Appendix).

The curve illustrating the relation between Hct and Hb content shows that when increase in Hb content occurs in the range of higher haemoglobinous levels it is accompanied by smaller increase in the Hct.

Therefore on the diagram representing Hct value in mammals with different body weights the distances between successive, increasingly higher haemoglobinous levels decrease (Fig. 15). It is clear from this diagram that Hct does not depend on the size of the animals and is uniform within the range of the same haemoglobinous level. Therefore the mean corpuscular haemoglobin concentration (MCHC) is also constant in animals represent-

ing the same haemoglobinous level, whereas in representatives of increasingly higher haemoglobinous levels MCHC is increasingly greater, because a uniform increase in Hb content is accompanied by an increasingly small rise in the Hct values.

In the light of this analysis »the law of constant haemoglobin concentration« formulated by Drastich (1928) would appear correct for each of the haemoglobinous levels taken separately, but it is not correct for animals characterized by different Hb content in their blood. It is probably for this reason that Enzmann (1934) found that Drastich's constant is not sufficiently exact for growing rats, since Hb content in a unit of blood volume in the animals he examined was at first very low and next increased intensively. MCHC increased together with it owing to the far slower increase in Hct. It would therefore appear that the interpretation of changes in Hct in mammals given above is in fact a general rule and explains the apparently contradictory facts observed by different authors.

A reply to the question as to why increases in Hct value are increasingly smaller at higher haemoglobinous levels is to be found in discussions of variations in number and size of RBC (section 2 and 3 of this chapter). If increases in the number of these cells are greater with a change in Hb content taking place in the range of its higher levels, there should also be greater increases in Hct. It is, however, a known fact that the size of blood cells decreases then and, as has been already shown, even slight changes in this value are very distinctly expressed in the change in total volume of RBC. It may therefore be assumed that despite the growth in increases of the number of these cells with change in Hb content taking place in the range of its higher levels, Hct value increases to a lesser extent owing to decrease in the size of RBC.

As already stated, Hct value is uniform in animals belonging to the same haemoglobinous level. Even abrupt changes in the number of RBC taking place in small mammals with a change in their body weight do not affect haematocrit value.

It may therefore be assumed that within the range of this same haemoglobinous level a larger number of RBC causes to the same degree of increase in their total volume as the smaller size of these cells causes decrease in Hct value. This same mechanism, observed in animals with the same body weight but belonging to different haemoglobinous levels, causes progressively smaller increase in the Hct value at higher haemoglobinous levels.

In the light of the facts given above a further conclusion arises relating to the significance of haematocrit in comparative studies and in diagno-



stics. As Hct is the same in animals representing the same haemoglobinous level it would be possible, not knowing the number and size of their *RBC* to assume, quite incorrectly, that the functional capacity of a unit of blood volume is similar in these animals. In addition the difference in Hct value in mammals is not in proportion to the differences in Hb content in their blood, and therefore without a knowledge of the number and size of *RBC* no conclusions can be drawn as to the capacity for oxygen carrying of a unit of blood volume. Haematocrit can thus only be of an auxiliary in haematological studies. Many authors decided not to define the number and size of *RBC*, limiting themselves only to measuring haematocrit (Morrison *et al.*, 1963a, 1963b; Sealander, 1965, 1966), but as can be seen from the data given this approach is incorrect. It would seem that for diagnostic purposes Hct can be used as a measure of the number of *RBC* only when it is known that their size has undoubtedly remained unchanged. It must, however, be remembered that even small differences in the size of these blood cells are of considerable importance to a change in their total volume.

#### 5. Total Surface Area of Red Blood Cells

The total surface area of red blood cells depends on mammals' body weight (Fig. 16) and also on Hb content in their blood (Fig. 17). Its size decreases with increase in the body weight of the animals. These changes take place very suddenly in small mammals and very slowly in larger and large animals. The relation between the value of total surface area of *RBC* and Hb content is not linear. The highly statistically significant correlation between these values (Fig. 7) obtained for *Microtidae* thus proves to be only part of this wider relation.

The mechanism increasing the total surface area of *RBC*, with unchanging Hb content, held to be specific of small mammals, also applies to larger and large animals. Inaccuracy of this type arose, and may also arise in the case of a number of other relations, because changes in the various physiological values take place very abruptly in small mammals, and are therefore far more easily perceived than very slow changes of these values in large animals.

The curve illustrating the relation between Hb content and total surface area of *RBC* shows that increase in the latter, always connected with the same degree of increase in Hb content, is greater if it takes place in the range of higher haemoglobinous levels. It follows from this that the greater the Hb content in the animals' blood, the relatively greater their total surface area of *RBC*. In other words, Hb content per unit of area of *RBC* in animals representing increasingly high haemoglobinous levels is

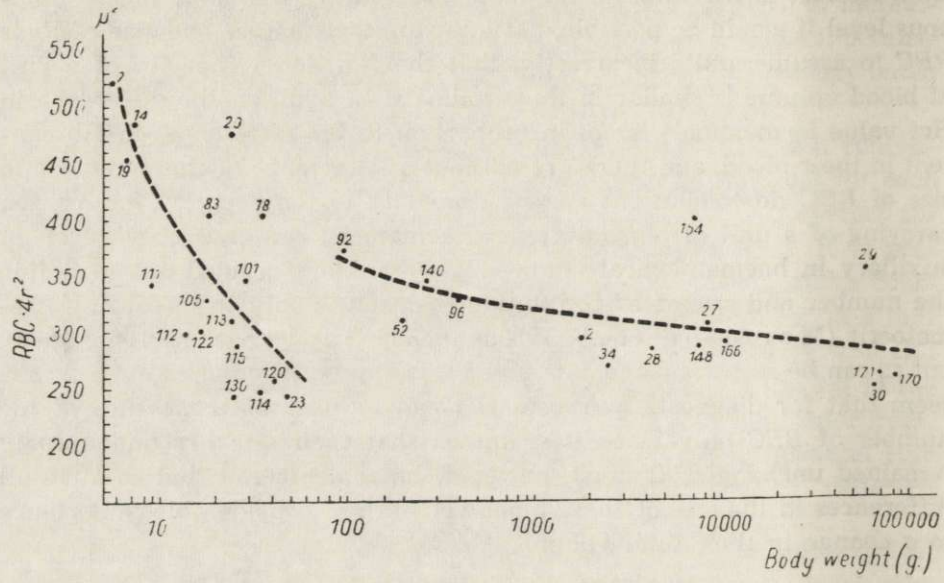


Fig. 16. Relation between total surface area of RBC in 1 mm<sup>3</sup> of blood and body weight of mammals. (Numbers indicate mammal species given in Appendix).

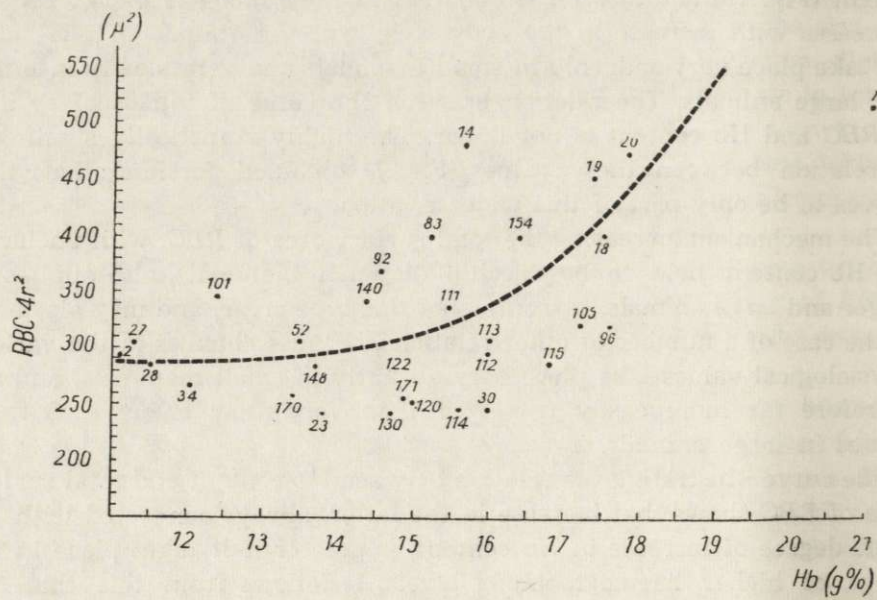


Fig. 17. Relation between total surface area of RBC in 1 mm<sup>3</sup> of blood and Hb content (g%) in mammals. (Numbers indicate mammal species given in Appendix).



increasingly smaller. Similarly in the range of the same haemoglobinous level, the smaller the animal the greater its total surface area of *RBC*, and thus the Hb content per unit of this area is smaller.

On these grounds the statement made by Bürker (1922) that Hb content per unit of area of *RBC* in mammals is constant cannot be considered as correct, and similarly it is impossible to agree with Čiževski's (1959) view that the total surface area of these cells in a unit of blood volume in mammals is uniform. Bürker's constant can be only very approximately correct for animals with body weights over 50 g and simultaneously representing the same (or very similar) haemoglobinous level. Even in this case, however, it will be correct only because the difference in the total surface area of *RBC* in these mammals is slight. It may be insufficient to examine this difference from the statistical aspect, as an estimate of the total surface area value is always burdened with some degree of error and even small differences may be of considerable functional significance in this context.

When analysing changes in the total surface area of *RBC* in mammals the fact is visible that these changes occur similarly to changes in the number of *RBC* depending on the body weight of the animals and on Hb content in their blood (Fig. 10). The number of *RBC* is of decisive importance in forming the value of their total surface area. Change in the diameter of these cells form an additional but very important mechanism, as it permits of further growth of the number of *RBC*. Therefore the same increases in Hb content are accompanied by increasingly intensive increase in total surface area of the blood cells as they occur in the range of increasingly higher haemoglobinous levels whereas the increase in Hct values is gradually smaller. Thus in consequence, within the range of each haemoglobinous level, animals of a given body weight have the greatest total erythrocytic surface area possible, with their smallest possible total volume. The essential nature of the mechanism increasing the capacity of a unit of the blood volume to carry oxygen would thus appear to be the increase in Hb content in blood and the increase in total surface area of the *RBC*.

#### 6. Significance of the Concept of Haemoglobinous Levels

When searching for the factor governing variation in blood values in mammals attention was directed primarily to the body weight of animals. The relation between these values characterizing the capacity of a unit of blood volume to carry oxygen with metabolic level, and thus indirectly also with the body weight of mammals, would appear completely sound. During the course of analysis it was found, however, that this relation

does not arrange all data in a sufficiently exact way. If there is a correlation between blood values and the body weight of mammals, then why do animals of often considerably different body weights have similar blood values, and conversely, data for animals with the same body weight often differ fairly considerably. The explanation of these facts is usually sought for in the characteristic features of the species or of whole groups of mammals, and they have been connected with the particular physiological requirements of these animals and their living conditions. Such explanations are undoubtedly correct, but these are only causes of the given demands made on the organism, not explaining the mechanism which is capable of ensuring that they are met.

The introduction of the concept of haemoglobinous levels makes it possible to explain part of the complicated mechanism ensuring that the organism receives the oxygen it requires. Analysis of the relation between blood values and body weight of mammals made in the range of different haemoglobinous levels provided the explanation for a number of these only apparently contradictory observations, since it showed why the statements of certain authors, often accepted as general regularities in mammals, are not correct, without at the same time throwing doubt on the correctness of the facts they observed.

The concept of haemoglobinous levels is of course a conventional concept and it is possible to distinguish an optimal number of them. The regularities found thus illustrate a certain continuity present in the variation in the blood values. Irrespective of whether the whole population or the same individual represents a different haemoglobinous level at different moments, a change in this level with a given body weight of the animals results in a strictly defined change in the blood values. The significance of this treatment of regularities of changes in the values examined consists primarily in its dynamism, since it permits of reaching conclusions, on the basis of static morphological measurements, as to physiological changes characterizing the capacity of a unit of blood volume to carry oxygen at every moment in the animal's life.

The method used for analysing changes in blood values permitted of making independent use of data obtained by different authors for the same species, since not only a given group of animals but even the same individual may at different moments represent a different haemoglobinous level. On this account the number of animals on which the authors based calculation of average blood values is also not important, since if the average value differed from the normal characteristic of the given group of animals, then all other blood values would also have to differ accordingly from the norm proper to them. These deviations cannot of course go beyond the limits of physiological variation in the values



considered, and therefore use was made only of those data in literature which apply to healthy animals living under given conditions described by the respective authors.

The introduction into the analysis presented here of data from literature may also give rise to some doubts, on account of the different study methods used by different authors, since all ways of counting and measuring *RBC*, all methods used to define Hb content in blood and Hct value are burdened with some degree of error. It would, however, appear that with so wide a range of material, including 126 species of mammals, with body weights ranging from a few grammes to over 100 kg, these errors do not distort the general picture of the regularities studied. This is shown by the fact that all the regularities found are consistently distributed and form a compact logical whole. An example of this is formed by the identical conclusions on intensity of changes in the particular blood values with even increases in Hb content in the blood, always arrived at twice on the basis of independently compared data. (Diagram presenting the relation between any given value and the body weight of mammals within a range of different haemoglobinous levels and a diagram presenting the relation between this value and Hb content in blood).

Without altering these general tendencies, the errors referred to may, however, significantly affect given values of the coefficients of equations expressing the relations examined, and therefore the material on which this double diagrammatic analysis of variation of blood values in mammals was based is fully sufficient only for ascertaining its general regularities. This analysis thus provides grounds for formulations of the kind such as, for instance, that the total surface area of *RBC* increases with constantly greater intensity when this increase takes place in the range of higher haemoglobinous levels, or the statement that within the range of the same haemoglobinous level the total surface area of *RBC* decreases with increase in the mammal's body weight. However, it is impossible on the basis of this material to make an exact calculation of how great the increases are in total surface area of *RBC* between different haemoglobinous levels, or to give equations exactly defining the degree of decrease in this area together with the increase in the animal's body weight. Similarly it can be said that *MCHC* in the range of the same haemoglobinous level is constant, but its true value for each of these levels cannot be calculated. Therefore in this study, general regularities were formulated for changes in blood values in mammals without setting them out in exact mathematical equation.

On the basis of some data in literature (Mott, 1966, 1967) it may be assumed that introduction of the concept of haemoglobinous levels to

analysis of variation in other physiological values characterizing the respiratory function of blood might also be of assistance in searching for general regularities. It would for instance appear likely that the percentage of body weight of mammals expressing the amount of blood circulating in the organism may prove to be constant within the same haemoglobinous level.

#### V. CHARACTERISTIC OF THE RESPIRATORY FUNCTION OF A UNIT OF BLOOD VOLUME

##### 1. An Attempt to Formulate an Equation Expressing the Possibility of a Unit of Blood Volume to Carry Oxygen

It is of course obvious that the capacity of a unit of blood volume to carry oxygen depends on the amount of haemoglobin present in this unit. The interrelations between blood values in *Microtidae* and analysis of variations in these values in mammals presented in this study show that the physiological sense of the mechanisms observed is the maximum size of the total surface area of *RBC* in a unit of blood volume with simultaneously minimal total volume possible. Therefore the value of the total surface area of *RBC* can be considered as the second factor of equal importance as Hb content, defining from the morphological point of view the capacity of a unit of blood volume to carry oxygen. The following equation has been accepted to describe this capacity:

$$F = \text{Hb} \times \text{RBC} \times 4r^2,$$

where Hb — amount of haemoglobin in mg/mm<sup>3</sup>, *RBC* — number of red blood cells in mln/mm<sup>3</sup>,  $4r^2$  — the measure of surface of one blood cell in  $\mu^2$ .

Value *F* is an abstract number, expressing the capacity of a unit blood volume to carry oxygen. It must be emphasised that this value characterizes a unit of the volume of blood circulating in the organism, as distinct from a static measurement of oxygen capacity, because the total surface area of *RBC* fulfils the relation between metabolic rate of the animals and the time of contact of these cells with oxygen in the lungs. It is known that haemoglobin takes up oxygen in the lungs extremely rapidly (K o r Ź u e v, 1964), but it is also known that if it is present in the blood cells this very considerably decreases (G i b s o n *et al.*, 1955). In animals with high metabolic level in which rapidity of linear flow of blood is greater (K l e i b e r, 1961) the time of contact of the various cells with oxygen in the lungs must be shorter than in animals with less intensive metabolism.



Thus within the same haemoglobinous level the greater total surface area of *RBC* in small animals enables correct and full use of the same amount of Hb which in large animals can be equally well used on a smaller total surface area of *RBC*. This mechanism leads to reduction in the amount of Hb per unit of surface of *RBC* in animals with greater metabolic rate, facilitating contact between pigment and oxygen. It is not only in the range of the same haemoglobinous level that the amount of

Hb per unit of surface area of *RBC*  $\frac{\text{Hb}}{\text{RBC} \times 4r^2}$  decreases with decrease

in mammals' body weight, but is also smaller in animals representing higher haemoglobinous levels.

In the light of these arguments it is not difficult to understand the fact that the value of this product in animals in normal physiological situations can decrease only by means of increase in the total surface of *RBC*, or by means of simultaneous increase in Hb content in blood and the more intensive increase in total surface area of *RBC*, but this value never decreases through decrease in the amount of haemoglobin in the blood.

It would thus appear that the equation enabling value *F* to be calculated on the basis of the amount of haemoglobin in the blood and value of the total surface area of *RBC*, includes all the regularities described here occurring in the blood values in mammals and should adequately describe, from the morphological aspect, the respiratory function of a unit of volume of the blood circulating in an organism.

Attempts may be found in literature at generalizing existing interrelations between blood values (Dunaway & Lewis, 1965; Russell *et al.*, 1951 Sealander, 1965). These are, however, fragmentary observations forming only part, as shown in the preceding sections of this study, of far wider regularities occurring in mammals. More general treatments of this problem are even far fewer. The concept of »haemoglobinous area« introduced by Götze (1923; cited after Koržuev, 1964) can be considered as an interesting attempt of this kind, but it would appear that the value 0.1 occurring in the equation given by this author is completely unnecessary, because its introduction into all calculations has not any comparative significance. Inclusion of the total volume of *RBC*, equivalent to Hct value, which is only an additional consequence of co-action between number and size of *RBC*, may even lead in certain situations to erroneous estimates of the respiratory function of a unit of blood volume. After eliminating the number 0.1 and the total volume of *RBC* from the denominator Götze's equation would express a similar content to that of the equation given in this study  $F = \text{Hb} \times \text{RBC} \times 4r^2$ . It would seem that the author, not having a suitable large

and varied amount of material, was unable to trace accurately the relations taking place between blood values. In considering probably all theoretical possibilities he found it necessary to introduce a total volume of RBC into the equation. The fundamental thought contained in Götze's equation is, however, correct and most certainly merits being remembered.

## 2. Possibilities of Application of an Equation Characterizing the Respiratory Function of a Unit of Blood Volume

Calculation was made of value  $F$  in accordance with the proposed equation for all the groups of *Microtidae* examined. It can be seen from the data in Table 7 that among the 5 laboratory species of *Microtidae* it is *C. glareolus* which has the highest  $F$  value. The capacity of a unit of blood volume for oxygen transport characteristic of this species is sta-

Table 7  
Average values  $F$  and confidence intervals for different groups of *Microtidae* examined.

Group	$F = \text{Hb} \times \text{RBC} \times 4r^2$	$F = \frac{\text{Hb}^2 - 0.0909\text{Hb}}{0.00026}$
<i>C. glareolus</i> , norma*	56.12 ± 2.88	53.7
<i>C. glareolus</i> , ♀♀ pregnant	45.89 ± 8.17	—
<i>C. glareolus</i> , ♀♀ lactating	43.87 ± 6.14	—
<i>C. glareolus</i> , Tatra Mts., June 66	70.91 ± 6.37	—
<i>C. glareolus</i> , Tatra Mts., Sept. 65	62.62 ± 6.30	—
<i>M. nivalis</i> , Tatra Mts.	38.37 ± 2.95	—
<i>L. lagurus</i> , norma*	44.85 ± 2.68	32.7
<i>M. agrestis</i> , norma*	48.38 ± 2.75	49.3
<i>M. arvalis</i> , norma*	49.65 ± 3.44	82.7
<i>P. subterraneus</i> , norma*	49.80 ± 2.87	42.7
<i>P. subterraneus</i> , 2-3 years old*	46.47 ± 4.62	42.7

\* Laboratory

tistically significantly greater than the average values  $F$  obtained for the other four species of these rodents. The lowest value  $F$  was found for *L. lagurus*, and it fails to differ statistically significant only from value  $F$  calculated for *M. agrestis*. *P. subterraneus*, *M. agrestis* and *M. arvalis* have very similar values  $F$  which statistically do not differ.

Average values  $F$  obtained for pregnant and nursing females of *C. glareolus* do not exhibit significant differences from each other, but are statistically significantly lower than the value of norm for this species.



Changes in the capacity of a unit of blood volume to carry oxygen observed in *P. subterraneus* and *C. glareolus* in their postnatal development take a different course in these two species. In the case of *P. subterraneus* value  $F$  is the same throughout the whole of the life span and even in old individuals (2—3 years old) does not differ statistically from the average value being the norm for this species (Fig. 18). With *C. glareolus*, on the other hand, postnatal anaemia is clearly marked and value  $F$  abruptly decreases during the first few days of life, after which it increases intensively and becomes stabilized about the 30th day of development (Fig. 19).

Seasonal changes in value  $F$  in *C. glareolus* under natural conditions form evidence that the unit of blood volume in these animals has the best capacity for oxygen transport in late autumn and spring (Fig. 20). In winter this value is relatively high, and after attaining a spring peak, declines sharply and reaches a minimum in August.

The average value  $F$  obtained for *M. nivalis* differs from this value in *C. glareolus* examined at the same time in both the Tatra Mountains and in lowland areas, being significantly lower (Table 7), while values  $F$  characteristic of mountain and plain populations of *C. glareolus* are statistically the same in both summer and autumn (Table 7). The conclusion can thus be confirmed that the capacity of a unit of blood volume to carry oxygen is the same in lowland and mountain populations of *C. glareolus*, which could explain why the area of occurrence of this species is so extensive (Kostelecka-Myrcha, 1969; Kostelecka-Myrcha *et al.*, 1970). It would therefore be interesting to examine  $F$  in different mammalian species occurring in mountains only and in populations of the same species living in areas situated at different heights above sea level. It is possible that the high value  $F$  in some species and low value  $F$  in other species or populations of this same species, living under conditions of lower partial oxygen pressure in the atmosphere is connected with the phylogenetic formation of these species.

In earlier publications containing the blood picture of several species of *Microtidae* at different times and under different conditions of their life, attempt was made to present this in a descriptive way and to compare the capacity of a unit of blood volume to carry oxygen (Kostelecka-Myrcha, 1966b, 1967). Values  $F$  for these different groups of animals calculated and statistically compared fully confirm this descriptive characterization. This fact deserves emphasis, as the final criterion of biological correctness of the equation accepted should be a check of its suitability for expressing different physiological and ecological situations of the organism. This equation fully meets the demands made on it.

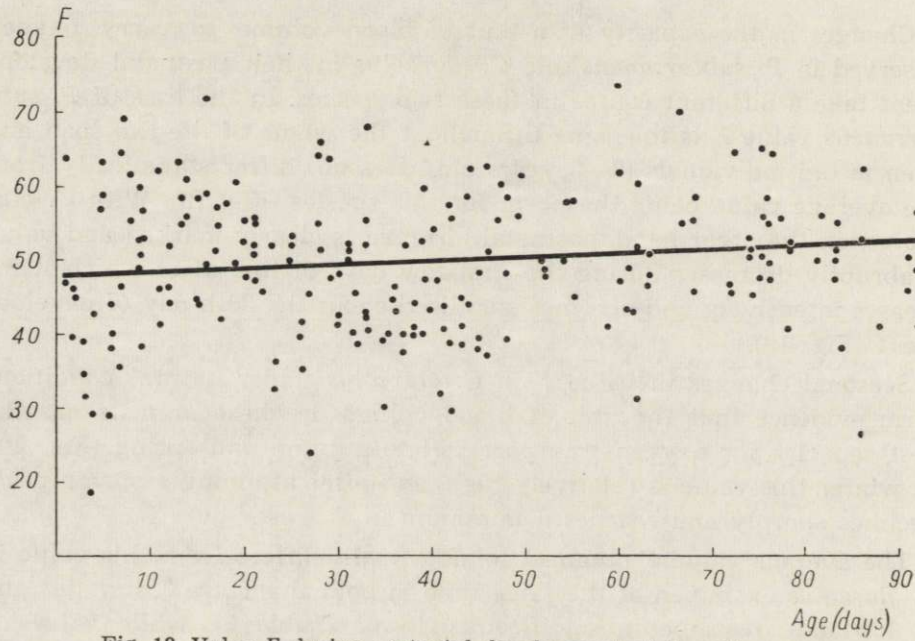


Fig. 18. Value  $F$  during postnatal development of *P. subterraneus*.  
 $y = 47.56 + 0.0464x$ ;  $r = 0.143$ ;  $n = 208$ .

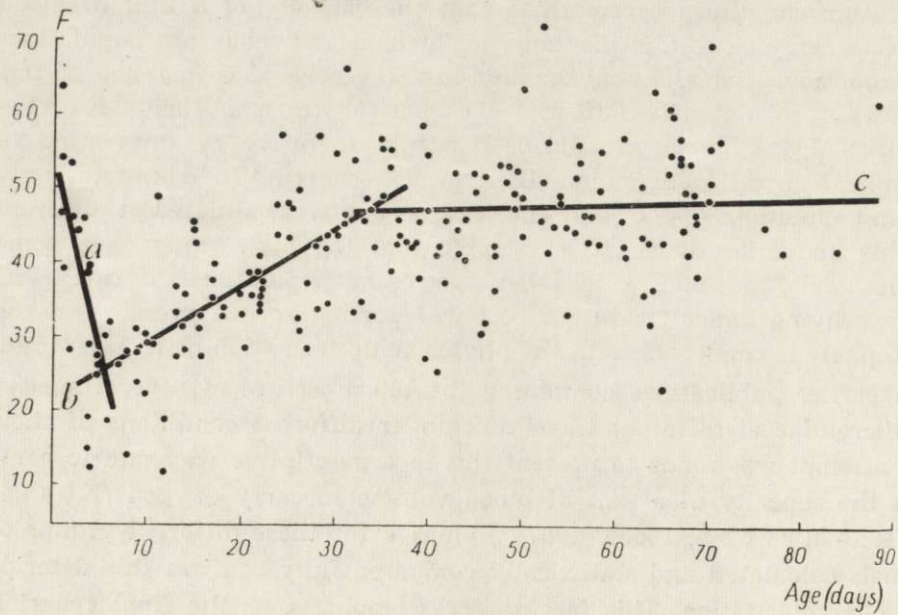


Fig. 19. Changes in value  $F$  during postnatal development of *C. glareolus*.  
 a) 1—6 days:  $y = 52.74 - 5.50x$ ;  $r = -0.718$ ;  $n = 20$   
 b) 7—30 days:  $y = 19.38 + 0.865x$ ;  $r = 0.637$ ;  $n = 65$   
 c) 31—88 days:  $y = 44.90 + 0.056x$ ;  $r = 0.088$ ;  $n = 113$ .



A knowledge of the all blood values does not explain the changes frequently observed, which may be of an adaptative character only, for maintaining value  $F$  in the range of the norm proper to the given species, subordinated to the organism's current metabolic needs. In pathological situations, however, deviation of value  $F$  from the norm may show that the compensating mechanisms are no longer able to maintain its normal value. Introduction of the equation expressing value  $F$  may thus be of significance in both comparative haematological and physio-

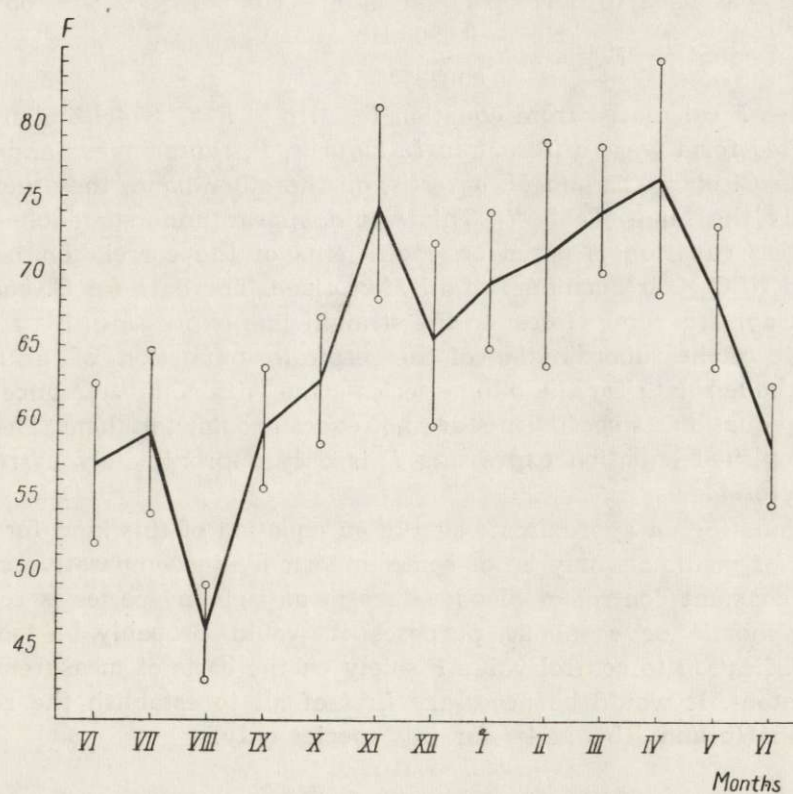


Fig. 20. Seasonal changes in value  $F$  in *C. glareolus*. The line contents average values  $F$  obtained for different months of the year. Vertical sections indicate size of confidence intervals.

logical studies, and may also prove useful in diagnostic practice. It is remarkable that this equation expressing the capacity of a unit of blood volume to carry oxygen in normal, healthy animals, also accurately describes the different forms of anaemia described by clinical researchers (Kassirskij & Aleksejev, 1970).

In evaluating the equation introduced from the practical point of view it must be admitted that it is not very convenient on account of the

necessity for ascertaining all the basic blood values for calculating value  $F$ . Taking the close correlation between Hb content and size of the total surface area of  $RBC$  in a unit of blood volume in *Microtidae* as a basis, an attempt was made at simplifying this equation. From conversion of the equation  $y = 0.0909 + 0.00026x$ , expressing the relation between Hb and  $RBC \times 4r^2$  it was established that  $RBC \times 4r^2 = \frac{Hb - 0.0909}{0.00026}$  and relation was used to develop equation  $F = Hb \times RBC \times 4r^2$ , obtaining the final equation:  $F = \frac{Hb^2 - 0.0909 Hb}{0.00026}$

Values  $F$  calculated from equation  $F = Hb \times RBC \times 4r^2$  and from its simplified form were different in *L. lagurus*, *P. subterraneus* and *M. arvalis*. In *C. glareolus* and *M. agrestis*, on the other hand, they were statistically the same (Table 7). This would appear understandable as the simplified equation is based on coefficients of the correlation between Hb and  $RBC \times 4r^2$ , common to all *Microtidae*. The data for *C. glareolus* and *M. agrestis* come closest to the straight line expressing this relation, example of the subordination of the respiratory function of a unit of and although data for the other species come within the tolerance limits of this equation its coefficients are not exact enough for them. Therefore the simplified equation expressing  $F$  is only approximately correct for all *Microtidae*.

Formulating an approximate simplified equation of this kind for larger groups of mammals may be of some importance in comparative studies, but if constant control of blood values in any given species is required for diagnostic or economic purposes it would probably be too great a simplification to control value  $F$  solely on the basis of measurement of Hb content. It would be necessary first of all to establish the relation between Hb and  $RBC \times 4r^2$  for this species only.

### 3. Relation Between $F$ and Metabolic Level in Animals

Additional confirmation of the correctness of the equation presented above can be obtained by checking whether changes in value  $F$  are in fact connected with changes in the metabolic level of animals. Seasonal variations in value  $F$  and metabolic level of *C. glareolus* may be a good example of the subordination of the value of the respiratory function of a unit of blood volume to the animals' metabolic requirements. The average daily metabolic rate (ADMR) of *C. glareolus* given by Górecki (1968) calculated per metabolic unit of body weight ( $kg^{0.75}$ ) shows that the voles' oxygen requirements are higher in winter than in summer. Compar-



Table 8  
Blood indices and values *F* for *S. araneus* and *C. glareolus* in winter.

Index	<i>S. araneus</i> Nov. 15 — Febr. 25	<i>C. glareolus</i> December
Hb mg/mm <sup>3</sup>	0.211	0.198
RBC mln/mm <sup>3</sup>	24.05	14.02
Hct %	52.8	52.5
Diameter RBC μ	4.65	4.87
MCHC ‰	39.6	37.6
<i>F</i>	109.2	65.8
n	19	14

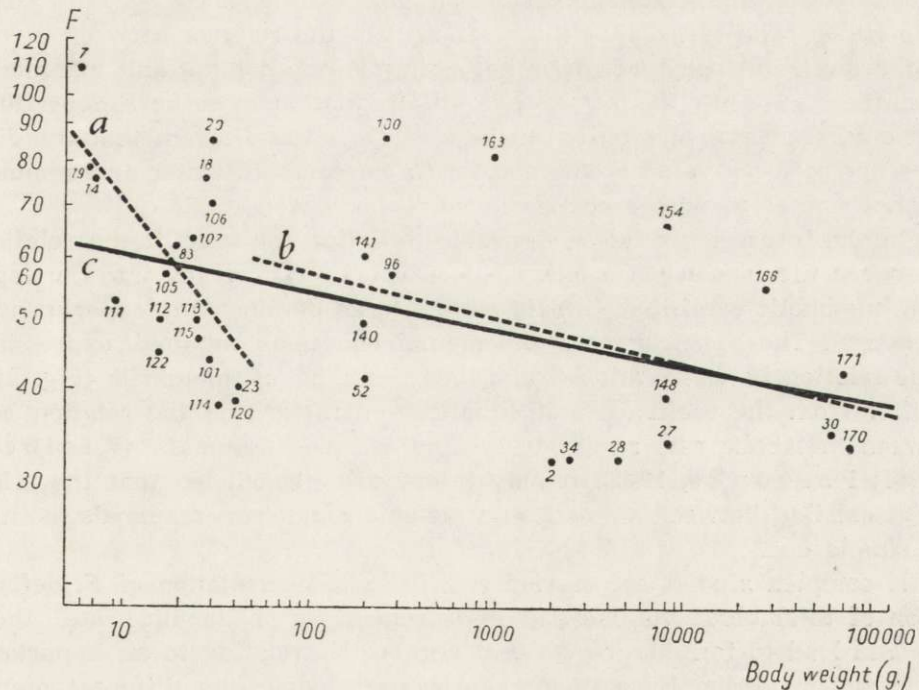


Fig. 21. Relation between value *F* and body weight of mammals.  
(Numbers indicate mammal species given in Appendix).

- a) mammals with body weight up to 50 g:  $y = 143.2x^{-0.310}$ ;  $r = -0.615$ ;  $n = 18$
- b) mammals with body weight over 50 g:  $y = 77.25x^{-0.064}$ ;  $r = -0.453$ ;  $n = 17$
- c) total regression:  $y = 68.39x^{-0.052}$ ;  $r = -0.477$ ;  $n = 35$ .

ison of value *F* for *S. araneus* and *C. glareolus* examined in winter (Table 8) also permits of finding that the greater value *F* in shrews is probably connected with the metabolic level of this species, which is higher than in *Microtidae* (Gębaczynski, 1965; Grodziński & Górecki, 1967).

The existence of a definite connection between value  $F$  and metabolic rate suggests that there is a statistically significant relation between this value and the body weight of mammals (Fig. 21). Value  $F$  decreases in a linear way on a logarithmic scale together with increase in the animal's body weight, these changes taking place far more intensively in mammals with body weights of less than 50 g than in larger mammals. The considerable variation in this value in species with similar body weight can be explained by the fact that calculations were made on the basis of data obtained by different authors using different methods. It would, however, seem that these variations may also have their biological causes. Some of them can be surmised from the different metabolic levels occurring in homoiothermic animals distinguished by Poczopko (1971), who stated that the coefficient of the relation between metabolic level and body weight is not uniform for all birds and mammals. Another cause may be intraspecific differentiation in value  $F$  depending on environmental factors. It can be seen from the diagram that the difference between value  $F$  obtained for *C. glareolus* in winter and summer is not connected with a change in voles' body weight.

In the future it would be desirable to define the type of the relation between the capacity of a unit of blood volume for oxygen transport and the metabolic rate of mammals on the basis of abundant experimental material. The coefficients of exponential equations obtained, expressing the relation between value  $F$  and body weight of mammals (Fig. 21), differ from the coefficients of equations characterizing the relation between metabolic rate and body weight of these animals (Kleiber, 1961; Poczopko, 1971). It may therefore be concluded that the relation existing between value  $F$  and metabolic rate of mammals is not a simple one.

If complex studies are carried out, including calculation of  $F$ , definition of total blood volume and measurement of metabolic rate, they should lead to formulating general regularities relating to an important mechanism of supplying mammal organisms possessing different metabolic requirements with oxygen.

#### VI. SUMMARY

The mechanism regulating the capacity of a unit of blood volume in mammals to carry oxygen consists in corresponding changes in Hb content and size of the total surface area of RBC ( $RBC \times 4r^2$ ) in this unit of volume.

The amount of Hb in a unit of blood volume does not depend on the animals' body weight. Values of all other indices characterizing the res-



piratory function of a unit of blood volume depend both on the body weight of mammals and on the amount of Hb in their blood.

The introduction of the concept of a haemoglobinous level, represented by animals with the same Hb content in the blood, made it possible to examine variation in blood values in mammals in relation to their body weight and simultaneously to the blood Hb content. It also permitted to set in order apparently contradictory facts and to find their correct position among the general regularities of changes in blood values presented in this paper. Whole populations, and also single individuals represent different haemoglobinous levels at different times. A change in haemoglobinous level always leads to a strictly defined changes in all blood values. This treatment of variation of these values in mammals is thus a dynamic treatment, despite the fact that it is based on static morphological measurements.

The size of the total surface area of *RBC* within the range of the same haemoglobinous level decreases with increase in mammals' body weight, these changes taking place more sharply in small (up to 50 g) than in large animals.

The close correlation between Hb content and  $RBC \times 4r^2$  is illustrated in *Microtidae* by a straight line forming part of the relation common to mammals, which takes a non-linear course. The total surface area of *RBC* thus increases the more intensively with the same increases in Hb content, the more the latter occur in the range of higher haemoglobinous levels. Hence the conclusion that the same amount of Hb may function over a different area, and therefore B ü r k e r's statement (1922) cannot be considered as a general rule in mammals.

Within the same haemoglobinous level the amount of Hb per unit of area of *RBC* decreases with decrease in the body weight of mammals. The growing Hb content in the blood is also accompanied by decrease in its amount per unit of area of *RBC*. The essence of this mechanism, permitting of quicker contact of haemoglobin with oxygen, is always increase in the total surface area of *RBC* and never decrease in the amount of haemoglobin in the blood.

The number of *RBC* decreases with increase in the body weight of mammals within each haemoglobinous level. In small mammals (up to 50 g) these changes take place abruptly, and in large mammals slowly. The relation between the number of these cells and Hb content in a unit of blood volume is illustrated in *Microtidae* by a straight line, which is part of non-linear relation common to mammals. Increases in the number of *RBC* accompanying the same rises in Hb content are thus greater when they take place in the range of higher haemoglobinous levels.

The size of *RBC*, on the other hand, within each haemoglobinous level increases with the rise in the body weight of mammals. The higher the haemoglobinous level, the smaller the size of these cells.

Changes in the number and size of *RBC* thus occur in accordance with a reverse and close relation between these values, which in *Microtidae* is characterized by an exponential equation.

The relation between the size of *RBC* and Hb content in the blood of *Microtidae* is not statistically significant. The straight line expressing this relation has a tendency to decline, due to the fact that a larger amount of Hb is associated with a larger number of *RBC*, which in turn is accompanied by their smaller size.

Changes in the size of these cells do thus not directly affect increase in Hb content or total surface area of *RBC*, but in the mechanism leading to increase in the capacity of a unit of blood volume to carry oxygen these changes are of considerable importance. Even a slight reduction in the size of *RBC* provides considerable opportunity for increase in their number. As a result increase in their total surface area becomes possible without changes in their total volume within the same haemoglobinous level. More intensive increase in the total surface area of *RBC* during a change in blood Hb content taking place at higher haemoglobinous levels, with simultaneously smaller intensity of Hct increase, is also made possible by decrease in the size of *RBC*.

Within the same haemoglobinous level Hct does not change and therefore *MCHC* value is constant. In animals representing a higher haemoglobinous level *MCHC* is greater, since the same increase in Hb content is accompanied by increasingly less intensive rise in Hct. The law of constant Hb concentration formulated by Drastich (1928) is therefore correct only for each of the haemoglobinous levels separately. This is confirmed by the non-linear relation obtained for mammals between Hct value and amount of Hb in a unit of blood volume.

Some mountain and diving mammals have a higher Hb content in their blood than would arise from this relation. It may therefore be assumed that all the relations characterizing the respiratory function of a unit of their blood value are shifted to a higher level.

The analysis presented led to formulation of the equation  $F = \text{Hb} \times \text{RBC} \times 4r^2$ , describing the capacity of a unit of blood volume to carry oxygen. This is a dynamic characteristic, as distinct from the static measurement of oxygen capacity since the size of the total surface area of *RBC* fulfils the relation between metabolic rate of mammals and the time their *RBC* are in contact with oxygen in the lungs.

Value *F* calculated for different species of *Microtidae* provides a good characteristic of differences in the respiratory function of a unit of the



volume of blood circulating in the organism of these animals in different physiological and ecological situations. It was found that value  $F$  decreases with an increase in the body weight of mammals. This relation is expressed in a logarithmic scale by straight lines, suggesting a relation between value  $F$  and metabolic rate of animals.

A simplified equation expressing  $F$  on the basis of a knowledge of Hb content only in a unit of blood volume, arrived at on the basis of the relation between Hb and  $RBC \times 4r^2$  may be of theoretical and practical importance in certain comparative studies and in diagnostics.

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#### APPENDIX

##### LIST OF MAMMAL SPECIES USED IN COMPARATIVE STUDIES

M — males, F — females

No. Species, sex, reference	No. Species, sex, reference
<i>MARSUPIALIA</i>	
1 <i>Didelphis marsupialis virginiana</i> <sup>79</sup>	6 <i>Sorex f. fumeus</i> , M <sup>79</sup>
2 <i>Didelphis virginiana</i> <sup>87</sup>	7 <i>Sorex araneus</i> , this paper
	8 <i>Sorex minutus</i> , this paper
<i>INSECTIVORA</i>	
3 <i>Cryptotis p. parva</i> , F <sup>79</sup>	9 <i>Blarina brevicauda talpoides</i> , M <sup>79</sup>
4 <i>Sorex c. cinereus</i> , F <sup>79</sup>	10 <i>Blarina brevicauda talpoides</i> , F <sup>79</sup>
5 <i>Sorex c. cinereus</i> , M <sup>79</sup>	11 <i>Erinaceus europaeus</i> <sup>3</sup>
	12 <i>Hemiechinus albulus tauricus</i> <sup>45</sup>

## CHIROPTERA

- 13 *Plecotus townsendi ingens*, M<sup>79</sup>  
 14 *Plecotus auritus*<sup>31</sup>  
 15 *Pipistrellus s. subflavus*, M<sup>79</sup>  
 16 *Pipistrellus s. subflavus*, F<sup>79</sup>  
 17 *Myotis grisescens*, F<sup>79</sup>  
 18 *Myotis myotis*<sup>31</sup>  
 19 *Myotis nattereri*<sup>31</sup>  
 20 *Nyctalus noctula*<sup>31</sup>  
 21 *Phyllostomus discolor*<sup>89</sup>  
 22 *Carollia perspicillata*<sup>89</sup>  
 23 *Artibeus jamaicensis*<sup>89</sup>  
 24 *Artibeus lituratus*<sup>89</sup>

## PRIMATES

- 25 *Tupaia glis*, M<sup>38</sup>  
 26 *Tupaia glis*, F<sup>38</sup>  
 27 *Macaca nemestrina*, M<sup>72</sup>  
 28 *Macaca nemestrina*, F<sup>72</sup>  
 29 *Pan troglodytes*<sup>46</sup>  
 30 *Homo sapiens*<sup>46</sup>

## LAGOMORPHA

- 31 *Sylvilagus floridanus alacer*, M<sup>79</sup>  
 32 *Sylvilagus floridanus alacer*, F<sup>79</sup>  
 33 *Oryctolagus cuniculus*<sup>9</sup>  
 34 Rabbit<sup>22</sup>  
 35 Rabbit<sup>81</sup>  
 36 *Lepus timidus*<sup>46</sup>  
 37 *Lepus europaeus*<sup>46</sup>  
 38 *Lepus europaeus*<sup>57</sup>

## RODENTIA

- 39 *Sciurus carolinensis*, M<sup>32</sup>  
 40 *Sciurus carolinensis*, F<sup>32</sup>  
 41 *Sciurus carolinensis*<sup>33</sup>  
 42 *Marmota marmota*<sup>37</sup>  
 43 *Marmota monax*<sup>73</sup>  
 44 *Marmota monax*<sup>33</sup>  
 45 *Marmota monax*<sup>33</sup>  
 46 *Marmota monax*<sup>34</sup>  
 47 *Cynomys ludovicianus*<sup>33</sup>  
 48 *Citellus columbianus*, M<sup>79</sup>  
 49 *Citellus undulatus*<sup>86</sup>  
 50 *Citellus undulatus*<sup>37</sup>  
 51 *Citellus suslica*<sup>46</sup>  
 52 *Citellus pygmaeus*<sup>60</sup>  
 53 *Citellus tridecemlineatus*<sup>74, 83</sup>  
 54 *Citellus tridecemlineatus*<sup>33</sup>  
 55 *Citellus l. lateralis*, M<sup>79</sup>  
 56 *Spermophilus tereticaudatus*<sup>33</sup>  
 57 *Amnospermophilus harasii*<sup>33</sup>  
 58 *Tamias striatus lysteri*, M<sup>79</sup>  
 59 *Tamias striatus lysteri*, F<sup>79</sup>  
 60 *Tamias striatus venustus*, M<sup>79</sup>  
 61 *Eutamias minimus consobrinus*, M<sup>79</sup>  
 62 *Eutamias minimus consobrinus*, F<sup>79</sup>  
 63 *Dipodomys ordii*, M<sup>79</sup>  
 64 *Thomomys talpoides fossor*, M<sup>79</sup>  
 65 *Perognathus hispidus*, M<sup>79</sup>

- 66 *Oryzomys p. palustris*, M<sup>79</sup>  
 67 *Oryzomys p. palustris*, F<sup>79</sup>  
 68 *Oryzomys palustris texensis*, F<sup>79</sup>  
 69 *Reithrodontomys fulvescens aurantius*, M<sup>79</sup>  
 70 *Reithrodontomys fulvescens aurantius*, F<sup>79</sup>  
 71 *Peromyscus crinitus auripectus*, F<sup>79</sup>  
 72 *Peromyscus maniculatus osgoodi*, F<sup>79</sup>  
 73 *Peromyscus maniculatus rufinus*, M<sup>79</sup>  
 74 *Peromyscus maniculatus rufinus*, F<sup>79</sup>  
 75 *Peromyscus maniculatus ozarkianum*, M<sup>79</sup>  
 76 *Peromyscus maniculatus ozarkianum*, F<sup>79</sup>  
 77 *Peromyscus maniculatus rufinus*<sup>85</sup>  
 78 a—h *Peromyscus maniculatus*<sup>78</sup>  
 79 *Peromyscus polionotus*<sup>79</sup>  
 80 *Peromyscus leucopus noveboracensis*, M<sup>79</sup>  
 81 *Peromyscus leucopus noveboracensis*, F<sup>79</sup>  
 82 *Peromyscus l. leucopus*, F<sup>79</sup>  
 83 *Peromyscus l. leucopus*, F<sup>20</sup>  
 84 a—i *Peromyscus l. leucopus*<sup>78</sup>  
 85 *Peromyscus l. leucopus*<sup>11</sup>  
 86 *Peromyscus boylii attwateri*, M<sup>79</sup>  
 87 a—g *Peromyscus boylii*<sup>78</sup>  
 88 *Peromyscus nuttalli flammeus*, M<sup>79</sup>  
 89 *Onychomys leucogaster*, M<sup>79</sup>  
 90 *Sigmodon h. hispidus*, M<sup>79</sup>  
 91 *Sigmodon h. hispidus*, F<sup>79</sup>  
 92 *Sigmodon h. hispidus*<sup>0</sup>  
 93 *Sigmodon hispidus texianus*<sup>35</sup>  
 94 *Neotoma floridana osagensis*, M<sup>79</sup>  
 95 *Neotoma floridana osagensis*, F<sup>79</sup>  
 96 *Mesocricetus auratus*, M<sup>82</sup>  
 97 *Mesocricetus auratus*, F<sup>82</sup>  
 98 *Mesocricetus auratus*<sup>6</sup>  
 99 *Mesocricetus auratus*<sup>55</sup>  
 100 *Mesocricetus auratus*<sup>23</sup>  
 101 *Cricetulus grisens*<sup>60</sup>  
 102 *Lemmus sibiricus*<sup>54</sup>  
 103 *Clethrionomys gapperi galei*, M<sup>79</sup>  
 104 *Clethrionomys gapperi galei*, F<sup>79</sup>  
 105 *Clethrionomys glareolus*<sup>50</sup>  
 106 *Clethrionomys glareolus* (Tatra Mts. — June)<sup>50</sup>  
 107 *Clethrionomys glareolus* (Tatra Mts. — Sept.)<sup>50</sup>  
 108 *Clethrionomys glareolus* (Lowland — Dec.)<sup>50</sup>  
 109 *Clethrionomys glareolus* (Lowland — June)<sup>50</sup>  
 110 *Clethrionomys rutilus dawsoni*<sup>80</sup>  
 111 *Pitymys pinetorum*<sup>20</sup>  
 112 *Pitymys subterraneus*<sup>47</sup>  
 113 *Microtus arvalis*<sup>47</sup>



114 <i>Microtus nivalis</i> <sup>49</sup>	
115 <i>Microtus agrestis</i> <sup>47</sup>	
116 <i>Microtus pinetorum nemoralis</i> , M <sup>79</sup>	
117 <i>Microtus pinetorum nemoralis</i> , F <sup>79</sup>	
118 <i>Microtus montanus fusus</i> , F <sup>79</sup>	
119 <i>Microtus longicaudus mordax</i> , M <sup>79</sup>	
120 <i>Microtus oeconomus</i> <sup>58</sup>	
121 <i>Microtus oeconomus chachlovi</i> <sup>54</sup>	
122 <i>Lagurus lagurus</i> <sup>47</sup>	
123 <i>Lagurus lagurus</i> <sup>66</sup>	
124 <i>Hesperomys sorella</i> <sup>61, 62</sup>	
125 <i>Phyllotis darvini limatus</i> <sup>61, 62</sup>	
126 <i>Phyllotis darvini chilensis</i> <sup>61, 62</sup>	
127 <i>Phyllotis pictus</i> <sup>61, 62</sup>	
128 <i>Mus musculus</i> <sup>61, 62</sup>	
129 <i>Mus musculus</i> <sup>79</sup>	
130 <i>Mus musculus</i> <sup>60</sup>	
131 White mouse, H <sup>70</sup>	
132 White mouse, CBA <sup>70</sup>	
133 White mouse, C <sub>57</sub> <sup>70</sup>	
134 White mouse, C <sub>3</sub> H <sup>70</sup>	
135 White mouse, dba <sup>70</sup>	
136 <i>Rattus norvegicus</i> <sup>8</sup>	
137 <i>Rattus rattus</i> <sup>81</sup>	
138 White rat, Wistar <sup>71</sup>	
139 White rat, Sprague-Dawley <sup>76</sup>	
140 White rat <sup>21</sup>	
141 White rat <sup>1</sup>	
142 <i>Apodemus sylvaticus ciscaucasicus</i> <sup>41</sup>	
143 <i>Glis glis</i> <sup>46</sup>	
144 <i>Zapus p. princeps</i> <sup>79</sup>	
145 Guinea pig <sup>24</sup>	
146 <i>Chinchilla lanigera</i> <sup>48</sup>	
147 <i>Chinchinilla sahamae</i> <sup>61, 62</sup>	
148 <i>Myocastor coypus</i> <sup>18, 34</sup>	
CETACEA	
149 <i>Tursiops tursio</i> <sup>46</sup>	
150 <i>Delphinus delphis</i> <sup>46</sup>	
151 <i>Phocaena phocaena</i> <sup>46</sup>	
152 <i>Phocaena phocaena</i> <sup>46</sup>	
	CARNIVORA
	153 Dog <sup>58</sup>
	154 <i>Vulpes fulva</i> <sup>46</sup>
	155 <i>Vulpes fulva</i> <sup>2</sup>
	156 <i>Alopex lagopus</i> <sup>2</sup>
	157 <i>Ursus americanus</i> <sup>90</sup>
	158 <i>Ursus americanus</i> <sup>15</sup>
	159 <i>Ursus americanus</i> <sup>15</sup>
	160 <i>Ursus americanus</i> <sup>77</sup>
	161 <i>Ursus americanus</i> <sup>77</sup>
	162 <i>Mustela erminea</i> <sup>46</sup>
	163 <i>Mustela vison</i> <sup>46</sup>
	PINIPEDIA
	164 <i>Phoca vitulina</i> <sup>46</sup>
	165 <i>Eumetopias stelleri</i> <sup>46</sup>
	ARTIODACTYLA
	166 <i>Sus scrofa</i> <sup>52</sup>
	167 <i>Lama glama</i> <sup>46</sup>
	168 <i>Odocoileus virginianus</i> <sup>83, 84</sup>
	169 <i>Odocoileus h. hemionus</i> <sup>4</sup>
	170 <i>Rangifer tarandus</i> , M <sup>28</sup>
	171 <i>Rangifer tarandus</i> , F <sup>28</sup>
	172 <i>Rangifer tarandus groenlandicus</i> <sup>16, 17</sup>
	173 Cow (swedish) <sup>46</sup>
	174 Cow of Dagestan breed <sup>46</sup>
	175 <i>Bos zebu indicus</i> <sup>56</sup>
	176 <i>Gazella subgutturosa</i> <sup>46</sup>
	177 Goat <sup>46</sup>
	178 Merino sheep, russian breeding <sup>46</sup>
	179 Sheep of Gissar breed <sup>46</sup>
	180 Sheep of Dagestan breed <sup>46</sup>
	181 <i>Capra ibex sibirica</i> <sup>46</sup>
	182 <i>Capra falconeri</i> <sup>46</sup>
	183 <i>Ovis ammon poli</i> <sup>46</sup>
	184 <i>Ovis ammon vignei</i> <sup>46</sup>
	185 <i>Ovis musimon</i> <sup>46</sup>

Alina KOSTELECKA-MYRCHA

PRAWIDŁOWOŚCI ZMIAN WSKAŹNIKÓW CZERWONOKRWINKOWYCH  
CHARAKTERYZUJĄCE ODDECHOWĄ FUNKCJĘ KRWI SSAKÓW

Streszczenie

Przeprowadzono analizę wzajemnych zależności pomiędzy czerwonymi wskaźnikami u 1072 osobników należących do 6 gatunków *Microtidae*. Zależności te opracowano statystycznie, obliczając współczynniki korelacji, równania regresji oraz granice ufności i tolerancji tych równań. Zbadano także pionowe przekroje poprzeczne rozpatrywanych zbiorów przedstawiających niektóre zależności (Fig. 2, 4, 6, 8, Tabela 3).

Analiza ta była punktem wyjścia do prześledzenia ogólnej zmienności czerwono-krwinkowych wskaźników u ssaków. W tej części pracy oparto się na badaniach własnych przeprowadzonych zarówno na *Microtidae*, jak również na dwóch gatunkach *Soricidae* oraz *Sus scrofa* L., a także wykorzystano podane w literaturze wartości wskaźników krwi innych ssaków. Dysponowano ogólnie danymi dla 126 gatunków należących do 10 rzędów. Przeanalizowano zależność wartości poszczególnych wskaźników krwi od ciężaru ciała tych zwierząt.

Mechanizm regulujący zdolność jednostki objętości krwi ssaków do transportu tlenu polega na odpowiednich zmianach zawartości Hb i wielkości sumarycznej powierzchni czerwonych krwinek ( $RBC \times 4r^2$ ) w tej jednostce objętości.

Ilość Hb w jednostce objętości krwi nie zależy od ciężaru ciała zwierząt (Fig. 9). Wartości wszystkich pozostałych wskaźników, charakteryzujących oddechową funkcję tej jednostki objętości, zależą zarówno od ciężaru ciała ssaków jak i od zawartości Hb w ich krwi.

Wprowadzenie pojęcia poziomu hemoglobinowego, reprezentowanego przez zwierzęta o jednakowej zawartości Hb we krwi, umożliwiło zbadanie zmienności wskaźników czerwono-krwinkowych u ssaków w zależności od ich ciężaru ciała i równocześnie od ilości Hb we krwi. Wprowadzenie tego pojęcia pozwoliło uporządkować pozornie sprzeczne ze sobą fakty i znaleźć właściwe ich miejsce w wyprowadzonych ogólnych prawidłowościach zmian wskaźników czerwono-krwinkowych u ssaków. Całe populacje, a także poszczególne osobniki reprezentują w różnych momentach różne poziomy hemoglobinowe. Zmiana poziomu hemoglobinowego pociąga za sobą zawsze ściśle określoną zmianę wszystkich wskaźników czerwono-krwinkowych. Takie ujęcie zmienności tych wskaźników u ssaków jest więc ujęciem dynamicznym mimo, że opiera się na morfologicznych, statycznych pomiarach.

Wielkość sumarycznej powierzchni czerwonych krwinek w zakresie tego samego poziomu hemoglobinowego maleje ze wzrostem ciężaru ciała ssaków, przy czym zmiany te zachodzą gwałtowniej u małych (do 50 g) niż u dużych zwierząt (Fig. 16).

Ścisłą korelację między ilością Hb a  $RBC \times 4r^2$  ilustruje u *Microtidae* linia prosta (Fig. 7), będąca częścią ogólnej dla ssaków zależności, której przebieg ma charakter nie liniowy (Fig. 17). Sumaryczna powierzchnia czerwonych krwinek zwiększa się więc tym intensywniej przy jednakowych wzrostach ilości Hb, im odbywają się one w zakresie wyższych poziomów hemoglobinowych. Wypływa stąd wniosek, że ta sama ilość Hb może funkcjonować na różnej powierzchni, wobec czego twierdzenia Bürkera (1922) nie można uznać za prawidłowość ogólną u ssaków.

W zakresie tego samego poziomu hemoglobinowego ilość Hb przypadająca na jednostkę powierzchni krwinek zmniejsza się wraz ze zmniejszaniem się ciężaru ciała ssaków. Wzrastającej zawartości hemoglobiny we krwi towarzyszy także zmniejszanie się jej ilości przypadającej na jednostkę powierzchni czerwonych krwinek. Istotą tego mechanizmu, umożliwiającego szybszy kontakt hemoglobiny z tlenem, jest zawsze wzrost sumarycznej powierzchni krwinek, nigdy zaś zmniejszenie się ilości hemoglobiny we krwi.

Liczba czerwonych krwinek maleje wraz ze wzrostem ciężaru ciała ssaków w zakresie każdego poziomu hemoglobinowego (Fig. 10). U małych ssaków (do 50 g) zmiany te przebiegają gwałtownie, a u większych powoli. Zależność liczby czerwonych krwinek od zawartości Hb w jednostce objętości krwi ilustruje u *Microtidae* linia prosta (Fig. 3), która jest częścią ogólnej dla ssaków zależności nie liniowej (Fig. 11). Przyrosty liczby czerwonych krwinek towarzyszące jednakowym wzrostom ilości Hb są więc tym większe, im odbywają się w zakresie wyższych poziomów hemoglobinowych.



Wielkość czerwonych krwinek natomiast w zakresie każdego poziomu hemoglobi nowego rośnie wraz ze wzrostem ciężaru ciała ssaków (Fig. 12). Im wyższy poziom hemoglobiny, tym wielkość tych komórek jest mniejsza (Fig. 13).

Zmiany liczby i wielkości czerwonych krwinek układają się więc w myśl odwrotnej i ścisłej zależności zachodzącej pomiędzy tymi wskaźnikami, którą u *Microtidae* charakteryzuje równanie wykładnicze (Fig. 1).

Zależność między wielkością krwinek a zawartością Hb we krwi *Microtidae* jest statystycznie nieistotna (Fig. 5). Prosta wyrażająca tę zależność ma tendencję spadkową, wynikającą z faktu, że większa ilość Hb związana jest z większą liczbą krwinek, której z kolei towarzyszy mniejsza ich wielkość. Zmiany wielkości tych komórek nie mają więc bezpośredniego wpływu na wzrost ilości Hb i sumarycznej powierzchni czerwonych krwinek, ponieważ wzrostowi liczby towarzyszy zmniejszanie się ich rozmiarów. W mechanizmie prowadzącym do zwiększenia zdolności jednostki objętości krwi do transportu tlenu, zmiany te mają jednak istotne znaczenie. Nawet niewielkie zmniejszenie się wielkości krwinek daje bowiem duże możliwości zwiększenia ich liczby. W rezultacie możliwe się staje zwiększenie ich sumarycznej powierzchni, bez zmiany ich sumarycznej objętości w zakresie tego samego poziomu hemoglobinowego. Intensywniejsze zwiększenie sumarycznej powierzchni krwinek podczas zmiany zawartości Hb odbywającej się w zakresie wyższych poziomów hemoglobinowych, przy równocześnie mniejszej intensywności wzrostu Hct, umożliwia także malejąca wielkość krwinek.

Wielkość czerwonych krwinek modyfikuje w istotny sposób zależność zachodzącą między Hct i RBC, co również świadczy o tym, że nawet niewielkie jej zmiany wyrażają się ostro w sumarycznej objętości tych komórek. Wartość hematokrytu jest więc tylko koniecznym następstwem współzależności zachodzącej między liczbą i wielkością krwinek, której istotnym fizjologicznym sensem jest zwiększenie ilości Hb i sumarycznej powierzchni czerwonych krwinek. Określenie wartości Hct nie może więc zastąpić znajomości liczby i wielkości tych komórek.

W zakresie tego samego poziomu hemoglobinowego Hct nie zmienia się (Fig. 15), wobec czego również wartość MCHC jest stała. Natomiast u zwierząt reprezentujących wyższy poziom hemoglobinowy MCHC jest większa, ponieważ jednakowym wzrostem ilości Hb towarzyszy coraz mniej intensywny wzrost Hct. Prawo stałej koncentracji Hb, sformułowane przez Drasticha (1928) jest więc słuszne tylko dla każdego z poziomów hemoglobinowych oddzielnie. Potwierdza to otrzymana dla ssaków nie liniowa zależność między wartością Hct a ilością Hb w jednostce objętości krwi (Fig. 14).

Niektóre ssaki górskie i nurkujące mają wyższą zawartość Hb we krwi, niż by to wynikało z tej zależności. Można przypuszczać więc, że wszystkie zależności charakteryzujące funkcję oddechową jednostki objętości ich krwi są przesunięte na wyższy poziom.

Przedstawiona analiza doprowadziła do sformułowania wzoru  $F = Hb \times RBC \times 4r^2$ , charakteryzującego zdolność jednostki objętości krwi do transportu tlenu. Jest to charakterystyka dynamiczna w odróżnieniu od statystycznego pomiaru pojemności tlenowej, ponieważ wielkość sumarycznej powierzchni czerwonych krwinek realizuje związek z tempem metabolizmu ssaków i czasem kontaktu ich czerwonych krwinek z tlenem w płucach.

Obliczone  $F$  dla różnych gatunków *Microtidae* dobrze charakteryzuje różnice w oddechowej funkcji jednostki objętości krwi krążącej w organizmie tych zwierząt, znajdujących się w różnych sytuacjach fizjologicznych i ekologicznych (Fig. 18, 19, 20, Tabela 7 i 8).

Stwierdzono, że wartość  $F$  maleje wraz ze wzrostem ciężaru ciała ssaków. Zależność tę wyrażają na skali logarymicznej linie proste, sugerujące związek wielkości  $F$  z tempem metabolizmu zwierząt (Fig. 21).

Uproszczony wzór wyrażający  $F$  na podstawie znajomości wyłącznie zawartości Hb w jednostce objętości krwi, wyprowadzony w oparciu o zależność Hb od  $RBC \times 4r^2$  może mieć znaczenie teoretyczne i praktyczne w niektórych badaniach porównawczych i w diagnostyce.