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ENERGY METABOLISM AS RELATED TO BODY SIZE AND RESPIRATORY SURFACES, AND ITS EVOLUTION

BY

AXEL M. HEMMINGSEN

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1.
INTRODUCTION

The relation between standard (basal) energy metabolism and body weight can be mathematically formulated by the equation

$$\text{metabolism} = k \cdot \text{body weight}^n$$

or

$$\text{log. metabolism} = \text{log. } k + n \cdot \text{log. body weight}$$

The linear relation in question usually results from smoothing of data grouped about the straight line representing the function in a diagram in which log. metabolism is plotted against log. body weight. Then n is the tangent of the angle at which the straight line is inclined to the axis of abscissae. If the scatter is small, graphical smoothing or eye-fitting often suffices. If the smoothing is made by the method of the least sum of squares the accuracy, or rather inaccuracy, of constants log. k and n can be expressed by their standard deviations (cf. e. g. HEMMINGSEN, 1933, pp. 150—51 and 156; or diss.: pp. 16 and 20—21; or KITTEL, 1941, p. 538; or HALD, 1952, or other statistical handbooks). Though there is a growing understanding of the necessity of this, regrettably many authors have not made statistical tests to ensure the justification of their conclusions. In the discussions to follow, published n values based on evidently too scattered data have not been considered. Sufficient time has not been available to subject all data under discussion to statistical tests, so that it has been necessary to take many n values based on reasonably slight scatter at their published face value.

In his thesis ZEUTHEN (1947) was the first to publish a comprehensive study of n, by him termed e (*loc. cit.*, p. 80), throughout the animal kingdom, excepting *Protozoa*, but including marine larvae down to body weights of 0.1—1 μg. He found a gradual average decrease in n from nearly 1.0 to less than 0.7 with body weight increasing from 1 μg up to between 1 g and 1 kg; and with further increase in weight, a gradual average increase in n up to 1 ton (*loc. cit.*, pp. 132—133; notably fig. 48, in which "percentage decrease in metabolism per unit body weight at a 10 times magnification of the animals", which varies inversely with n, is plotted against body weight). The question whether or not these gradual changes in n applied only to short lines oscillating about an over-all line with constant n, or they represented changes in the over-all n, or there was no over-all n at all, did not become an object of attention, because the above-mentioned double logarithmic plotting was not used (*loc. cit.*, pp. 128 and 146—149).

Hemmingsen (1950) demonstrated that provided rigorous demands are made upon standard conditions the over-all n is uniform (about 0.73), not only in homoiothermal animals as demonstrated notably by Kleiber (1932, pp. 320—21), Brody *et al.* (1932, 1934), and Brody (1945, fig. 13.7 on p. 370), but with a considerably lower k also in poikilothermal animals (and at least some plants) down to body weights of about 0.1—1.0 mg. This was visualized by plotting in the above equation log. metabolism against log. body weight (as in figs. 1—9 and 11—12 of this paper). It was shown (*loc. cit.*, fig. 1) that below body weights of 0.1—1.0 mg the metabolism values fall below an extrapolation of the straight line representing the poikilothermal animals down to 0.1—1.0 mg body weight, and appears to correspond to an n value nearer to 1.0, at least down to weights at about 0.1—1 μg. The data for still smaller organisms (yeast and bacteria) also fall below the line (*loc. cit.*, fig. 2 on p. 17, which compares plants with animals). The question of n at these still smaller body weights will be discussed in chapter 2.

Adopting the same double logarithmic plotting and drawing in supplementary data from his own work and other sources, especially as regards unicellular organisms, Zeuthen (1953) accepted that n is practically uniform and nearly identical (0.75—0.76) in homoiothermal and poikilothermal animals down to a certain body weight (Zeuthen thinks 40 mg rather than 0.1—1.0 mg), and then—with further decrease in body weight—1.0 or nearly so (he thinks 0.95), down to about 0.1—1.0 μg. In the unicellular organisms below 0.1—1.0 μg cell weight he found "a very significant regression of metabolic rate with size" (p. 4) but with "a very ill-defined slope" (n) of the straight line, n being about 0.7 (p. 4) or ⅔ (p. 9).

A study of the points representing unicellular organisms in Zeuthen's fig. 1 shows that not only is the slope "very ill-defined", but the points representing the metabolism of the bacteria and of the ciliate *Tetrahymena* would fall about an extrapolated prolongation of the poikilotherm line; and those of the flagellates, on a prolongation of the "crustacean" line with the slope 0.80. Of the points representing the unicellular organisms only the point representing the amoeba *Mayorella* really falls below a prolongation of the "crustacean" line drawn; and only slightly.

According to *loc. cit.* (p. 2) Zeuthen, owing to unknown influences of acclimatization, applied to the data on poikilothermal and unicellular organisms a temperature correction only in a few cases, but states that in arriving at the slope 0.7 for the unicellular organisms some "regard has been paid to the fact that temperature differences exist between the different groups of experiments" (p. 4).

The highest metabolism values of some unicellular organisms, e. g. bacteria, were obviously too high to be comparable with the basal or resting values of metazoans on which the lines representing homotothermal and poikilothermal animals, as adopted by Zeuthen, were based. And the oxygen intake of bacteria at 37° C. and marine larvae at 13° C. were plotted in the same coordinate system without any allowance for the influence of temperature on metabolism—which for the difference between 13° and 37° C. must be assumed to correspond at least in some animals (Krogh, 1916, tables XV—XVI, pp. 93—95) to more than a 6 times (about 0.8 log. decade) difference in metabolism. We shall try in the next chapter to allow for the influence of activity and temperature in treating similar data.

Speaking of poikilothermal organisms in general, the metabolism of eurythermal species may be less influenced by temperature than that of stenothermal species (cf. Schlieper, 1950:

Bläsing, 1953), and some acclimatization of metabolism to temperature may take place, especially but not exclusively in marine poikilotherms (cf. references by Hemmingsen, 1950, pp. 10—12; Scholander, Flagg, Walters, and Irving, 1953; Rao and Bullock, 1954; Bullock, 1955; Prosser, 1955; Dehnel and Segal, 1956; Tashian, 1956; Roberts, 1957 a and b; and Démeusy, 1957). Wells (1935a) found the influence of temperature to depend on body weight in the fish *Fundulus*, but Job (1955) found such an influence in the fish *Salvelinus fontinalis* only on active metabolism, not on standard metabolism. Other examples of absence of acclimatization are quoted by Bullock (1955, p. 323). Even "reversed acclimatization" has been described (Berg, 1953).

Omission of temperature corrections in comparisons between organisms of different size would be justifiable only if acclimatization were absolute; that is, if any changes in metabolism from a specific standard value (characteristic of each body weight) due to temperature changes were only temporary, and if the available measurements were all made in the absence of any temperature influence on the supposed standard, or after reversion to it from temporary changes due to temperature. None of these conditions are fulfilled. It is, therefore, to be expected in general that the scatter of metabolism values will be considerably reduced by applying a temperature correction, for instance on the basis of Krogh's curve (1916) or by means of some value of Q_{10} for van't Hoff's curve, even when the latter may be rather ill-defined. We shall check this expectation later in connection with figs. 2 and 9 (chapters 3 and 4).

As standard metabolism values for comparison at different body weights it is endeavoured in general to obtain measurements which are as "basal" as possible. In cases where acclimatization is known to occur, it is natural therefore to prefer measurements obtained by acclimatization to higher temperatures, to such obtained by acclimatization to lower temperatures, because when corrected to a certain common temperature, the former will be lower than the latter. Still, if several acclimatization temperatures have been used, it seems reasonable to choose the result obtained with the one nearest to the temperature to which correction is made.

Corrections for temperature applied in this paper have been obtained by reference to Krogh's curve (1916, p. 96; cf. Hemmingsen, 1950, p. 10) unless otherwise available. The heat production in Cal. has been calculated from the respiratory exchange by reference to Krogh (1916, p. 10), unless otherwise available.

2.

STANDARD ENERGY METABOLISM RELATED TO BODY (CELL) WEIGHT IN UNICELLULAR ORGANISMS

In the author's opinion metabolism values of unicellular organisms cannot be compared with those of poikilothermal metazoans unless in both groups the best approximations to accepted comparable "standard" ("basal") conditions are chosen for comparison. It seems self-evident that for bacteria the high values of oxygen consumption per cell during the growth of the population should be discarded and comparisons made on the basis of the low constant level obtained afterwards, which presumably is a much better approximation to "basal" or "standard" metabolism. It seems also self-evident that all measurements should be corrected to the same temperature. These demands are satisfied in fig. 1 of this paper.

The data representing in fig. 1 the relation between "standard" energy metabolism corrected to 20° C. and body (cell) weight in unicellular organisms have been obtained from Fenevessy and Reiner (1928; cf. Brand, 1935, table on p. 203, and Jahn, 1941, table on p. 362); from Zeuthen (1943, p. 511); from Smith and Kleiber (1950, fig. 1 on p. 135; there are misprints in the corresponding table 2 on p. 134); from the sources quoted and treated by Hemmingsen (1950, text and figs. 1—2); from Scholander, Claff, and Sveinsson (1952, fig. 1 on p. 179 and sources discussed on p. 180); and from the sources quoted by Zeuthen (1953, pp. 3—4), except that the data of Pace and Kumura (1946) on *Pelomyxa* were preferred to those of Pace and Belda (1944) because their cultures were bacteria-free. A specific gravity of 1.0 has been assumed in expressing volumes as weights. The weights

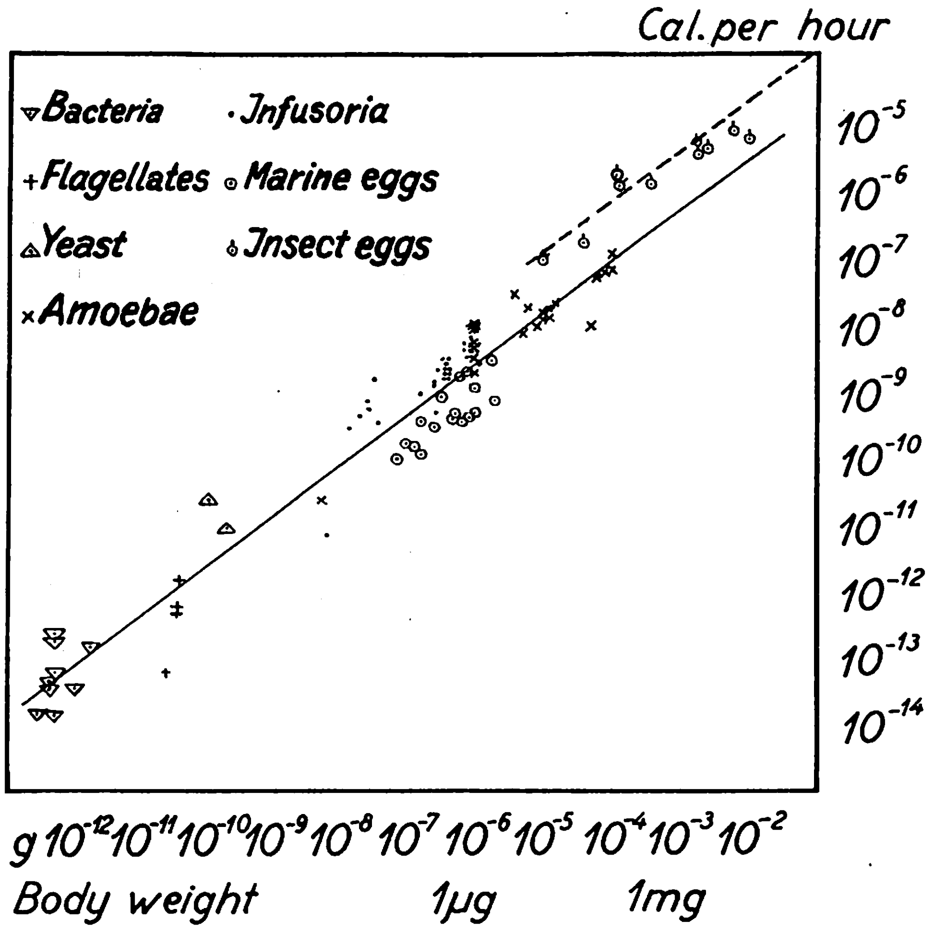

Fig. 1.

The relation between standard energy metabolism at 20° C. and cell weight in unicellular organisms. The authorities of the data are given in the text. The straight whole line which corresponds to $n = 0.756 \pm 0.021$ has been obtained by mathematical smoothing of all the values represented excepting those obtained on insect eggs, which are seen to fall nearer to the broken line which is a prolongation of the line for poikilothermal animals (cf. fig. 2). Both marine and insect eggs were fertilized.

given by Zeuthen (1953, p. 4) for *Chaos chaos* exceed 10 times those given by Scholander, Claff, and Sveinsson (fig. 1 on p. 179). According to Andresen (1956, p. 79) the volumes of different specimens of *Chaos chaos* vary extremely, dependent on the number of nuclei (5—1000 or more).

Data on fertilized marine and just laid insect eggs have been included in fig. 1, although of course even unfertilized eggs are not, strictly speaking, unicellular organisms.

In some of the marine eggs represented in fig. 1 the respiration is known to rise on fertilization; in others, to fall; and in still others, to remain practically unaltered (cf. Ballentine, 1940 b, table 1 on p. 218; for *Ciona*, also Holter and Zeuthen, 1944; and for the surf clam *Spisula*, Sclufer, 1955, with still other references). Now, according to Whitaker (1933; cf. also Needham, 1942, p. 563) the respiratory rates (metabolism per unit volume or weight) of the eggs of the various groups are more uniform shortly after than before fertilization. This would occur if n were nearer to 1.00 after than before fertilization. There may apparently be a tendency towards such a difference in n, but the main reason is a decreased scatter of the metabolism values after fertilization, not only when calculated per unit volume or weight but also when plotted in a diagram as fig. 1. It thus seems that, after all, fertilized eggs may constitute a better basis for comparison than unfertilized eggs.

Whereas the data on the marine eggs represented in fig. 1 place them among the unicellular organisms, those on the insect eggs evidently approach or nearly fit the lower end of the (broken) poikilotherm line.

The data on eggs of *Bombyx* ($10^{-3.9}$ g) and *Acilius* ($10^{-2.8}$ g) represented in fig. 1 are identical to the data represented at the lowest end of the poikilotherm line published by Hemmingsen (1950, fig. 1). Different values for weights and metabolism of *Bombyx* eggs possibly of different races (e. g. Hsueh and Tang, 1944) have not been included here.

Fig. 1 thus neatly accounts for the different levels of the data on marine eggs and insect eggs in Smith's and Kleiber's fig. 1, from where the other egg data were taken (except one measurement by Zeuthen (1943) on the egg of a polychaetous worm).

The egg of the sea urchin *Arbacia* (**Warburg**, 1908) is represented in fig. 1 both by a point from **Krogh** (1916, p. 145, as adopted by **Hemmingsen**, 1950, pp. 11—12) and by a point from **Smith** and **Kleiber**, because the two authorities employed somewhat different methods of calculation. Two data on amoebae and two on infusorians coincide in the figure.

It should be added that the position of data on some mammalian eggs in **Smith**'s and **Kleiber**'s fig. 1 of body sizes similar to those of the marine eggs may perhaps be best interpreted as being grouped about—or rather, as they scatter very much, the center of gravity of them being placed near—the lower end of the poikilotherm line.

Not only the energy metabolism of the female sex cells here represented by marine eggs, but also that of spermatozoa (e. g. bovine, cf. **Lardy**, **Ghosh**, and **Plant**, 1949, with references), fall into line with the *Protista,* and would be represented in fig. 1 by points in the region of the flagellate points.

It will be seen from fig. 1 that from bacteria at the weight of 10^{-6} μg (= 10^{-12} g) up to the giant amoebae weighing about 10^{-1} mg (= 10^{-4} g), *the average relation of unicellular metabolism to cell weight will be best represented by a straight line, which is, at least approximately, parallel to the (broken) prolonged metazoic poikilotherm line and situated about 0.9 logarithmic decade (in terms of the ordinate scale) below the latter.* In other words: the metabolism of unicellular organisms is on the average about 8 times lower than the metabolism which imaginary equally sized poikilothermal multicellular animals would have, if their metabolism were to be obtained by extrapolation of the metazoic poikilotherm line to the same microscopic sizes.

The straight whole line drawn in the figure was obtained by the smoothing method of the least sum of squares, excluding insect eggs but including marine eggs, and corresponds to $n = 0.756 \pm 0.021$. Without marine eggs (and again without insect eggs) n becomes 0.772 ± 0.020.

Though marine eggs, especially when fertilized, may be said not to be unicellular organisms in a narrow sense, it is, on the other hand, an obvious possibility that their lower metabolism relative to the numerous measurements on infusorians and also some on amoebae within the same range of body weights (cf. fig. 1) is due to their immobility. Even at rest fast swimming, highly active infusorians may have a relatively high metabolism, and though the amoebae are very sluggish they are certainly more active than eggs. The n value obtained with the inclusion of marine eggs may therefore well represent a better approximation to a unicellular standard line than the value obtained without these eggs.

If no corrections had been made for temperature in fig. 1, n would probably have turned out smaller, because many of the experiments at lower cell weights were made at 37° C. In order to test whether the correction for temperature has actually led to a more uniform picture in terms of a smaller dispersion, it has been preferred, therefore, to compare the deviations of the data, with and without corrections, from a line, the inclination of which was determined more independently of the corrections than the line in fig. 1. This will be done in the next chapter.

3.

STANDARD ENERGY METABOLISM RELATED TO BODY WEIGHT IN UNICELLULAR ORGANISMS AND METAZOANS

The question now arises whether the values of n for unicellular organisms differ significantly from the n common to homoiothermal and poikilothermal metazoans above 0.1—1.0 mg. This n was taken in the earlier publication (**Hemmingsen**, 1950) to be 0.73 as also advocated by the U. S. National Research Council on the basis of the work of **Brody** and coworkers (**Brody**, 1945, pp. 370 and 390: 0.734 and 0.732).

Kleiber (1947, p. 528) found for the 10 groups of mammals (rat to steer) from his earlier data (**Kleiber**, 1932) $n = 0.739 \pm 0.03$ and for 26 groups of more recent own and other data also on mammals (mouse to cow) 0.756 ± 0.05 (3 printed lines later 0.004 is substituted for the latter standard deviation, so it is not clear which of them is meant). Since according to this n is very nearly 0.75, and this is a less complicated figure than 0.73, and furthermore does not differ significantly from 0.73, Kleiber (*loc. cit.*, p. 534) favours the adoption of $n = 0.75$ in preference to 0.73.

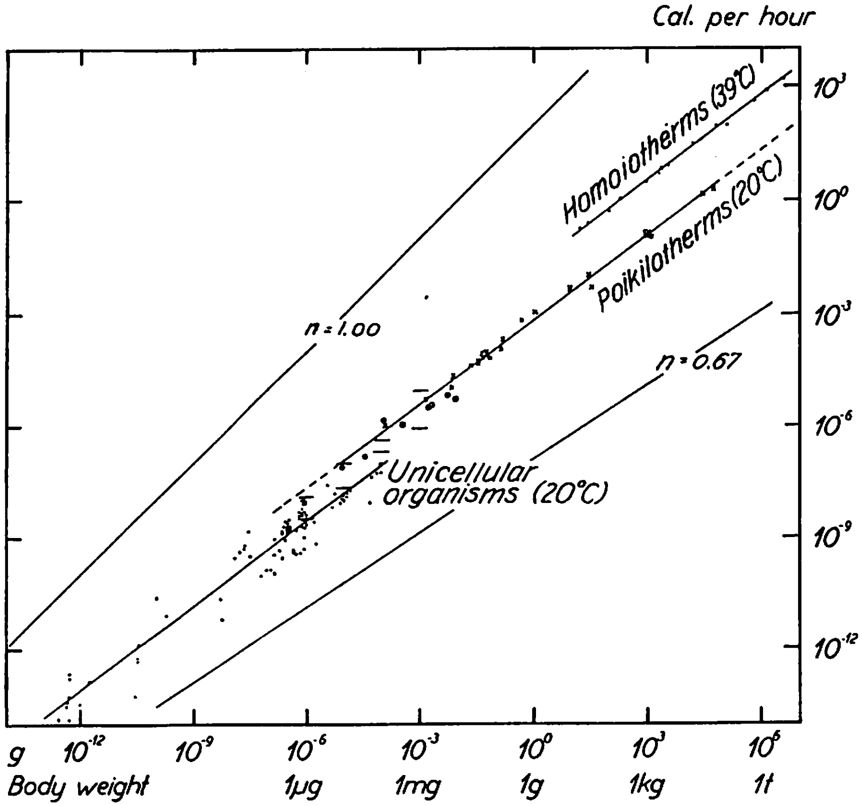

Fig. 2.

The relation of standard energy metabolism to body weight in unicellular organisms including marine eggs (points, representing data from fig. 1) and in poikilothermal and homoiotermal *Metazoa* (crosses and points, respectively, representing data from Hemmingsen, 1950, fig. 1). The three straight lines representing this relation for the three groups of organisms in question have been obtained by smoothing of the data by means of the method of the least sum of squares assuming n to be identical in the three groups. Their common inclination corresponds to $n = 0.751 \pm 0.015$. For comparison the data from Smith and Kleiber (1950, fig. 1 on p. 135) on insect eggs are plotted as circles. The short horizontal lines represent ranges as read from

The data representing homoiotherms (corrected to 39° C.) and poikilotherms (corrected to 20° C.) in fig. 1 of the earlier publication (Hemmingsen, 1950), and reproduced in fig. 2 of this paper (together with the data on unicellular organisms and eggs from fig. 1), have been found by smoothing to correspond to $n = 0.739 \pm 0.010$ and 0.738 ± 0.0095, respectively.

The values of n for unicellular organisms with (0.756 ± 0.021) or without (0.772 ± 0.020) marine eggs do not differ significantly neither from the n values calculated by Kleiber for homoiotherms nor from those calculated by me for homoiotherms and poikilotherms. There seems thus to be no reason for believing that the close correspondence of the n for unicellular organisms with the n common to homoiothermal and poikilothermal animals does not, in fact, represent actual identity. *A collective smoothing of the three groups of data (including marine eggs) on the assumption of an identical n value, that is of parallelism of the three straight lines representing them in fig. 2, gives* $n = 0.751 \pm 0.015$. The lines drawn in fig. 2 represent the result of such a collective smoothing. We shall, for brevity, in the following pages refer to these 3 lines as "the unicellular line", "the poikilotherm line" and "the homoiotherm line".

The data are not quite ideal for such a statistical collective smoothing, because the variance about the line is significantly much greater of the "unicellular data" than of the other two groups of data, and the distribution of the unicellular data (in logarithms of course) about the smoothed line is not ideally normal. The deviations from normality are, however, distributed over

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Zeuthen (1947, fig. 46 on p. 128) and here corrected to 20° C. These data include Zeuthen's measurements on marine larvae mostly at 16° C., and the vertical ranges in question reflect therefore the position and trend — though not exactly the vertical dispersion — of these measurements as later plotted by Zeuthen (1953 in fig. 1 on p. 3) without correction for temperature. Data obtained by Overgaard Nielsen (1949) on soil nematodes would also fall within them (cf. Zeuthen, 1953, pp. 4—5; fig. 2). The vertical dispersion at body weights near 1 mg in Zeuthen's plotting is much less than the corresponding vertical range in this figure, at least partly because the latter includes some data other than marine larvae.

the whole range of unicellular body weights (mainly along the lower edge of the dot diagram) and there is no biological justification for omitting them. Anyway, there is no better method available for smoothing the data.

A test of the justifiability of the temperature corrections applied to the data on unicellular organisms has been made by comparing the deviations of the points from the unicellular line in fig. 2, with and without correction for temperature, because this line is more independent of the corrections than the line in fig. 1. We shall use the term log. decade for log 10.

The temperature corrections applied have moved 29 of the points that after correction fall above the line, 6 of those that after correction fall below the line, and 2 of those that after correction fall on the line, nearer to the line than they would have been without the corrections. Of these, 3 would have been on the other side of the line without corrections. 1 of the points that after correction fall above the line and 21 of those that after correction fall below the line have been moved away from the line by the correction. The average movement of the 37 which have come nearer to the line is 0.24 log. decades; and of the 22 which got away from the line, 0.16. The remaining points were not corrected being obtained at 20° C. The sum of the movements towards the line is 8.71 log. decades; and the sum of the movements away, 3.62. There is no doubt, then, that the corrections for temperature have considerably reduced the dispersion about the line, and there is, therefore, reason to believe also, that the determination of the unicellular line and its slope has been less in error than a determination in the absence of temperature corrections would have been.

In the equation

$$\text{log. Cal per hour} = \text{log. } k + 0.751 \times \text{log. body weight in g}$$

constant log. k which represents the vertical position of each line in fig. 2 is

for homoiotherms: -1.706 ± 0.111 (+ 35 % − 25 %)
for poikilotherms: -3.161 ± 0.068 (+ 17 % − 15 %)
for unicellular organisms: -4.074 ± 0.110 (+ 35 % − 25 %).

The vertical differences between the two first (3.161 − 1.706) is 1.455 ± 0.130 logarithmic decades, corresponding to a 28.6 (± 8—10) times difference between the energy metabolism of homoiothermal and poikilothermal animals of equal body weights. The corresponding difference between poikilotherms and unicellular organisms is 4.074 − 3.161 = 0.913 ± 0.130 corresponding to a 8.1 $(^{+3}_{-2})$ times difference.

There is no reason to suspect that the lower position of the unicellular line relative to the poikilotherm line should be due to a lower content of solids of the unicellular organisms. The nitrogen content is expressly known for bacteria, yeast (see HEMMINGSEN, 1950, pp. 13, 16 and 18), and the marine *Arbacia* eggs (KROGH, 1916, p. 145; BALLENTINE, 1940 a) to be about 2—3 % as in presumably all the metazoans represented in fig. 2; and the dry matter of a ciliate (ORMSBEE, 1942) and an amoeba (REICH, 1948) is known to be 10 %. Doubtlessly, the same picture as in fig. 2 would be obtained if the abscissae had been in terms of body nitrogen (cf. ZEUTHEN, 1953, fig. 1).

The slopes of the 2 straight lines marked $n = 1.0$ and $n = 0.67$ in fig. 2 testify that evidently n for the unicellular organisms (as well as for homoiotherms and poikilotherms) differs considerably from 1.0 (proportionality of metabolism to body weight) and also distinctly from 0.67 (proportionality to body surface assuming constant shape). In fact all the n values obtained by mathematical smoothing, for unicellular organisms with or without marine eggs, for poikilotherms and for homoiotherms, as well as the over-all value 0.751 ± 0.015 differ significantly from both 1.00 and 0.67 at very high levels of statistical significance.

Some of the authors from whom the data on unicellular organisms were drawn, calculated n within the narrow range of body (cell) weights of their data. Thus SMITH and KLEIBER (1950) found $n = 0.66 \pm 0.11$ for the insect eggs and $n = 0.82 \pm 0.065$ for the marine eggs. The standard deviations show that none of these n values differ significantly from $n = 0.751 \pm 0.015$, the common slope for unicellular poikilothermal and homoiothermal animals; and their average, "weighted" or not, is very near to 0.75.

HEMMINGSEN (1950, pp. 22—23) from the scarcer data then treated attempted an extrapolation of $n = 1$ below weights of 1 μg at different levels for micro-plants and micro-animals. No doubt the interpretation of ZEUTHEN (1953, p. 4) that at weights below the transitional section of his diagram, i. e. below 0.1 μg, there is a very significant regression of metabolic rate with size, is correct. As quoted above ZEUTHEN (1953, p. 4) mentioned $n = 0.7$ as an ill-defined figure or $n =$ about ⅔ (p. 9). The question has been whether the slope of the regression line could not be much better defined. I believe that I have done this in the present chapter.

SCHOLANDER, CLAFF, and SVEINSSON (1952) found $n = 0.55$ (no standard deviations calculated) for the combined measurements on two species of ciliates (*Bresslaua insidiatrix* and *Paramæcium caudatum*) and one species of giant amoebae (*Chaos chaos*).

On the basis of extrapolations of the straight line corresponding to this n, down to the body weights of bacteria and other unicellular organisms, these authors (*loc. cit.*, p. 181) found that "it would appear impossible to fit the data into any single rule, such as the 'mouse to elephant' curve (BENEDICT, 1938), or even the 'beech tree to egg of silkworm' curve discussed by HEMMINGSEN (1950)". A calculation of the standard deviation of the value $n = 0.55$ after the method of the least sum of squares as employed by SMITH and KLEIBER and myself would have been required to show the limitation of these extrapolations.

At any rate, all the apparently discrepant values of n just mentioned carry no weight when the whole much wider weight range from bacteria to giant amoebae is treated collectively as in figs. 1 and 2. They are, so to speak, drowned in the other data.

As shown by the treatment of the measurements by ZEUTHEN (1947) on marine larvae included within the pairs of limiting horizontal lines in fig. 2 and by ZEUTHEN's own treatment (1953, fig. 1), the transition from the unicellular region of the diagram to the poikilotherm line situated at a higher level (0.91 log. decade), takes place over a weight range from about 0.1—1 μg to 1 mg (or 40 mg according to ZEUTHEN), where metabolism is nearly proportional to 1.0 (0.95 according to ZEUTHEN). Also soil nematodes as studied by OVERGAARD NIELSEN (1949) fall within this range with $n = 0.9$ (ZEUTHEN, 1953, fig. 2 on p. 5).

As was pointed out by ZEUTHEN (1953) there are thus three phases in the relation of poikilothermal energy metabolism to body size. With allowance for the somewhat different treatment of the relevant data by HEMMINGSEN (1950) and in the present chapter as illustrated in fig. 2, these phases are: one for unicellular organisms represented by a line parallel to a prolongation to the left of the poikilotherm line (with $n = 0.75$) but on a lower level (phase 1); one for small poikilotherms weighing 0.1 μg to 0.1—1 or 40 mg with $n =$ approximating 1.0 (phase 2); one for poikilotherms and plants above 0.1—1 or 40 mg up to trees and giant reptiles with $n = 0.75$ (phase 3).

The discrepant views of ZEUTHEN (1953) who puts the body weights at which phase 2 stops and phase 3 begins at 40 mg, and of HEMMINGSEN (1950) who puts it at 0.1—1.0 mg, may, it seems, be reconciled as follows (cf. fig. 2): Phase 2 starts (at weights about 0.1 μg) before phase 1 stops (at giant amoebae of 0.1 mg), and ends (at 40 mg) after phase 3 has started (if not at mammalian eggs of 0.0001—0.001 mg, then at least at insect eggs of 0.01 mg). The evolutionary bearing of these phases will be discussed in chapters 11—14.

It has been contended that protozoans with more than one nucleus should not be called unicellular but acellular, and the remarkably high organization of the *Infusoria* has led to the idea (see HADŽI, 1953, p. 149; 1956; DE BEER, 1954, PAX, 1954) that lower metazoans of an organization similar to that of acoelous turbellarians may have evolved through cellular differentiation of some hypothetical multinucleate infusorians. It will be seen from figs. 1—2 that as far as energy metabolism is concerned both the amoebae largely represented by the multinucleate *Chaos chaos* and the binucleate and highly organized infusorians fall into line with the groups of mononucleate organisms. But while the metabolism values of giant amoebae fall below both the extrapolated metazoic poikilotherm line and the data from marine metazoic larvae and soil nematodes, the metabolism of the infusorians might well be imagined to coincide with that of the smallest metazoans of phase 2.

There is apparently a queer tendency among some students of n not to appreciate the meaning of comparisons of n between widely differing organisms such a bacteria and mammals (BERTALANFFY, 1957 a, p. 34, ll. 20—21) or animals and plants (LEH-

MANN, 1956, p. 18). We fail to see, how it is possible to underestimate the theoretical significance of the uniform regression of metabolic rate with size common to the whole organismal world. In chapters 11—14 we shall consider this universal phenomenon in the light of evolutionary theory.

4.

ENERGY METABOLISM RELATED TO BODY WEIGHT WITHIN LIMITED WEIGHT RANGES IN POIKILOTHERMAL METAZOANS (AND PLANTS)

There is apparently a consistent discrepancy between the value of $n = 0.73$—0.75 found by HEMMINGSEN (1950 and this paper) for the standard (basal) energy metabolism of poikilothermal metazoans (and some plants) down to 0.1 or even 0.01 mg, and the values published by many authors for various poikilotherm groups within narrower ranges of weights both intra- and interspecifically. It is true that KAYSER (1950) for his own measurements on smaller amphibia and reptiles and those of BENEDICT (1932) on larger reptiles, altogether from 5 to 5.3×10^4 g, ELLENBY (1951) for the isopod *Ligia oceanica* from 0.042 to 1.027 g, WILL (1952) for another isopod, *Oniscus asellus* L., BERG (1951, 1952, 1953) and especially BERG *et al.* (1958) for *Ancylidae* (*Gastropoda*) from 2 to 40 mg, and DAVISON (1956) for a crayfish from 0.004 to 20 g, found $n = 0.73$—0.75, or nearly so. (BERG *et al*, 1958: 0.716 ± 0.034; DAVISON: 0.76). But quite a number of other values of *n*, ranging from about 0.67 (proportionality to body surface) or even less, up to 1.0 (proportionality to body weight), have been reported for the same or various other groups, with a tendency, it seems, to values near 0.80—0.85. Most authors have not calculated the standard deviations of their *n* values, but some have found a statistically significant difference from 0.73—0.75 (from 0.74: WEYMOUTH *et al.*, 1944, 0.798 intraspecifically for one species of crab and 0.826 interspecifically for various crustaceans from 0.04 g to 532 g). Now, where lies the truth?

It was suggested by the author (1950, pp. 24 and 34) that deviations from the standard *n* within narrower ranges of body weights were likely to be masked by the dispersion of the data about the standard line for greater ranges. We shall try to compare such deviations with the standard line over its entire range.

Examples of different *n* values of poikilotherms from varying ranges of animal body weights may be found in numerous papers, quoted, for instance, by ZEUTHEN (1947, pp. 107—134; 1953; and 1955, pp. 469—473); FRY, 1957 (for fishes); and BERTALANFFY (1957 a, p. 29; and 1957 b, p. 221). The straight lines representing the log. Cal.-log. body weight relation from some of these and other examples, taxonomically grouped, are shown in figs. 3—8; and in the aggregate, in fig. 9. Most of the lines were drawn by the respective authors; a few, by myself by eye-fitting. They have all come to notice in an endeavour to cover the whole poikilotherm weight range and a reasonable number of taxonomical groups; and new examples, intra- as well as interspecific, as specified under figs. 3—8, were accumulated until the diagram in fig. 9 became too crowded. But they have been chosen with no conscious bias, and none were discarded because of too deviating slope or position. If there is a bias it is towards more recent publications in preference to older. No attention could be paid to publications where the experimental temperature was not mentioned or the scatter too large for a reasonably reliable determination of the slope to be obtained. All lines were corrected to 20° C. The weight limits are given in the legends of figs. 3—8 to facilitate identification of the lines, but do not in all cases correspond to the exact limits of the data with more than reasonable approximation. For convenience round ordinate and abscissa values near the extreme data (in terms of their logarithms) were often chosen from the published figures or smoothed data to define the lines in preference to the often less convenient exact extremes.

The standard poikilotherm line from fig. 2 is also reproduced in figs. 3—9. It will be seen that all these lines, which, relative to the whole poikilotherm range of body weights, we shall term "short range lines", have inclinations which oscillate about the inclination of the standard line. Their positions are in some ani-

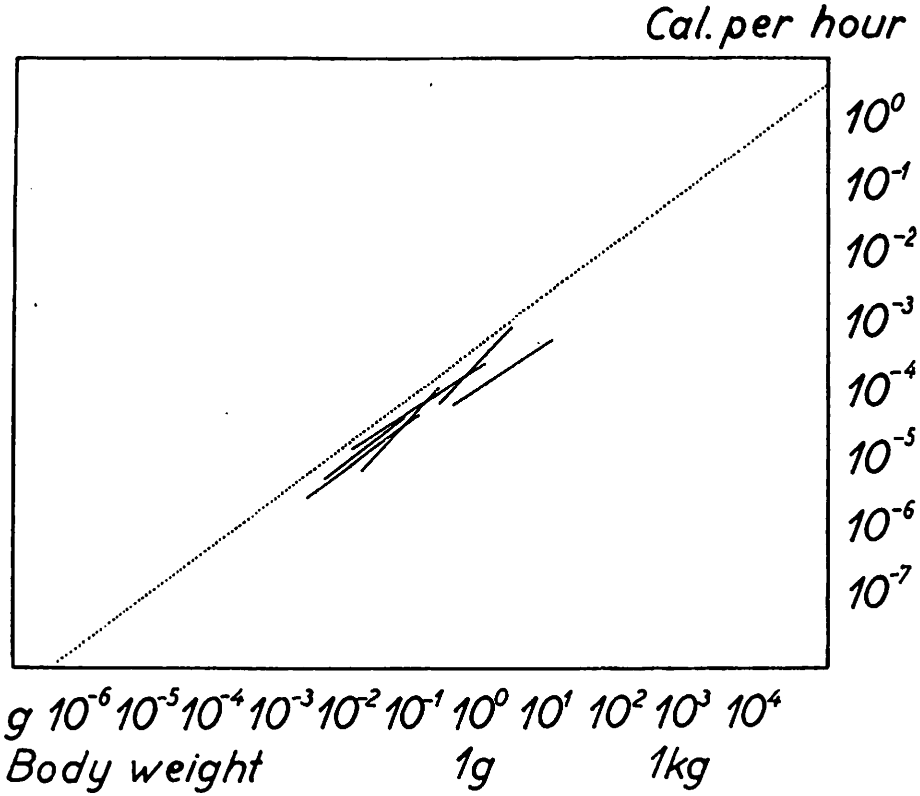

Fig. 3.

The relation of energy metabolism to body weight of some lower invertebrates (whole lines) as compared with the standard relation from fig. 2 for the entire poikilotherm range (dotted line). 20° C.
Four species of *Turbellaria* (2.2—16.9 mg), Whitney, 1942, table 1, p. 170; fig. 1, p. 171. *Planaria gonocephala* (4—65 mg), Bertalanffy and Müller, 1943, fig. 18. *Ascaris lumbricoides* (310 mg—9.7 g), Krüger, 1940, fig. 3, p. 568. *Glossiphonia complanata* and *Erpobdella octoculata (Hirudinea)* (10—100 mg and 15—200 mg), Mann, 1956, figs. 1, 2, p. 617. *Lumbricus* sp. (200 mg—2.5 g), Müller, 1943b, table 1, p. 448, (represents also fairly well the combined data of Thunberg (1905) and Lesser (1908) as from Krogh, 1916, p. 148). *Eisenia foetida (Oligochaeta)* (10—900 mg), Krüger, 1952, fig. 2, p. 4.
The ends (weight limits) of the lines are approximative.

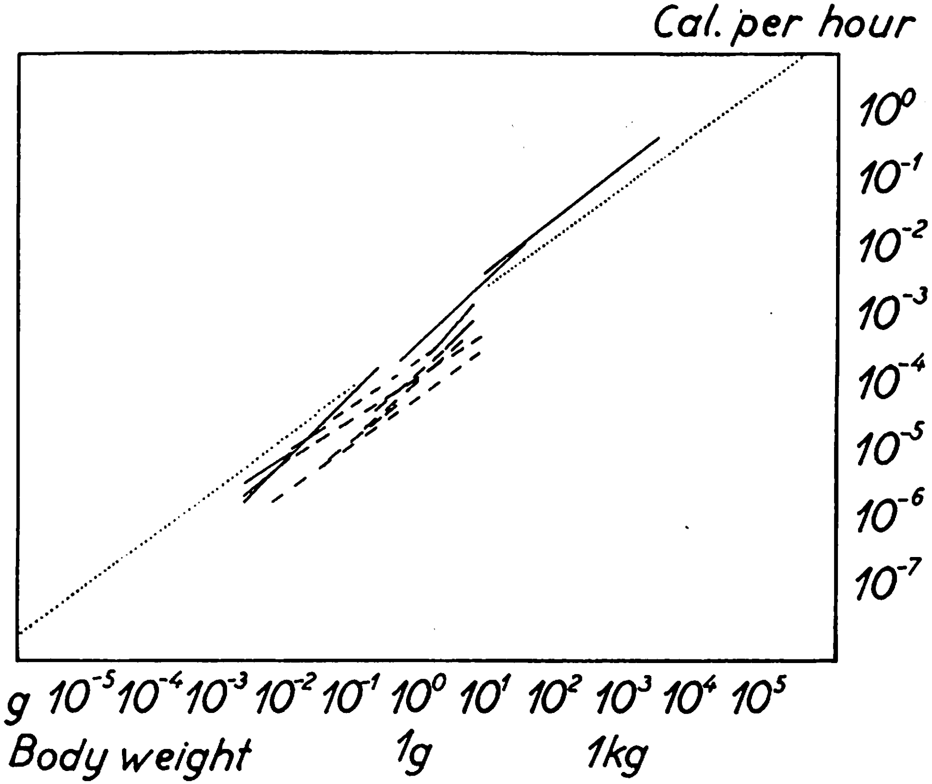

Fig. 4.

The relation of energy metabolism to body weight of some molluscs (whole lines: without shell; broken lines: with shell) compared with the standard relation from fig. 2 for the entire poikilotherm range (dotted line). 20° C.
Operculata (4.8 mg—4.6 g, with shell), Brand, Nolan and Mann, 1949, fig. 1, p. 202. *Limnaea stagnalis* (900 mg—4.6 g, without shell), Füsser and Krüger, 1951, fig. 5, p. 22. *Limnaea* (140 mg—1.70 g, with shell), Bertalanffy and Müller, 1943, fig. 12. *Planorbis corneus* (1.8—4.2 g, without shell), Füsser and Krüger, 1951, fig. 4, p. 22. *Planorbis* (32—280 mg, with shell), Bertalanffy and Müller, 1943, fig. 11. *Ancylus fluviatilis* (2—30 mg, without shell), Berg, 1952, fig. 8a, p. 242. *Ancylus fluviatilis* (10—35 mg, without shell), Berg, 1953, fig. 2, p. 338. *Acroloxus lacustris* (2—10 mg, without shell), Berg, 1952, fig. 8b, p. 244. *Helicidae* (390 mg—29 g, without shell), Liebsch, 1929, table 3, p. 185. *Cepaea vindobonensis* (120 mg—2.7 g, with shell), Bertalanffy and Müller, 1943, fig. 8. *Pulmonata* (13 mg—6.8 g, with shell), Brand, Nolan and Mann, 1949, fig. 1, p. 202. Brackish- and freshwater *Gastropoda* (2—200 mg, without shell), Berg and Ockelmann (unpubl.). *Dreissensia polymorpha* (40 mg—1 g, with shell), Ludwig and Krywienczyk, 1950, fig. 3, p. 465. Various *Cephalopoda* (7.1—2310 g), Krogh, 1916, table XLIV, p. 148.
The ends (weight limits) of the lines are approximative.

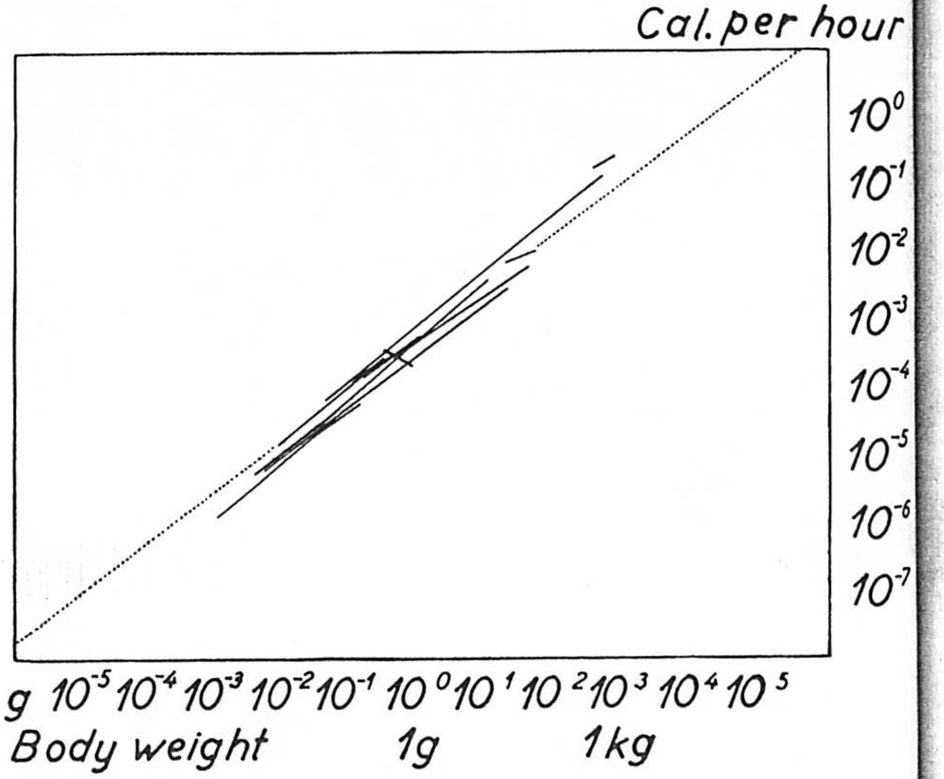

Fig. 5.

The relation of energy metabolism to body weight of some crustaceans (whole lines) as compared with the standard relation from fig. 2 for the entire poikilotherm range (dotted line). 20° C.

Various *Crustacea* (40 mg—532 g), Weymouth *et al.*, 1944, fig. 4, p. 59. Tropical *Crustacea* (30 mg—10 g), Scholander *et al.*, 1953, fig. 2, p. 72. *Asellus aquaticus* (3.6—60 mg), Will, 1952, fig. 5, p. 22. *Ligia oceanica* (150 mg—1 g), Ellenby, 1951, fig. 3, p. 496. *Porcellio scaber* (8—275 mg), Will, 1952, fig. 7, p. 23. *Armidillidium Pallasii* (30—130 mg), Müller, 1943b, table 3, p. 449. *Talitrus sylvaticus* (1—50 mg), Clark, 1955, fig. 1, p. 254. *Talorchestia* (110—240 mg), Rao and Bullock, 1954, fig. 1, p. 35. *Potamobius astacus* (17.6—50 g), Kalmus, 1930, table 9, p. 737. *Homarus vulgaris* (345—765 g), Thomas, 1954, fig. 5, p. 237. *Procambarus alleni* (4 mg—20 g), Davison, 1956, fig. 1, p. 266. *Emerita* (300—750 mg), Rao and Bullock, 1954, fig. 2. p. 36. *Pachygrapsus crassipes* (400 mg—40 g), Roberts, 1957 a, fig. 1, 234.

The ends (weight limits) of the lines are approximative.

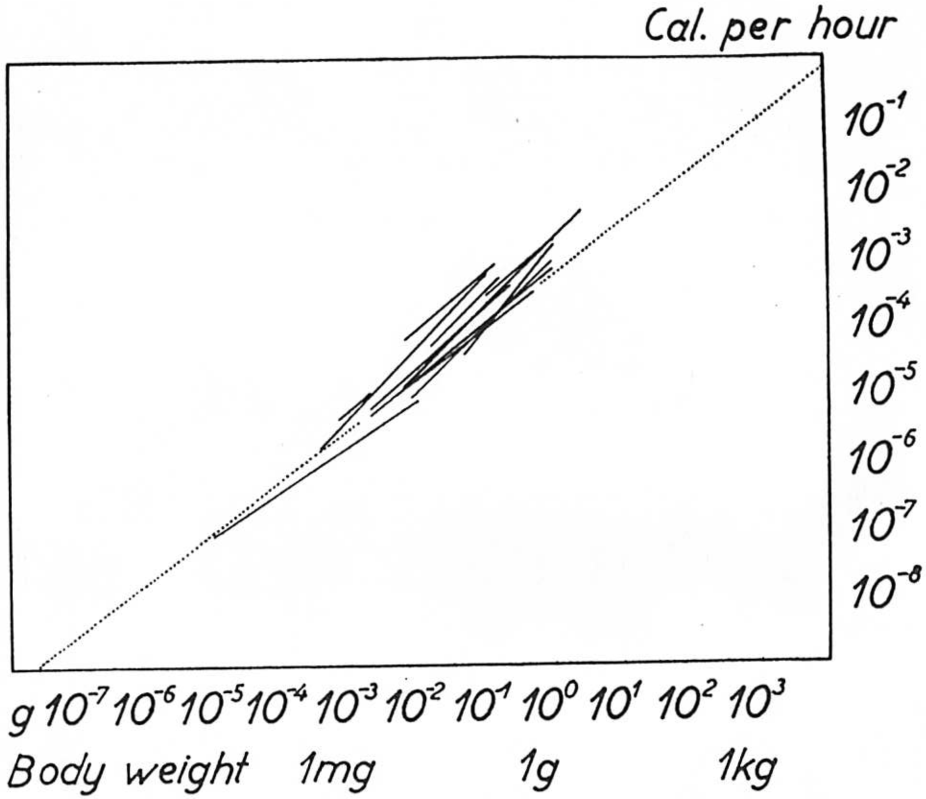

Fig. 6.

The relation of energy metabolism to body weight of some insects and a few spiders (whole lines) as compared with the standard relation from fig. 2 for the entire poikilotherm range (dotted line). 20° C. Insect eggs (10 µg—10 mg), Smith and Kleiber, 1950, fig. 1, p. 135. Arctic and tropical *Insecta* (6—130 mg), Scholander *et al.*, 1953, fig. 3, p. 73. Arctic and tropical *Insecta* (100 mg—1 g), Scholander *et al.*, 1953, fig. 4, p. 73. Arctic and tropical *Insecta* and *Arachnida* (2—500 mg), Scholander *et al.*, 1953, fig. 5, p. 74. Various *Insecta* (8—900 mg), Balke, 1957, figs. 5, 7, 8, 10, 12, 14, 15, pp. 422, 423, 425, 427. *Blatta germanica* — *Periplaneta americana* (47–912 mg), Gunn, 1935, table II, p. 187. *Dixippus morosus* (8—850 mg), Müller, 1943a, pp. 141—142. *Coleoptera* (7 mg—2.5 g), Kittel, 1941, fig. 18, p. 560. *Tenebrio molitor*, larvae (2–250 mg), Teissier, 1931, fig. 55, p. 219, Bertalanffy and Müller, 1943, fig. 4. *Diptera* (400 µg—100 mg), Kittel, 1941, fig. 9b, p. 549. *Diptera* (16—160 mg), Tetens Nielsen, 1935, fig. 19, p. 207. *Drosophila melanogaster*, prepupae (700 µg—2 mg), Ellenby, 1953, fig. 5, p. 484.

The ends (weight limits) of the lines are approximative.

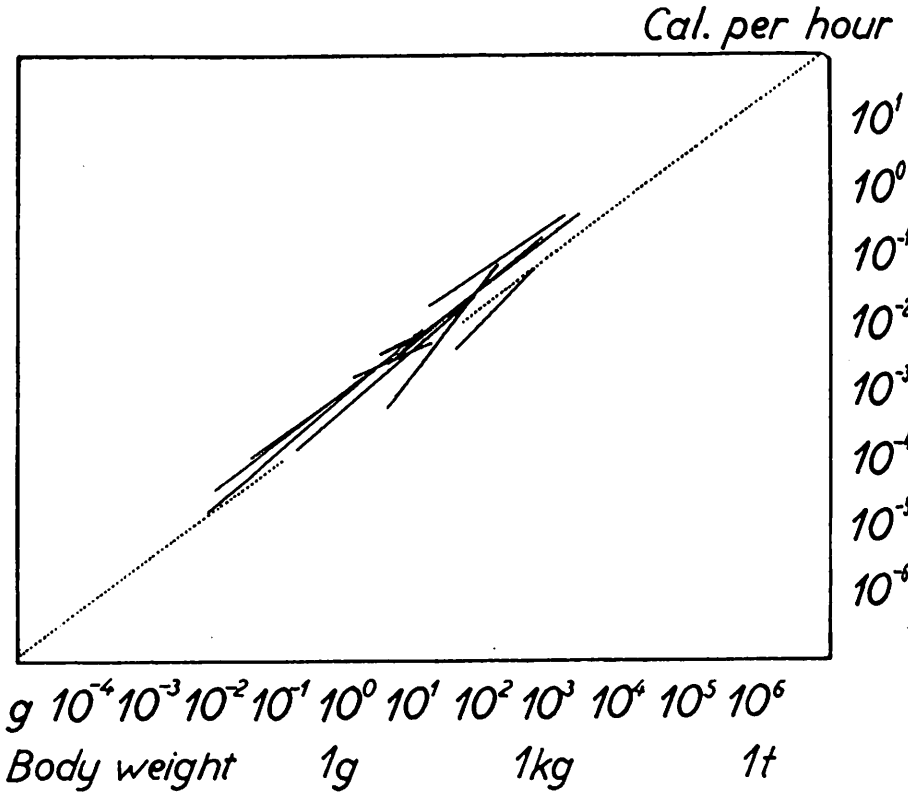

Fig. 7.

The relation of energy metabolism to body weight of some fishes (whole lines) as compared with the standard relation from fig. 2 for the entire poikilotherm range (dotted line). 20° C.

Various fishes (8 mg — 2000 g), Zeuthen, 1947, table 40, p. 116. Tropical fishes (150 mg—60 g), Scholander *et al.*, 1953, fig. 1, p. 72. Lungfish (31–450 g), extrapolation to first day of fasting, Smith, 1935, fig. 5, p. 346. *Chanos chanos* (6.9 mg—10 g), Viswanathan and Tampi, 1953, fig. 2, p. 151. *Salvelinus fontinalis* (3—600 g), Job, 1955, fig. 10, p. 13. *Cyprinus carpio* and *tinca* (12.2—1217 g), Krogh, 1916, table XLIV, p. 147. *Anguilla vulgaris* (3—135 g), Krogh, 1916, table XLIV, p. 147. *Lebistes reticulatus* (30—600 mg), Bertalanffy 1957b, fig. 3a, p. 225. *Fundulus parvipinnis* (2.4—7.6 g), Keys, 1931, fig. 13, p. 457. *Fundulus parvipinnis* (1-13.4 g), Wells, 1935b, fig. 1, p. 324.

The ends (weight limits) of the lines are approximative.

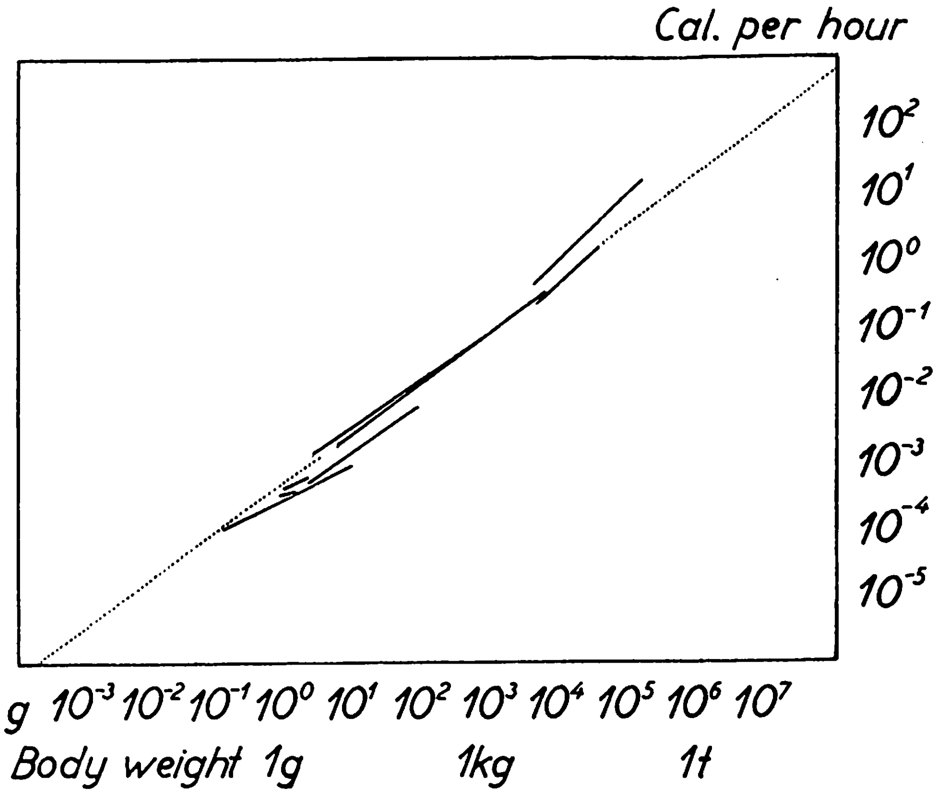

Fig. 8.

The relation of energy metabolism to body weight of some amphibians and reptiles (whole lines) as compared with the standard relation from fig 2 for the entire poikilotherm range (dotted line). 20° C.

Various amphibians and reptiles (5—5000 g), Kayser, 1950, fig. 1, p. 364. *Plethodon* and *Eurycea (Salamandridae)* (0.66—1.17 g and 0.75—1.69 g), Vernberg, 1952, fig. 1, p. 247.*Hyla* and *Pseudacris* (100 mg—8 g), Davison, 1955, fig. 1, p. 411. Three species of *Rana (*2—600 g), Davison, 1955, fig. 1, p. 411. Tortoises without shell (3300—130000 g), Benedict, 1932, pp. 378—388. Three species of *Lacerta* (1.72—71 g), Kramer, 1934, p. 611. Snakes (3700—32000 g), Benedict, 1932, pp. 158—211.

The ends (weight limits) of the lines are approximative.

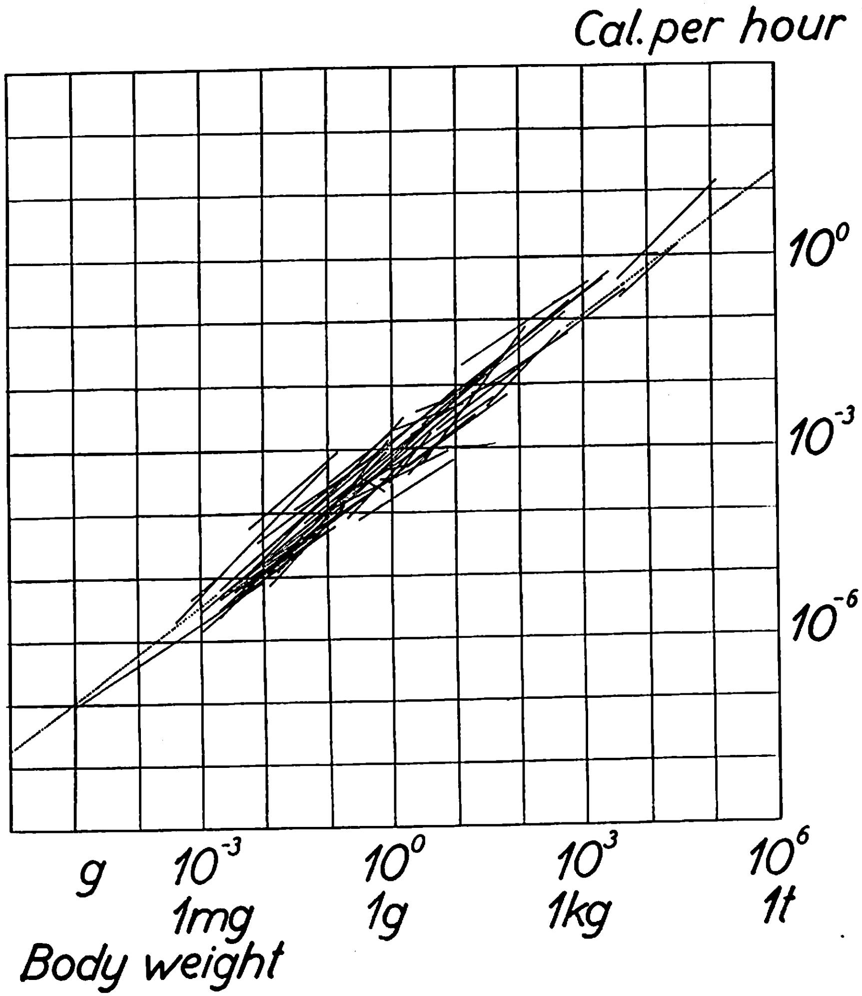

Fig. 9.

The relation of energy metabolism to body weight as found by various authors within shorter poikilotherm ranges (whole lines from figs. 3—8) as compared with the standard relation from fig. 2 for the entire poikilotherm range (dotted line). 20° C.

mal groups largely below the standard line (lower invertebrates in fig. 3, molluscs with shell in fig. 4), in others largely above (insects in fig. 6), and in still some others more or less evenly above and below (molluscs without shell in fig. 4, crustaceans in fig. 5, fishes in fig. 7, amphibians and reptiles in fig. 8). Naturally the metabolism of molluscs when referred to a body weight including the shell will be too low to be comparable with that of animals without such heavy, inert constituents.

Eight of the short range lines in fig. 9 consist actually of coinciding lines from one or related species studied at the same temperature. They will in the following considerations be treated as single lines.

In the aggregate fig. 9, where molluscs with shell are excluded, the short range lines in terms of the distances of their middles from the standard line are so evenly distributed about the standard line that the average of their (28) positive (above the standard line) and (24) negative (below the standard line) distances is only + 0.0064 log. decade; that is, they cancel practically out. As regards the inclination of the lines there is a preponderance of slopes steeper than the standard line over slopes less steep in the ratio of about 1.3.

A tendency towards the gradual decrease in *n* up to body weights between 1 g and 1 kg with a further increase in *n* up to 1 ton, postulated by Zeuthen (1947, pp. 132—33, especially fig. 48), may perhaps be traced in fig. 9, but is hardly significant statistically.

The temperature corrections applied have moved 16 of the short range lines which after the corrections, in terms of their middle points, fall above the line, and 11 of those that after correction fall below the line nearer to the standard line than they would have been without the correction. Of these 27 only 3 would have been on the other side of the line without correction. Only 11 (8 above, 3 below the line) have been moved away from the standard line by the temperature corrections. The average movement of the 27 which have come nearer to the line is 0.17 log. decade (0.18 without the 3 coming from the other side, and in which the approach is thus only a fraction of the distance moved); and the average movement of the 11 away from the line is 0.19 log. decade. The remaining short range lines have not been subject to corrections as they were obtained at 20° C. The sum of the movements towards the line is 4.7 log. decades, the sum of movements away from it, 2,1. There is no doubt, then, that the corrections for temperature have reduced the dispersion of the short range lines about the standard line.

It is important that the standard line has not been obtained on the basis of the short range lines at all, so that it is independent of any possible difference in distribution of the short range lines about the standard line near its ends. There are in fig. 9 more short range lines above than below the upper (right) part of the standard line, and more below than above its lower (left) part. Quite apart from the question whether this difference is statistically significant or not, it does not to the writer's mind affect the inherent likeliness of the standard line, as judged primarily from the rigid standard conditions under which it was obtained and secondarily from its parallelism to the homoiotherm line.

The most deviating position of a short range line *below* the standard line is that of *Ascaris* (cf. fig. 3). As one possible reason for this one might perhaps suspect natural acclimatization to the body temperature of the host. If the measurements had not been corrected from the temperature of 37° C., at which they were made, to 20° C., the line would fall very close to the standard line. Another possible explanation would be the extreme sluggishness of this worm, at least as observed by the author personally. Though its size and at a superficial glance its appearance was reminiscent of a rainworm, its movements were much like slow motion pictures of the latter. According to KRÜGER (1940, p. 548) the oxygen absorption (R. Q. = 1) of this normally anaerobe nematode is, in contrast to aerobe organisms, practically independent of movements. One way or the other its low metabolism may be associated with its anaerobiosis. But, of course, more than one factor may contribute.

An explanation of the most deviating position of a short range line *above* the standard line, that of some arctic and tropical insects (cf. fig. 6), cannot be sought in acclimatization, as the metabolism of the arctic and tropical insects in question fall at practically the same level at 20°. A relatively high muscular activity in the experiments is perhaps a reasonable explanation.

The characteristic feature about fig. 9 is that *very few short range lines fall in continuation of one another, and that slopes deviating from the slope of the standard line exist only within shorter ranges of body weights.* With increasing body weight short range lines with deviating inclinations do not continue, but other lines nearer to the standard line take over the rôle, so to speak. If we except the two lines mentioned with the most deviating positions, *the most deviating ends of short range lines above and below the standard line are seen to fall at about the same distance from the standard line over wide ranges of the latter. These facts seem to confer upon the standard line the rank of being really representative of the whole poikilotherm range.*—But how is the relation between the deviating positions and slopes of the short range lines and the position and slope of the standard line to be understood?

The standard line is based primarily on table XLIII on p. 145 in KROGH's book from 1916. In this table values of standard metabolism at 20° C. of different animals were put together. KROGH considered muscular tonus to be responsible for most metabolic differences, and it was reduced to a minimum in the measurements in question by urethane narcosis (frog, snake embryo, goldfish) or by choosing eggs and chrysalides or very quiet animals (*Culex* in winter, starved unnarcotized goldfish) as experimental objects. The animals were starved for weeks or months. It seems to be significant that at higher body weights the measurements by BENEDICT (1932) on lizards, large python and alligator fit the standard line very closely. BENEDICT likewise attached much importance to muscular relaxation in measurements on basal metabolism. It may also be significant that the measurements on beech trees without leaves, and certainly without muscular tonus, fit the line rather well at still higher weights.

Of especial significance is the fact that KROGH (*loc. cit.*, p. 146) was unaware of the fact that the values in question fitted so well the same *n* (about 0.75) as the values from homoiotherms. This is an indirect check that his establishment and selection of these values were not biased by any *a priori* expectation, and also that it cannot be true that no comparable standard metabolism values can be obtained in poikilotherms, as is stated by certain authors.

Why in later years Krogh (1941, p. 5) admitted "as a fact" that during rest sluggish forms have a lower metabolism than active ones, without mentioning the possibility of an influence of muscular tonus, is not easy to understand in view of his earlier work. The statement is sometimes made, that muscular tonus in smooth invertebrate muscles, e. g. in the adductor muscle of pelecypod shells, is unaccompanied by any increase in energy metabolism. This appears not to be correct, in as much as the metabolism of such muscles differs quantitatively rather than qualitatively from that of striated muscles (cf. Yapp, 1945, p. 153, and Scheer, 1948, p. 203).

The measurements on which the short range lines in figs. 3—9 were based, were made usually on animals at rest, and measurements obtained in periods of activity were discarded by the authors. But that does not mean that muscular tonus may not have played an important rôle. Resting metabolism is not the same as standard (basal) metabolism. There is, for instance, often a prolonged after-effect from muscular activity.

Actually some evidence exists that reduction of muscular activity or tonus may bring about a flattening of the slope, a diminution of n. The slope (n) was found to be in two series of experiments on non-narcotized normal and spayed female rats 0.943 ± 0.081 and 0.820 ± 0.086. In two similar series with somnifen narcosis n was 0.752 ± 0.047 and 0.594 ± 0.041 (Hemmingsen, 1933—34, fig. 9 and table 5). In meal-worms (*Tenebrio molitor*) n was found to be 0.90 or 0.95 in feeding active larvae and about 0.8 in starving resting larvae (Teissier, 1931, pp. 219—223). Similar results in meal-worms were obtained by Bertalanffy and Müller (1943). It may be suspected, therefore, that some if not all of the short range lines which fall above the standard line might be lowered in position and also in inclination, thus approaching the standard line, if more rigid standard conditions were observed, for instance narcosis.

Also, the deviation from 0.73—0.75 of the n value 0.64 for some birds as found by Brody (1945, p. 371) may similarly be suspected to be due to relatively higher muscular tonus in the smaller birds, as the upper part of the corresponding line, and some not included data on doves and pigeons (*loc. cit.*, pp. 370, 389 and 390), very nearly coincide with the mammalian line.

There may in some cases be other reasons for deviating slopes. The deviating steep slopes for tortoises without shell (cf. fig. 8) may be due to a relatively too high metabolism of the giant tortoises as an adaptation to the habitual burden of the shell, even when the measurements are obtained at rest. And the steep snake slope (cf. fig. 8) may be due to a relatively too low metabolism in the smaller snakes because of the prolonged starvation (days, weeks or months).

As found by Tetens Nielsen (1935) and Krogh (1941, p. 7) for insects the energy metabolism decreases with the length of the starvation period; and presumably this holds for invertebrates in general (cf. Hemmingsen, 1950, p. 14). It might be suggested, then, that comparable standard values might be best approximated shortly after the post-absorptive stage has been reached. However, as mentioned above the standard line is based on experiments in which the animals were starved for weeks or months. Most authors have employed some shorter period of starvation. But even if the same period of starvation were employed in small and large animals they may not be strictly comparable from a nutritional point of view. It can thus only be hoped that some approximation has been obtained in most cases. Differences in nutritional stage—varying from hardly any to more or less prolonged starvation—may, therefore, to some extent contribute to the variation, both in slope and position, of the short range lines under discussion.

Kayser (1950, pp. 373—374) found $n = 0.94$ for small mammals in lethargy (cf. chapter 10). However, this high value of n, interpreted by Kayser as proportionality of metabolism to body weight, is due to the fact that the body temperature (from 4.3° C. in the smallest to 10° C. in the largest species) was positively correlated with body size. When the caloric output of each of the 14 animals is corrected to 20° C., the metabolism values approach the poikilotherm standard line ($n = 0.75$; cf. fig. 12) with regard to both position and n.

In some cases slopes have even been found to vary with temperature and season (Rao and Bullock, 1954, and Clark, 1955, for two species of amphipods; Dehnel and Segal, 1956, for the American cockroach; Job, 1955, for active but not standard metabolism in the speckled trout *Salvelinus fontinalis;* Wells, 1935, for the fish *Fundulus*), or from quite unknown reasons (Ellenby, 1953, for prepupae of *Drosophila;* Kittel, 1941, for *Vanessa urtica*), or even within ontogeny (Michal, 1931, for growing, feeding meal worms; Zeuthen, 1955, with the qualifications stated in chapter 13).

It is self-evident that only those short range lines, or parts of them, that fall above the standard line can be imagined to deviate from the standard line on account of muscular activity including muscular tonus. So, since the short range lines are distributed at random about the standard line the obvious conclusion is that all sorts of varying conditions and experimental errors together with the variations inherent in all biological materials, including taxonomic differences, have produced the random variation about the independent standard line, which, in contrast to most short range lines, was obtained under especially rigid standard conditions.

Berg *et al.* (1958, fig. 15) adduce evidence that for 9 series of experiments with *Ancylus fluviatilis* n approaches the value 0.70—0.73 or thereabout with rising correlation coefficient; whereas with lower coefficients there are values both above and below this value. In other words, factors which reduced the dispersion of the data about the straight line, brought in these experiments n closer to 0.73.

It seems quite likely, but it is hardly possible to prove definitely, that the n of some of the short range lines in fig. 9 may actually be significantly different from the n of the all-over standard line, even when exactly comparable conditions were virtually established. If short range lines with such truly deviating slopes are represented in fig. 9, evidently they—just like any other short range lines in the figure—do not extend over more than a few log. weight decades with their deviating inclinations. The evolutionary significance of this will be discussed in chapter 14. In the next two chapters (5 and 6) we shall discuss some attempts that have been made to explain differences in slope of short range lines, evidently on the assumption that they are significantly different under comparable conditions.

5.

METABOLIC TYPES AND GROWTH TYPES

According to Bertalanffy (1941, and several later publications; for references see 1957 a and b) there are three metabolic types corresponding to certain growth types: 1) $n = 0.67$ in lamellibranchs (sometimes generalized into "molluscs"), isopod crustaceans (sometimes generalized into "crustaceans"), fishes and mammals (sometimes generalized into "vertebrates, especially fishes"); growth attaining a steady state. 2) $n = 1.00$ in insect larvae, *Orthoptera*, annelids, *Helicidae;* growth exponential, interrupted by metamorphosis or seasonal cycles. 3) n intermediate between 0.67 and 1.00 in *Planorbidae, Limnaea;* growth attaining a steady state.

Examples which are in agreement with this scheme as regards the correspondence of certain n values with certain animal groups are found in a table given by Bertalanffy (1957 a, table 6 on p. 29; 1957 b, table 5 on p. 221). Others might have been quoted, for instance $n = 0.952 \pm 0.018$ for *Periplaneta orientalis* by Will (1952). But the same table contains many examples of intraspecific n values which contradict the scheme. Apart from the contradictory fact that in the scheme itself $n = 1.0$ for *Helicidae* though it is a mollusc and that also the intermediate value stated for freshwater pulmonates does not agree with the generalization of $n = 0.67$ for molluscs, some of the examples which agree with the scheme have been quoted with a bias. The n value of the prosobranch snail *Lithoglyphus naticoides* Pfeiffer, for instance, does not correspond with surface proportionality, as it is 0.858 ± 0.059, and the essential fact about the n of the annelid *Eisenia foetida* in this connection should not be illustrated by merely querying its surface proportionality but by stating its definite difference from 1.0.

As evidence which is not in agreement with the scheme, beyond that found in Bertalanffy's own table, may be quoted intermediate n values for crustaceans and fishes (Scholander *et al.*, 1953: interspecifically: 0.85) and for fishes (several authors quoted by Fry, 1957, pp. 35—36 intra- or interspecifically: 0.5—0.9, mostly 0.67—0.85). Also in the vertebrate groups reptiles (Kayser, 1950, interspecifically) and mammals (Kleiber, 1932, 1947, and Brody, 1945, interspecifically) n (0.73—0.75) is definitely higher than 0.67. Berg and Ockelmann (unpublished) found even $n = 1.0$ in certain molluscs interspecifically.

The allegation that $n = 1.00$ in insect larvae and *Orthoptera* does not hold either. In starving, resting *Tenebrio* larvae Teissier (1931) found $n =$ about 0.8 (0.90—0.95 in feeding, active ones). In arctic and tropic insect larvae Scholander *et al.* (1953) found n interspecifically $= 0.80$. In cockroaches Davis and Slater (1926) found intraspecifically a definite fall in metabolic rate with rising weight; Gunn (1935), interspecifically $n = 0.75$—0.80; and Dehnel and Segal (1956), intraspecifically a doubtless regression of metabolic rate with size at a lower level in nymphs than in adults, but with n varying according to acclimatization. In grasshoppers Bodine (1921), Bodenheimer *et al.* (1929) and Butler and Innes (1936) found intraspecifically n to be lower than 1.00; as it seems, even equal to or near to 0.67. The often repeated statement that in insects there is no regression of metabolic rate with size (e. g. also Buddenbrock, 1939, p. 598; Lehmann, 1956, p. 30) is not in agreement with actual fact as a general statement (cf. also Wigglesworth, 1950, p. 414).

Data treated by Edwards (1953, figs. 26 and 27 on pp. 105—106) appear to suggest that $n = 1.00$ in *Holometabola* and 0.67 in *Hemimetabola*. But there are authorities (some of them not included in the quotations by Edwards), who have found n in some *Hemimetabola* to be very nearly 1.00 (e. g. Will, 1952, for *Periplaneta;* Müller, 1943 a, for *Dixippus;* Balke, 1957, for nymphs of various *Odonata*) or, what is of course less contradictory, 0.75—0.80 (Gunn, 1935, for cockroaches; Balke, 1957, for nymphs of *Perla*); and there are others who have found n intermediate in *Holometabola* (e. g. Balke, 1957, for larvae of *Sialis* and *Hydropsyche;* Hsueh and Tang, 1944, for *Bombyx* larvae; Kittel, 1941, for *Vanessa* (sometimes); Teissier, 1931, for *Tenebrio* larvae; Ellenby, 1953, for prepupae of *Drosophila* ($n = 0.55$ and 0.78); Scholander *et al.*, 1953, for some arctic and tropical insects and insect larvae).

Roberts (1957a, p. 239) who in agreement with Bertalanffy's scheme found $n = 0.66$ for a crab, *Pachygrapsus crassipes,* could not, however, find the characteristics of growth which Bertalanffy has assigned for the 0.67 proportionality, to hold for this species. And in silkworm larvae Hsueh and Tang (1944, p. 74) found n varying though the growth was exponential.

According to Zeuthen (1955, p. 470) n changes regularly in the course of ontogenetic development, so that there would be many more metabolic types which should be related to growth than the three suggested by Bertalanffy. Some of these changes postulated by Zeuthen are, however, not well established (see chapter 13). Bertalanffy (1957a) himself admits that the trout species studied by Job (1955) has an intermediate n and a growth curve deviating from what he had postulated as typical for fishes. He concludes himself that different metabolic and growth types may exist within a systematical group. But 9—10 lines previously he had stated that surely n is a group or species specific characteristic. One wonders what exactly, if anything, is left of the original theory. There is much to indicate that n as measured within shorter weight ranges is not a species specific characteristic. As exemplified by references in chapter 4 it may vary not only with state of nutrition and muscular tonus, but with temperature and season, or from quite unknown reasons, or even during ontogeny.

With n varying as much as the examples show, within any group with allegedly (or at least at first allegedly) uniform growth type, it seems impossible to accept Bertalanffy's generalizations unless a statistically significant correlation between n and growth type can be demonstrated on a much larger number of examples than the few ones which Bertalanffy has repeatedly published.

Furthermore, the random distribution of short range lines with their individual n values about the standard poikilotherm line with its over-all n of 0.75 in fig. 9 of this paper appears to call for a critical mentality as regards n values determined within short ranges of body weights, even when they apparently differ significantly from 0.75.

6.

METABOLIC TYPES AND TYPES OF RESPIRATORY APPARATUS

Ludwig (1956), **Sattel** (1956), **Kienle** and **Ludwig** (1956), **Kienle** (1957) and **Balke** (1957), all from **Ludwig**'s laboratory in the Zoological Institute of the University of Heidelberg, are of opinion, on the basis of own and quoted investigations, that $n = 2/3$ in purely gill-breathing invertebrates and $n = 1$ in *Lumbricus,* insects and terrestrial and some aquatic pulmonate snails. Intermediate n values are rare according to **Sattel**. They are recorded from the same laboratory by **Krywienczyk** (1952 a) for a prosobranchiate, *Lithoglyphus naticoides* Pfeiffer (0.858 ± 0.059) and (1952 b) for some fresh-water pulmonates (0.808 ± 0.056 and 0.897 ± 0.057) and by **Will** (1952) for an isopod, *Porcellio scaber* L. (0.835 ± 0.044). Such intermediate values are explained by **Ludwig** (1956) in some cases by the animals having respiratory organs of two types, e. g. skin and tracheae in insects, gills and air-breathing organs in some isopods. A confirmation of **Ludwig**'s conclusions is seen by **Balke** (1957) in the gradual rise in n with decreasing share of the tracheal gills in respiration in a series of nymphs and larvae of different genera of aquatic insects. According to **Sattel** (1956) for *Bombyx* larvae and **Balke** (1957) for nymphs of *Odonata* proportionality of tracheal surface to body weight is an important basis for the proportionality of metabolism to body weight in insects.

A similar basis for the same proportionality of metabolism to body weight in pulmonate land snails could not, however, be found by **Balke** (1957) for *Helix pomatia,* the lung surface being (according to her fig. 4) proportional to weight 0.74. (Whether this value 0.74 is actually significantly different from 1.0 is however, doubtful in view of the considerable scatter of the points, and a statistical test is lacking).

It should be remembered also that the principal part of the exchange of gases in the tracheal system of insects takes place

in the finest branches, the tracheoles, which were not measured; and, furthermore, that over wider ranges of body weights inner tracheal surface cannot increase in proportion to body weight, except at the expense of tracheal cross section area. And the latter sets a limit to body size in the *Tracheata* (**Krogh**, 1920, p. 110).

Similar doubts regarding the general validity of the opinion of the Heidelberg group must be felt as for the **Bertalanffy** theory: There are both intra- and interspecifically gill-breathing invertebrates with n significantly different from $2/3$ and insects and pulmonate snails with an n nearer to $2/3$ than to 1.0 (for quotations see preceding chapters 4—5).

The allegation by **Sattel** (1956, p. 90) that surveys, as that by **Zeuthen** (1953), which do not allow for works by German authors, easily lead astray, may be in this connection returned (by an entirely neutral), the Anglo-Saxon references in point missing in the papers of the Heidelberg group.

Finally, the same caution against short-range n values as concluded the preceding chapter, is relevant here.

7.

BODY SURFACE AND SPHERE SURFACE

Is body surface proportional to a fractional power of the body weight differing from 0.67? The question was raised in the earlier paper (**Hemmingsen**, 1950, p. 47—48) whether body surface might not be more nearly proportional to the 0.73 than to 0.67 power of the body weight when different organisms of extremely different size and organization were considered. **Ellenby** (1945, 1951, 1953) has found cases within shorter weight ranges where, although metabolism is not proportional to a $2/3$ power of the weight, it nevertheless is proportional to the surface area.

Body surface measurements are plotted in fig. 10 against body weight from many sources as specified under the figure.

The straight line drawn in fig. 10 represents the relation between the (body) surface of a sphere and its (body) weight

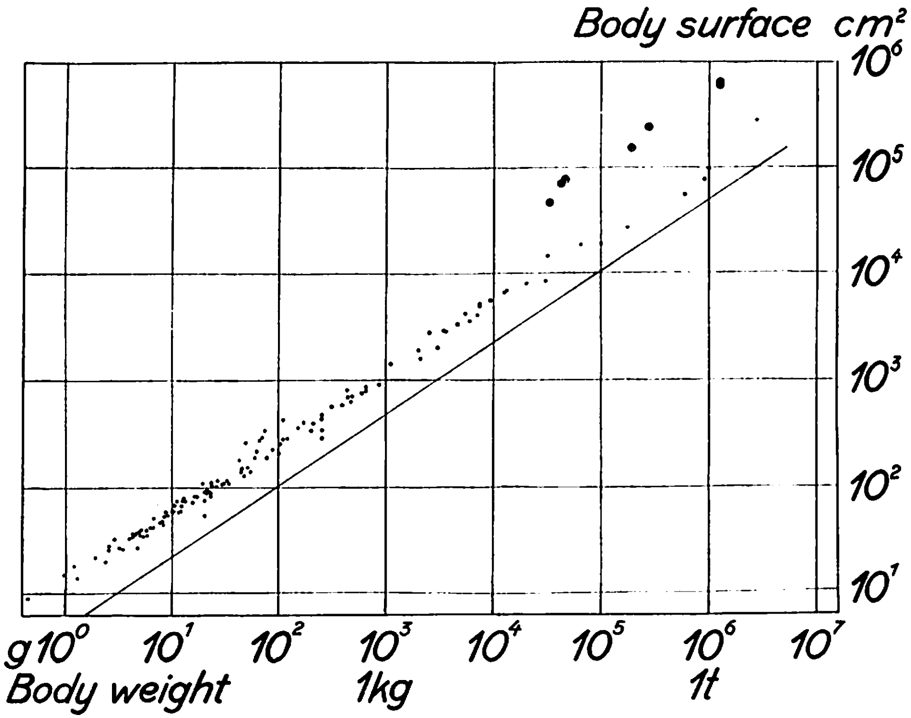

Fig. 10.

The relation of body surface to body weight in vertebrates. The points surrounded by a circle represent beech trees. The authorities of the data are in approximate order of body sizes of organisms: Fishes *(Tinca, Esox, Salmo, Pleuronectes flesus, Anguilla, Crenilabrus, Labrus: 0.44 g—2 kg),* Jan Boëtius (unpublished). Frogs (3.5—32 g), lizards (3—13 g), Fry, 1914, p. 191. *Rana esculenta* (23 and 50 g), Krogh, 1904, p. 404. Lizards *(Lacerta muralis* and *viridis, Anguis fragilis:* 5—26 g) and Ringed Snake (47—109 g), Inaba, 1911, pp. 7–8. Tench (*Tinca:* 211 g), frog (44 g), rabbit (3.6 kg), Voit, 1930, pp. 239, 244, 245. Dogs (7 and 30 kg), pigs, (3 and 100 kg), horses (175 and 900 kg), monkeys (2.5 and 5.5 kg), man (6 and 65 kg), Brody, Comfort and Matthews, 1928, pp. 8, 30, 33 and 51. Snakes (rattle-snake, small and large python, boa: 3.5—32 kg), Benedict, 1932, p. 146. Rats (20 and 250 g), cattle (20 and 600 kg), Brody, 1945, pp. 360, 361. Giant shark (2.75 t), rhinoceros (1 t), Hemmingsen, 1950, pp. 30 and 43. Beech trees without leaves and roots (30 kg—1.3 t), Møller, Nielsen and Müller, 1954, tables 2—4 on pp. 277—281.

assuming a specific gravity of 1.0. Naturally, the inclination of this line corresponds to a proportionality power of 0.67.

Of the unicellular organisms represented in fig. 1 not a few are spherical in shape (the bacterium *Sarcella, Saccharomyces,* marine eggs); and most of the others have surfaces exceeding those of spheres of equal volume by rarely more than what corresponds to 0.1 decade in the log. ordinate system (*Photobacterium phosphorescens:* 12 %, i. e. 0.05 decade, *Escherichia coli:* 34 %, i. e. 0.13 decade, the ciliates *Colpidium* and *Paramaecium:* 19—22 %, i. e. about 0.08—0.09 decade; calculated on the basis of data of Pütter, 1924, table 7 on p. 108, and Harvey, 1928, table 1). Similar figures probably hold for other ciliates. Only the flagellates represented (*Trypanosomidae, Astasia klebsii*) and certain amoebae are likely to deviate by higher figures. The surface values of the unicellular organisms represented in fig. 1 will, therefore, fall either on, or in most other cases less than 0.1 decade above, a line representing the relation between surface and volume of spheres.

It will be seen from fig. 10 that the points representing the body surfaces of the metazoic animals in question are grouped parallel to the sphere line; that is, also corresponding to a proportionality power of 0.67. An average line through the points would fall about 0.30 logarithmic decade above the sphere line, meaning that on the average the body surface is roughly 2 (antilog. 0.30) times higher in the animals under study than in spheres of equal weight or volume. In organisms of extreme shapes as the python ($10^{4.5}$ g) and the beech trees (especially marked in fig. 3) the surface is about 3 and 10 times, respectively, greater than in a sphere of equal weight and volume. These facts agree well with the values 9—11.8 for the constant k in the formula

$$\text{body surface in cm}^2 = k \cdot \text{body weight}^{0.67}$$

as tabularized by Benedict (1938, p. 175) for various birds and mammals weighing 8 g—14 kg; because this is about double the value of k for sphere surface (4.83). The value of k (13.96) found by Krüger (1940) for *Ascaris* is 2.9 times 4.83, and this corresponds well with the above mentioned figure 3 for the much larger python of similar shape.

The surface areas of spherical eggs will naturally be represented by the straight line in fig. 10. If body shape had not varied from the egg to the great body sizes in question, in other words if these latter organisms had retained spherical shape, the points representing them in figure 10 would have fallen on the straight line, assuming a specific gravity of 1.0.

The surface area of an egg with a radius of 1 mm, say, would fall where the line cuts the abscissa $10^{0.62-3}$ g (4.2 mg) and the ordinate $10^{0.10-1}$ g (0.126) cm², i. e. somewhere to the left of and below the diagram in fig. 10. If from this point a straight line is drawn to the point representing the body surface of a large python of $10^{4.5}$ g, the tangent of its inclination angle, that is the power of the body weight to which surface area is proportional, will be found to be 0.735. A straight line from the same point to the points representing the body surfaces of cattle or horse of $10^{5.8}$ g corresponds to a power of 0.69—0.70. It would of course be possible to construct lines with values between these, and also lines with values of 0.75, say, by choosing larger eggs.

A little calculation (cf. fig. 10) will show that since spherical egg surface must fall on the sphere line and corresponding adult body surface 0.3 log. decade above the sphere line, the power 0.73 (tangent of the inclination angle) for a straight line connecting egg and adult coordinates, will require a body weight difference of 4.77 log. decades; the power 0.727, 5.00 decades (100.000 times), between egg and adult anywhere within the weight range of fig. 10. With the power 0.75 the required weight difference would be 3.61 decades (4100 times). In other words the power would be nearly 0.73 or 0.75 for allometric body surface increase from an egg of *Bombyx* egg size (about 0.1 mg) to some adult of 10 g or 0.41 g respectively, or from an egg of *Acilius* egg size (about 1 mg) to some adult of 100 g or 4.1 g, respectively. For a man of 65 kg a spherical embryonic stage of 0.65 g or 16 g, respectively, would be required. The rise in surface from egg to adult would, however, hardly be represented by a straight line in fig. 10, as the rise from the sphere line to the adult surface level occurs rather early in life.

But even if such linearity were assumed for the increase in body surface when we pass the whole way from the coordinates of insect eggs in fig. 2 at the lowest end of the poikilotherm line to those of adult animals at higher weights, e. g. to the alligator through about 10 log. decades corresponding to a 10 milliard times weight difference, the body surface would rise with a power that would be lower than the power 0.75 with which the metabolism varies, though it would be above 0.67.

Elting and Brody (1926, fig. 12 on p. 18) also published a double logarithmic plot of the relation between body surface area and weights in vertebrates including all the available data which were to their knowledge recorded in literature. The logarithmic decades of their two coordinate axes were not drawn to equal lengths. In their figure the data from 25 g to 1 ton body weight would fall about a line representing a variation of the area with the ⅔ of the body weight but with a tendency for areas to vary with a somewhat lower power at weights above 10 kg, and especially within the species. The tendency towards a different intraspecific power, notably a lower power exists also in the material in fig. 10, in which not only the adult weight but also younger animals are included within some of the species. Lower powers have been found also for the surface area of beech trees (about 0.60, data from Müller, Møller and Nielsen, 1954, tables 2—4, pp. 277—81), *Aphis rumicis* and *Blattella germanica* (0.60 and 0.63, respectively, Simanton, 1933), fruit fly (*Drosophila*) prepupae (0.52—0.57, Ellenby, 1953, pp. 485—486), rat (0.60—0.66; see Hemmingsen, 1933—34, pp. 18—19, from Lee; and Brody, 1945, p. 361), and according to Brody (1945, p. 403) horse (0.64), swine (0.63), sheep (0.57) and cattle (0.56—0.60). Somewhat higher powers were found for man (0.69—0.70, according to Brody, 1945, pp. 362 and 367) and dog (0.70 according to Brody, 1945, p. 362). All such intraspecific deviations from the power 0.67, are evidently drowned when widely varying body weights from different species are considered, as in fig. 10. Formally, they bear to the over-all power the same relation as the values of *n* of short range lines in fig. 9 to the over-all value of *n* of the poikilotherm standard metabolism line.

In conclusion: Though body surface from egg to adult or from young to adults may vary with powers of the body weight which are below or above 0.67, *the body shape of young or adult vertebrate animals is sufficiently constant to ensure an over-all* *variation of the body surface with the 0.67 power of the body weight when animals of different species with widely varying body weights are considered. The energy metabolism thus definitely varies interspecifically over similar wide weight ranges with a higher power of the body weight than the body surface.*

8.

ENERGY METABOLISM AND RESPIRATORY SURFACES

To what extent may the higher levels of the energy metabolism of multicellular plants, poikilothermal and homoiothermal metazoans relative to that of unicellular organisms be related to qualitative or quantitative differences in respiratory surfaces? Subscribing to Krogh's conclusions (1941, pp. 17—20) we tacitly assume throughout this paper that diffusion alone is responsible for the gas exchange through respiratory surfaces.

As pointed out by Hemmingsen (1950, p. 23) the lower level relative to the poikilotherm line of the metabolism of the organisms with body weights less than about 0.1—1.0 mg may have something to do with a lower level of organization below this limit. A diameter of 1 mm (i. e. 0.52 mg, assuming a specific gravity of 1.0) is according to Krogh (1941, pp. 22—24) about the limit above which diffusion alone without development of internal circulation or special respiratory surfaces usually is not sufficient to ensure in spherical aquatic animals the necessary oxygen supply, when the metabolism is fairly high. Similarly, Zeuthen (1953, p. 9, second column) quotes Goddard (1945) for putting the limit at about 1 mg; and writes that the possibility of a causal connection between beginning anaerobiosis in animals above 1 mg and the reduced rate of rise in metabolism above 40 mg cannot be ignored (cf. also chapter 12).

As shown by Zeuthen (1953, pp. 3—4) and seen from fig. 2 of this paper the metabolism values of the smallest metazoans rise from the unicellular line already at body weights below 1 μg; that is, before the upper (right) end of the unicellular line, which is at about 0.1 mg. And they reach the metazoic poikilotherm line

at 40 mg (Zeuthen, *loc. cit.*). This is after the beginning (left end) of the poikilotherm line which is at 0.01 mg (insect eggs) or even perhaps 0.0001—0.001 mg (mammalian eggs). Insect eggs (though air-filled spaces in the chorion may *connect* with the surroundings) or mammalian eggs have developed no special respiratory surfaces, and according to the above mentioned limit at about 0.5—1 mg they should hardly need them, so at these weights there is no explanation of the vertical difference between the unicellular and the poikilotherm metazoic lines in terms of qualitative or quantitative surface differences.

Some increase in body size above the small sizes in question (above which sphere surface would be too small for sufficient oxygen to pass through) is possible by the mere increase in body surface resulting from any deviation from spherical shape. To what extent the metabolism of the small animals in which this type of respiration is realized, fall on or below the poikilotherm line in question might be worth an inquiry. Some perhaps belong to the marine larvae or soil nematodes which connect the unicellular and the poikilotherm lines. As mentioned in chapter 7 nematode shape corresponds to a body surface about 3 times spherical surface.

A further increase in body weight above the small sizes in question is made possible by two means: 1) increased convection (internal circulation; external ventilation) and 2) further increase of surface.

There is apparently not much *internal* convection at unicellular sizes, though there must be some, especially where there are contractile vacuoles, and in many forms (*Amoeba, Paramaecium*) food vacuoles are carried about the cell by rotation movement (cyclosis) apparently of the fluid endoplasm. But, with the exception of immobile eggs with a specific gravity nearly equaling that of the surrounding water, some *external* convection will generally aid the respiration also of organisms of unicellular size by replacing the absorbed oxygen.

In comparatively small organisms, such as aquatic eggs and embryos, and even earthworms (allegedly even up to the 2 m long eastern *Megascolecidae!*), increased circulation of blood just below the surface is sufficient to enable some increase in size beyond the 1 mg limit without development of special respiratory organs. Also in some *Amphibia* cutaneous respiration suffices or is predominant. There are *Salamandridae* without or with rudimentary lungs. Gill and lung exstirpation in axolotls and lung exstirpation in frogs is without much effect on basal metabolism. But with continued increase in size usually the respiratory surface is also increased.

Evidently the higher level of poikilotherm energy metabolism relative to unicellular metabolism may be brought about at smaller sizes by means other than surface increases in excess of body surface. But it may still be instructive to see in what quantitative relation surface increases in excess of the ordinary body surface, stand to the vertical difference between unicellular and poikilotherm lines.

As already pointed out the unicellular line in fig. 2 falls about 0.91 ± 0.13 decade (corresponding to a $8.1\,{}^{-2}_{+3}$ times difference) below the extrapolation of the poikilotherm line. If the higher level of poikilothermal metazoic (or multicellular plant) metabolism over unicellular metabolism had been made possible merely by an increased body surface over the surface of the usually more or less spherical unicellular organisms, the body surfaces of poikilothermal multicellular organisms (including plants) above 40 mg should be increased over the surface of spheres of equal volumes also by 0.91 logarithmic decade (8.1 times). We shall in the discussions to follow have to take the figure 0.91 at its face value, yet remembering that its standard deviation is rather considerable.

There may at a superficial glance appear to be a flaw in this argument, because unicellular metabolism is not proportional to body surface but to the power 0.75 of body weight. We know, that the metabolism of the more or less spherical unicellular organisms fall on the unicellular line in fig. 2; but their surfaces, on an extrapolation of the drawn line in fig. 10. We are, however, virtually asking why the metabolism of metazoans does not fall on a direct continuation of the unicellular line, and if we want to see whether differences in surfaces may be causative we must compare the difference between the line on which poikilotherm metazoic metabolism actually falls and the direct continuation of the unicellular line, with the difference between metazoic surfaces and the surfaces which the unicellular organisms would have had if they had grown to the same sizes; just as we would do it at the body weights at which both unicellular and metazoic organisms exist.

In beech trees without leaves and roots the conditions outlined may well be at least approximately fullfilled: Their metabolism values fall parallel to and relatively close to the poikilotherm line; somewhat (about 0.3 log. decade) below it when not corrected for N-content, and not much higher above it if corrected for N-content (Hemmingsen, 1950, fig. 1 on p. 11, and pp. 15—16). It may thus not fall far from 0.91 ± 0.13, or roughly one decade, above the extrapolated unicellular line, as in poikilotherms. And in fig. 10 of this paper their surfaces are seen to fall also about one log. decade above the sphere line.

The energy metabolism of sprouting peas and lupine seeds as measured in terms of carbon dioxide output, fall very close to the energy metabolism of poikilothermal animals of similar body weight, e. g. a snake embryo, or a *Bombyx chrysalis* (cf. Hemmingsen, 1950, p. 15 and fig. 2 on p. 17). But as at least the peas are more or less sphere-shaped there are no external surfaces to account for their metabolism being so much higher than corresponding to an extrapolation of unicellular metabolism. There may be some internal convection. It is also possible that the metabolism in the sprouting stage is too high to correspond to standard conditions in poikilotherms or that direct calorimetry would give, as it does with corns of wheat, considerably lower results than the employed method of measuring carbon dioxide output (cf. Hemmingsen, 1950, p. 19).

As already demonstrated at least the body surfaces of the vertebrates represented in fig. 10 are increased by only about 0.3 decade (corresponding to only a 2 times difference) above the surfaces of spheres of equal weight. This is only about ⅓ of the vertical difference between unicellular and poikilotherm lines. We shall have to assume roughly similar figures for not too deviating shapes of invertebrates, for which measurements are scarce. The above mentioned good agreement in this respect (body surface = 3 × sphere surface) between an invertebrate and a vertebrate with widely differing sizes but the same *deviating* shape (*Ascaris* and *Python*) suggests that such an assumption cannot be much in the wrong.

Now, actually the surfaces of many metazoans have become enlarged by invagination (lungs) or evaginations (gills) to form extra respiratory surfaces. So the next question would be whether the extent of such extra respiratory surfaces alone or considered in addition to the body surface proper agrees better with the vertical difference in fig. 2 of 0.91 decade between unicellular and poikilotherm lines.

For several reasons complete correspondence is in no way to be expected. The conditions for diffusion are different in water and air; the lungs and gills are usually much better adapted to the exchange of gases than the body surfaces, especially in land animals; part of the internal respiratory space is in some animals ventilatory rather than respiratory; some animals ventilate their respiratory organs, others do not; or, only when active; in some animals the gas exchange is directly between air and tissue cells (tracheates), in others blood is mediatory; the oxygen carrying power of the different respiratory pigments differ; the blood circulation differs; and what is especially important, the lungs or gills of many metazoans, even sometimes their body surfaces, are more effective transmitters of oxygen owing to their vascularization than unicellular cell surfaces (and those of beech trees); though, on the other hand, the respiratory epithelial membranes are likely to be thicker and thus less favorable to oxygen transmission than the unicellular membrane.

But let us try audaciously, nevertheless, to see just what quantitative relation the body surface + additional respiratory surfaces bear to the difference between unicellular and poikilotherm standard (basal) metabolism. It might not seem entirely out of the question theoretically that in some cases surface increase with slow blood flow through the vascularized area might serve primarily basal metabolism and increased blood flow superbasal levels.

Apart from the homoiothermal mammals, we shall consider mainly available measurements from such animal groups (tracheates, fishes, amphibians) as contributed to the establishment of the poikilotherm line in fig. 2 and among which were the data selected by **Krogh** (1916, p. 145) from own and other sources as having been made under rigid standard conditions. Thus we shall not consider many lower marine invertebrates which have a low percentage of solids and, therefore, when plotted in terms of actual body weight have a low metabolism falling below the standard poikilotherm line; though some larger forms have enlarged external (*Spongia*) and internal (*Coelenterata*) surfaces along which water currents carry oxygen to the tissues.

To my knowledge no data are available for a satisfactory estimate of the aggregate internal respiratory surfaces of tracheates. Presumably the gas exchange takes place mainly in the countless tracheoles of less than 1 μ in diameter though no doubt also to some extent in the tracheae proper and in air sacs. For the purpose of proving that diffusion alone would supply the tissues with sufficient oxygen **Krogh** (1920) measured the length and aggregate cross section area of the tracheae in the chilopod *Scutigera* and the *Cossus* larva, but was not concerned with their inner area. Approximate assessments, more reliable perhaps in *Scutigera* by reference to **Haase** (1885, fig. 11 on plate XIII) than in *Cossus* show that the inner area of the tracheae can hardly correspond to more than a fraction of the body surface. The same applies to measurements, largely relative, made by **Sattel** (1956) of the inner surface of tracheae exceeding 2 μ in diameter in small silkworms. Whether the inner aggregate area of the tracheoles when added to this (and perhaps to the body surface) may correspond more or less to the 0.91 log. decade (8.1 times) difference from the corresponding sphere area cannot be decided from available data, but the large oxygen absorption recorded for flying insects suggests a very considerable aggregate absorbing surface in the tracheoles (cf. **Krogh**, 1941, p. 122) at least in such forms.

Tracheal gill area in *Aeschna* nymphs was found by **Koch** (1936) to be 7 cm^2 corresponding to an external surface of 3 cm^2. This would mean a body + gill surface approximately a little over 6—7 times the corresponding sphere area.

Calculations on the basis of measurements by **Pütter** (1909, pp. 148—155, or 1911, p. 315) of gill areas in some species of molluscs (7), crustacea (4), and fishes (7) give body + gill surfaces 2—5 (mostly 3—5) times the corresponding sphere surfaces.

Similar figures (gill + body surface area 2—6 times corresponding sphere area) may be calculated from measurements of **Hesse** (1910) and **Kienle** (1957) on *Helix pomatia*, **Riess** (1881) on a pike, **Price** (1931) on the fish *Micropterus dolomieu*, **Schöttle** (1931) on gobiiform fishes, **Dubale** (1951) on 34 tropical species of fish, the terrestrial forms having according to the two latter authors a reduced gill surface compared with aquatic species. A similar trend was found in the gill area of 16 species of crabs (Gray, 1957), which according to an orientating survey have body + gill areas 3—7 times the corresponding sphere surfaces (correlated with habitat and metabolic activity). (On the other hand the teleost *Erythrinus unitaeniatus* which can breathe completely through either gills or lungs, has a slightly greater area of the latter (quoted from Yapp, 1945, p. 114)).

Incidentally, Price (*loc. cit.*) found gill area in cm^2 = weight in $gms^{0.785} \times 8.65$; that is, running practically parallel to energy metabolism.

More recent measurements of gill area in 31 species of fish were published by Gray (1953 and 1954). According to Gray (1953, p. 286) an average toadfish (*Opsanus tau,* fam. *Batrachoididae*) weighs 233 g and (1954, p. 222) has 197 mm^2 gill area per g; i. e. a total gill area of 458 cm^2. Its body surface (1953, fig. 2 on p. 288) is about 350 cm^2. The sum is 808 cm^2 which is 4.4 times the external surface which the fish would have had if it had been sphere-shaped.

The gill area of the active menhaden (*Brevoortia tyrannus,* fam. *Clupeidae*) is roughly 10 times that of the sluggish toadfish at the same weight; and the moderately active sheeps-head (*Archosargus probatatocephalus,* fam. *Sparidae*) and tautog (*Tautoga onitus,* fam. *Labridae*) occupy an intermediate position (Gray, 1954, p. 224). The body surface of a menhaden of 233 g would be about 300 cm^2 (1953, extrapolation of fig. 2 on p. 288); i. e. a total of 4880 cm^2, which is well 26 times the area of an equally sized sphere. The 4—26 times increase in body + gill surface over equally sized spheres is seen to include an 8.1 times increase in some moderately active fishes, corresponding as an approximate average to the 8.1 times difference in level of metabolism between the more or less spherical unicellular organisms and the poikilothermal metazoans.

The skin in fishes has little respiratory function, but in some more or less active species gill area alone will of course correspond to the said difference.

Estimations by Wikgren (1953) also correspond to about an 8 times larger surface of the gills of the lamprey than of a corresponding sphere.

In the afore-mentioned molluscs, crustaceans and fishes with body + gill areas less than 8.1 times (2—6 times) the corresponding sphere surfaces, the basal (standard) metabolism corresponding to the poikilotherm line must be supposed to exceed the hypothetical (extrapolated) unicellular metabolism not only (or perhaps as in certain amphibians without lungs not necessarily at all) by means of the excess of respiratory surface proper over sphere surface but also (or entirely) by means of the vascularization of it or of the body surface, the blood flow being further increased at superbasal levels.

Whether in the fishes in which the respiratory surfaces exceed the sphere surface by just about 8.1 times (and the skin surface can be ignored), the correspondence has any real meaning is equally problematic on account of the vascularization.

Some highly active, schooling, fast swimming, streamlined fishes cannot at all be kept under standard conditions, as they ventilate their gills only by opening their mouth during constant swimming and can be kept only in ring-shaped or huge basins. To consider the fraction of the large gill surface which exceeds sphere surface 8.1 times (it seems the entire gill surface may exceed it even 26 times) as reflecting the excess of basal (standard) over sphere metabolism would seem to be highly fictive and just as problematic as in the less active.

According to Krogh (1904 a, p. 403) the respiratory lung surfaces of a frog (*Rana esculenta*) are about 100 cm^2 (the surface of 100 cm^2 given for one frog lung by Krogh (1941, p. 62) must be a slip of the pen, for in the original paper (1904a) this is the surface of both lungs). The respiratory surface of the lungs is 0.73 times that of the skin (p. 405) which leaves the frog of 40 g with the skin surface of 137 cm^2, and accordingly a total surface of 237 cm^2. This is about 4 times the area of an equally sized sphere. Some aquatic amphibians have a smaller lung area, e. g. the unialveolar lung of *Proteus* (Krogh, 1941, fig. 34 on p. 62); some other amphibians (Krogh, 1941, fig. 36 on p. 63) and some reptiles, especially *Varanidae, Chelonia,* and *Crocodilia,* have a larger area.

As shown by Krogh (1904 a) and Dolk and Postma (1927) the respiration of the frog under basal conditions is mainly cutaneous. In other words the difference between basal metabolism of the frog and the corresponding hypothetical sphere (extrapolated unicellular) metabolism is brought about by increased internal convection, the vascularized lung surface serving respiration mainly at superbasal levels, so that apparently in the frog it would have no direct meaning to ascribe part of the metabolism difference in question to the lung surface.

However, no matter our afore-mentioned interpretative difficulties, we are left with the fact that the body + respiratory surfaces of the poikilotherms under consideration—to the extent figures have been calculated—exceed the corresponding sphere surfaces by figures (2—26) which, when they do not coincide with 8.1, fall on both sides of this figure, though mainly below, but that at any rate they are of the same order of magnitude. Figures of lower order of magnitude will of course exist in forms in which the respiratory function of the skin is supplemented by smaller extra surfaces than in the forms considered. I have not found data to decide whether or not figures of higher order of magnitude may occur, e. g. in reptiles.

For man 90 m² is suggested as a fairly probable figure for the surface of the lung in middle position (Zuntz, 1882, p. 90; Krogh, 1941, p. 63). Correspondingly, Aeby (1880, pp. 90—91) calculated 79 m² for a male and 63 m² for a female lung at rest, and 130 and 104 m², respectively, at maximal inspiration (cf. Winterstein, 1921, p. 236). At a body weight of 65 kg the body surface is 1.72 m² (Brody, 1945, p. 369). This is only about 2 % of the sum 91.72 m²; and this is about 117 times (90 is 115 times) the surface of an equally sized sphere (equivalent to a difference of 2.069 and 2.061 decades, respectively, in the logarithmic system). As can be calculated from fig. 2, by adding the vertical difference between the unicellular line and the extrapolated poikilotherm line (0.913 log. decade) to the vertical difference between the poikilotherm line and the homoiotherm line (1.455 log. decade), the homoiotherm line, or the extrapolation of it, is situated 2.368 ± 0.156 decades above the unicellular line, or the extrapolation of it (corresponding to a 233 $^{+100}_{-70}$ times difference). The standard deviation is considerable but let us discuss the figure at its face value. For one thing allowance must be made for the increase in diffusion coefficient with a rise in temperature from 20° to 39° (to which latter temperature all metabolism measurements on homoiotherms called in to produce the homoiotherm line were corrected). This rise enables a higher difference in metabolism to exist than what corresponds to a difference in the respiratory area. The diffusion constant for oxygen through animal tissues increases from 20° 1 % per degree (Krogh, 1919), that is 0.076 log. decade from 20° til 39°. This is not much. But in order to exclude this and other possible temperature influences from the comparison it would appear more correct to consider the metabolism of man corrected to 20° C.

The subtraction from the 2.368 decades of the difference between the standard metabolism of a curarized dog at 39° and 20° (illustrated appr. in fig. 11: 0.455 log. decade) will be seen to bring the difference between the standard metabolism of man and hypothetical equally sized unicellular organisms at 20° down to 1.913 decades (82 times), i. e. deviating only by a figure equal to or slightly less than the standard deviation 0.156 (about 1.43 times) from the differences (2.069 and 2.061, that is 117 and 115 times) between the assessed average 1) respiratory + body surfaces and 2) respiratory surface only, of man and the surface of a sphere of size equal to the body.

To make the point clear: The surface of the lungs of man appears to exceed the surface of a sphere of equal volume and weight (assuming a specific gravity of 1.0) about as much as his temperature-corrected standard energy metabolism exceeds the standard energy metabolism, which at the same temperature such a sphere would have if it could be calculated by extrapolation from the relation between standard energy metabolism and cell weight in the more or less spherical unicellular organisms.

Quite apart from the considerable uncertainty involved in the standard deviation this rather close correspondence may appear to be a coincidence. For it seems, again, that the respiratory surface difference in question cannot possibly represent the whole difference between hypothetical unicellular sphere metabolism and homoiotherm metabolism, since there is also an immense qualitative difference between the respiratory surface of a unicellular organism and the richly vascularized lung surface. One might, for instance, suspect the lung surface not to be as large as estimated (cf. Winterstein, 1921, p. 237) or to be adapted to an average metabolism above the basal.

It may also be argued that the area of respiratory surfaces must be expected to be adapted to maximal, not to standard (basal), metabolism. Maximal metabolism, however, is in general brought about by increased ventilation and blood flow, and this tends to keep the diffusion gradient (tension difference) as small as possible, in spite of the increased combustion. At rest the gradient is small in man, the oxygen consumption being only about $^{1}/_{10}$ of what could actually be absorbed by diffusion. Equilibrium between alveolar air and blood is established shortly after entrance of the blood into the lung capillaries (from Lundsgaard, 1953). In other words the actual resting lung surface could serve a 10 times rise in metabolism without extra blood flow. During maximal work (up to a 20 times rise over basal metabolism) the oxygen tension in the venous blood falls and the tension difference increases and perhaps the lung capillaries widen or more of them open. But clearly the area of respiratory surface necessary for resting and maximal metabolism may not differ as much as might perhaps be thought.

Still, in animals with high *average normal* muscular activity the lung or gill area *is* larger than in less active species. Lung area is larger, for instance, in the dolphin (*Delphinus*) than in man, and lower in a sloth than in a housecat of equal size (Schultze, from Winterstein, 1921, p. 237); and as shown by Gray (as quoted above) higher in active than in sluggish crabs or fishes. It is maintained (e. g. Krogh, 1941, p. 5) that the resting (also standard (basal)?) metabolism is likely to run parallel with this. It might thus fall above the standard line in especially active and below it in especially sluggish species. To what extent muscular tonus is involved under standard conditions is not always clear, however.

In the discussion above we have taken the vertical distances between the unicellular, poikilotherm and homoiotherm lines at their face values, tacitly assuming that, being the most probable values, they are likely not to be much in the wrong notwithstanding their rather large standard deviations. The standard deviations in question derive their large magnitude mainly from the large scatter of the "unicellular data". The "poikilotherm and homoiotherm data", as chosen, scatter much less; and particularly the vertical position of the homoiotherm line is likely to be virtually much better defined than its standard deviation as above given suggests. For it agrees well with the corresponding lines calculated by Kleiber (1932 and 1947), Benedict (1938), and Brody (1945). And if their data after correction to the same temperature (39° C.) were drawn in, doubtlessly a smaller standard deviation of k for the homoiotherm line and thus also for the vertical difference between the unicellular and homoiotherm lines would result.

The standard deviation 0.130 of the figure 0.913 calculated for the vertical distance between unicellular and poikilotherm lines, and corresponding to a $8.1\,^{+3}_{-2}$ times difference, means, according to usually accepted statistical concepts, that with a probability of 0.68 the true value will deviate less than the standard deviation; that is, it will be between 0.783 and 1.043, corresponding to a 6.1—11.0 times difference. With a probability of 0.95 it will be between ± two times the standard deviation, that is 0.653—1.173, corresponding to a 4.5—14.9 times difference. And with a probability of 0.997 it will be between ± three times the standard deviation, that is 0.523—1.303, corresponding to a 3.3—20.1 times difference. Thus, the conclusion that the difference between respiratory surface and corresponding sphere surface of many poikilotherms (2—26 times) is of the same order of magnitude as the 8.1 times difference between unicellular and homoiotherm lines, would not be affected even if the figure 8.1 were in error to the extent of three times its standard deviation.

The standard deviation 0.156 of the vertical difference 2.368 between unicellular and homoiotherm lines, corresponding to $233\,^{+100}_{-70}$ times, is equivalent to a probability of 0.68 that the difference is 2.212—2.524, corresponding to 163—334 times, of 0.95 that it is 2.056—2.680, corresponding to 114—479 times, and of 0.997 that it is 1.900—2.836, corresponding to 79—686 times. Supposing only the scatter of the unicellular data contribute to the standard deviation, the figures would be 181—301, 141—387, and 109—499. Should the error turn out to be as large as any of these possibilities, the arguments must of course be altered correspondingly. But even with the most extreme possibilities, which have a probability which is less than 0.003, the temperature-corrected difference (1.900—0.455 = 1.445, and 2.836—0.455 = 2.381, corresponding to 28 and 240 times) between unicellular and homoiotherm lines is of the same order of magnitude as the assessed difference between respiratory surface of man and the corresponding sphere surface (115 times).

However, the extreme unlikeliness, or rather virtual impossibility, of the extreme figures calculated is additionally obvious from the fact that the lowest of them, 1.445, equivalent to a 28 times difference, would reduce the vertical difference between the unicellular and homoiotherm lines to practically the face value of the difference between the poikilotherm and homoiotherm lines, which is 1.455. The latter figure appears to be for the reasons above stated quite well established, probably much better than its calculated standard deviation would imply, so the extreme possibility in question would be equivalent to the vertical difference between unicellular and poikilotherm lines being zero, which is absurd. If only the "unicellular scatter" is considered in calculating the standard deviation, the extreme figures 28 and 240 with a probability of less than 0.003, become 38 and 171.

We shall try to summarize this chapter as follows:

The energy metabolism of beech trees exceeds the hypothetical extrapolated unicellular metabolism of a sphere of equal weight by about as much as the tree surface exceeds the sphere surface.

In many poikilotherms the standard energy metabolism exceeds the hypothetical extrapolated (at the lowest weights the actual) unicellular metabolism (of a sphere of equal weight) more than their body + respiratory surfaces exceed the corresponding sphere surface. And in some cases no respiratory surfaces (as developed in excess of body surface) are responsible at all for the rise of poikilotherm metazoic basal metabolism over unicellular metabolism. Unknown factors as in insect eggs or increased internal convection, in particular cutaneous vascularization are in such cases responsible. In connection with vascularization the increased surface constituting gills and lungs serve in some cases rather to enable superbasal metabolism than to participate in basal metabolism. In some poikilothermal vertebrates, perhaps also in some insects, the respiratory surfaces exceed the corresponding sphere surface as much or more than corresponding to the vertical difference between unicellular and poikilotherm standard lines in fig. 2 (e. g. some highly active and moderately active fishes), but vascularization of the respiratory surfaces complicates comparison. In the tracheates internal convection (movement of body fluids) plays a minor role, the surface increase in the form of tracheae and tracheoles being mainly responsible both at basal and superbasal metabolism levels, and in reptiles where skin respiration is reduced the internal surface increase in the form of lungs must be largely responsible also for basal metabolism. It may or may not be a coincidence that *the excess of body + additional surfaces (present) appear to be in many forms of the same order of magnitude (2—26) as the excess of basal (standard) metabolism over extrapolated unicellular metabolism (8.1 $^{+3}_{-2}$ times).*

In homoiotherms, as exemplified by man, there seems to be a closer correspondence between metabolism over the unicellular level and increase of respiratory surface over the unicellular surface level. The correspondence is not easily understood.

As regards the jump in metabolism level from poikilotherms to homoiotherms, Zeuthen (1953, p. 9) states that "the real evolutionary problem" is how homoiothermal animals managed to establish so high a level of metabolism (much higher, than can be explained by the body temperature differences alone). He suggests that this high level may have been brought about by an extension similar to phase 2 in his examples of a recapitulation of the three-phased evolutionary curve during the ontogenesis of some animals (cf. chapter 13). Phase 2 which characterizes a growth phase from unicellularity to multicellularity with a rise in metabolism in proportion to body weight, is thought to have been prolonged in poikilotherms developing into homoiotherms.

This chapter may suggest that the evolution of poikilotherms into homoiotherms has been to a very great extent dependent on the increase in area of the respiratory surface, whereas the evolution of metazoic poikilotherms from unicellular organisms has not primarily been dependent on such an increase. A closer quantitative study of the rôle of the increase in respiratory lung area for the evolution of homoiothermism might be worth while.

In chapter 12 we shall discuss to what extent the rise of poikilothermal over unicellular metabolism may be explained by differences in *cellular* surfaces (theories of Zeuthen and Davison).

9.

MAXIMAL ENERGY METABOLISM

Is maximal energy metabolism in poikilothermal and homoiothermal animals proportional to the same fractional power of the body weight (0.75) as the standard (basal) metabolism? In natural selection, for instance in the struggle between preys and predators, it is primarily maximal rather than standard metabolism which has survival value; whereas on the other hand standard metabolism is likely to be a function of maximal metabolism (cf. von Döbeln, 1956, pp. 59—60).

Egg weight of different species of birds ranging in body weight from 2.8 g hummingbird to 113.4 kg ostrich, and milk production in rats, goats, cattle and man appear to vary nearly with the same fractional power (0.75) of the body weight as the standard basal metabolism (Brody, 1945, pp. 482—483). To Brody this indicates that the total metabolism parallels the basal metabolism (*loc. cit.*, p. 483).

Correspondingly, he found (*loc. cit.*, p. 910) that 1) the energy cost of standing above lying is about 9 % both in man, cattle and sheep. (Horses do not spend more energy during standing. They have an unusually powerful suspensory and check ligament and rest and sleep as well while standing as while lying), 2) the rate of oxygen consumption during average walking is double that of standing both in relatively larger and smaller animals, horses, cattle, sheep, men (p. 912). 3) The ratio of oxygen consumption of sustained hard work (carried on in a 8—10 hours day) to basal metabolism is approximately the same (about 3—8) in horse and man (pp. 915—916), 4) the maximal oxygen consumption in sustained muscular activity (maintained for shorter periods of time) is approximately 20 times the basal value (p. 917) both in horse and man (cf. Krogh, 1941, p. 7), 5) the maximal energy expenditure during maximal exertion for a few seconds (including the oxygen debt) is about 100 times the resting metabolism in horse and man (pp. 915 and 918).

These ratios are the same for 680 kg and 340 kg horse and for 68 kg man. They appear to be independent of body weight and species as such (p. 918) and would thus in fig. 2 of the present paper be represented by so many straight lines parallel with and above the homoiotherm line.

Similarly, approximate parallelism was found by Job (1955, figure reproduced by Fry, 1957, p. 35) between the straight lines representing in similar diagrams standard and active metabolism at different temperatures of a species of trout (*Salvelinus fontinalis*). And viewpoints to practically the same effect were advanced by Hill (1949, pp. 459—460) and Wilkie (1959) on general lines.

The energy metabolism of resting hummingbirds (*Calypte anna* (Lesson) and *Selasphorus sasin sasin* (Lesson)) as calculated from Pearson (1950, table 1 on p. 146) is about 4 times higher than if it fell on the homoiotherm line in fig. 2 (which line represents basal metabolism at 39° C.). This is doubtless because the nervousness and constant need for food of these tiny animals with a particularly high energy metabolism per unit body weight prevent the establishment of standard conditions. The metabolism of hovering hummingbirds was found to be 5.2—6.5 times the resting level; i. e. 21—26 times the metabolism which one must suppose they would have under real standard (basal) conditions. It is unknown whether the hovering metabolism in question was maximal metabolism. But the figures 21—26 correspond remarkably well with the above mentioned figures 20—21 for maximal oxygen consumption over basal metabolism in horses and man, and it seems that they may reasonably be assumed likewise to correspond to maximal sustained muscular activity in the hummingbirds.

Zeuthen (1942, pp. 44—46) calculated that in a pigeon flying at the speed af 70 km per hour the metabolism is about 27 times the metabolism of rest. The value of the metabolism of resting pigeons (from Krogh, 1904 b), on which Zeuthen's calculations were based, exceeds by the ratio 1.66 (0.22 in logs.) the basal value to be expected from the homoiotherm line in fig. 2. The average of basal values obtained by Riddle or Benedict (from Brody, 1945, fig. 13.7 on p. 370 and pp. 389 and 390) for doves and pigeons, actually fall close to, or rather, especially when corrected for presumable body temperature, slightly below, the homoiotherm line. The figure 27 should thus be raised to about 44 to represent the excess of the flight metabolism in point over standard (basal) metabolism. If in the pigeon the ratio of maximal sustained flight metabolism to basal metabolism should be represented by the figure 20 (cf. above: horses, man and hummingbirds), the corresponding speed would have to be 53 km per hour, as can be computed from Zeuthen (*loc. cit.*, by interpolation in table 1). This appears to be about the speed of winner pigeons in long distance flying races. Except under the influence of fair wind, a speed of 70—80 km per hour is reached only in specially trained homing pigeons, whereas the speed of the winner pigeons in ordinary short distance flying races is about 60—65 km per hour. If we take the speed, say 63 km per hour, of these winners (which, arriving first, have travelled at the highest speed) to represent the speed of maximal sustained flight, the figure will be 33.5.

From the maximum sustained power output of dogs climbing a treadmill (Dill *et al.*, 1932) or pulling a sledge (Taylor, 1957) the figures 18 and 12, respectively, can be calculated to denote the excess of the metabolism of maximum sustained work over basal metabolism, assuming the total production of energy (heat + work) to be 4 times the horse power output. It may be well to point out that both in the pigeon and the dog figures an uncertainty of the efficiency factor 4 is involved.

● Maximal sustained flight metabolism (insects and birds), including in insects other maximal values (cf. text); or maximal sustained work (mammals).

× Average flight (cruising) metabolism.

⊙ Flight metabolism, unknown whether maximal, presumably maximal sustained.

▽ Resting metabolism, in the insects corrected to 20 ° C.

+ Metabolism under curare (dog at 20° C.), or in torpidity (hummingbirds at 22°—24° C. environmental tp., here corrected to 20° C.), or at rest (bats at about 26° C. body tp., here corrected to 20° C.).

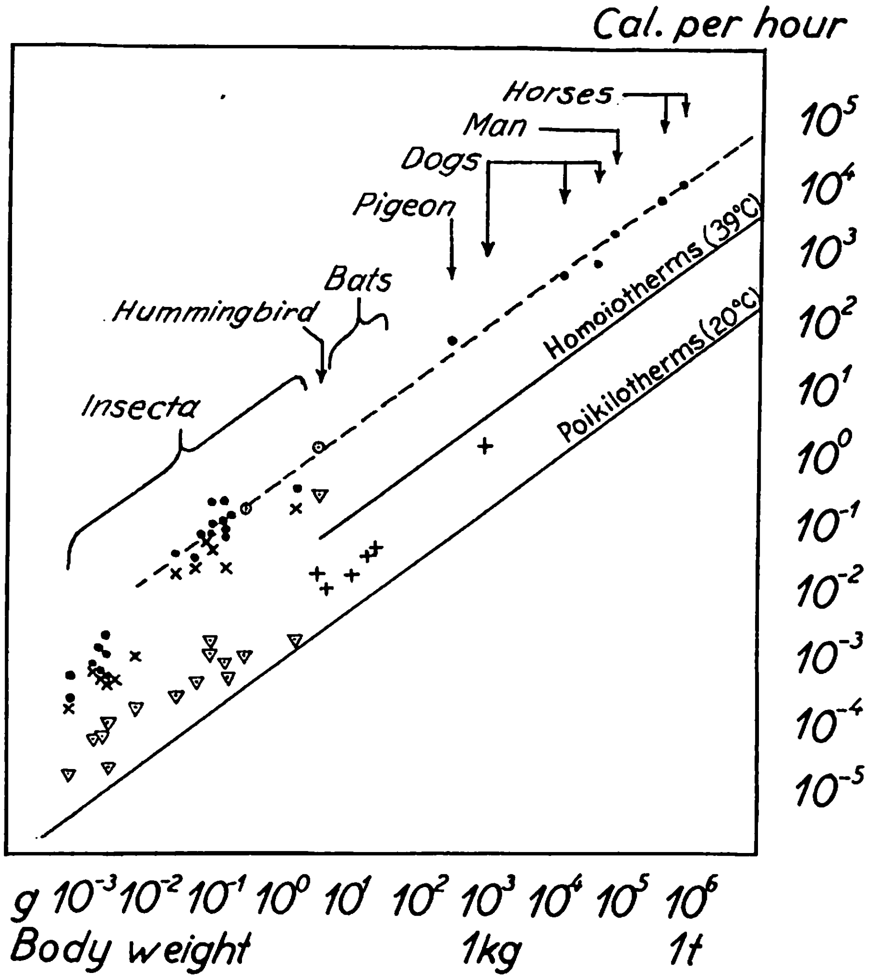

Fig. 11.

The relation between the energy metabolism during maximal sustained work or flight and the energy standard metabolism in some insects and homoiotherms. The two unbroken straight lines represent the relation of standard energy metabolism to body weight in homoiotherms at body temperatures of 39° C. and poikilotherms at 20° C. (cf. fig. 2).

On the basis of these figures for hummingbird, pigeon, dog, man and horse the relation to log. body weight of log. maximal energy metabolism during sustained flight or work for shorter periods of time, will be seen in a double logarithmic plot (fig. 11) to be well represented by a straight line situated practically parallel to and about 1.3 logarithmic decade above the homoiotherm standard energy metabolism line.

The metabolism of flight has been studied also in insects. In order of body weights the species of insects represented in fig. 11 are: species of *Drosophila, Simulium* and *Aëdes* of 0.9—8.1 mg (from Chadwick and Gilmour (1940) and Hocking (1953)), *Lucilia sericata* Mg. of 31 mg (from Davis and Fraenkel (1940)), *Tabanus septentrionalis* of 61.8 mg (from Hocking (1953)), *Apis mellifica* L. of 98.5 and 105 mg (from Jongbloed and Wiersma (1935) and Hocking (1953)), *Tabanus affinis* of 161.7 mg (from Hocking (1953)), *Lepidoptera* of the genera *Metopsilus, Saturnia* and *Vanessa* of 160—300 mg (from Krogh, 1941, pp. 1 and 129, quoting Zeuthen, and Zebe (1954)) and *Schistocerca gregaria* Forskål of 1.8 g (from Krogh and Weis-Fogh (1951) and Weis-Fogh (1952)). Hocking's data on flight metabolism (1953, p. 287; body weights on pp. 310—15 and 324) were calculated from the sugar consumption; and some of those on resting metabolism (1953, p. 288) from related species. Hocking (*loc. cit.*, p. 286) quotes some other similar data largely indirectly obtained.

The values of resting metabolism represented in fig. 11 by triangles were obtained by the respective authors at environmental temperatures of 19—30° C. (average 22° C.). A nonabsorptive stage was hardly ever ensured, and even the rest was dubious, notably in the blowflies and the bees. In the latter complete rest was obtained (according to Jongbloed and Wiersma) "when they had already flown". The metabolism ensured after flight is known in other insects (*Drosophila, Schistocerca*) to exceed the resting value before flight on account of the oxygen debt and this might well be the case in bees too. For the reasons mentioned, the resting values are seen in fig. 11 to fall above the basal (standard) values represented by the poikilotherm line even when corrected to 20° by means of "Krogh's curve" (Krogh, 1916, p. 96)—shown to be valid also for insects by Tetens Nielsen (1935, figs. 9 and 12 on p. 181 and 187)—or in the case of *Schistocerca* when corrected by means of the relation between oxygen consumption and temperature found by the respective authors on the actual species in question (Krogh and Weis-Fogh, 1951, fig. 2, p. 348). As shown previously (Hemmingsen, 1950, pp. 11—12) the standard energy metabolism at 20° C. of sluggish mosquitoes (from Ellinger, 1915) taken from a cellar in winter (and of some insect eggs, larvae and chrysalides) fall on the standard line.

At any certain body weight in fig. 11 the cross represents average cruising speed; the circle immediately above the cross, maximal cruising speed; and the next one above, if there is one, maximal speed bursts. In the case of *Apis* there is a third one on top representing maximal flight in the field. For the butterflies there are no crosses, only maximal flight values. A few data unfortunately coincide.

There are two groups of insect data: One between body weights of $10^{-1.5}$ and $10^{0.25}$ g, i. e. 31 mg and 1.8 g (blowfly to locust), and one between $10^{-3.1}$ and $10^{-2.1}$ g, i. e. 0.9 and 8.1 mg (fruit fly and mosquitoes). In the first group the maximal values are grouped about an extrapolation of the broken line which represents maximal sustained flight in birds and maximal sustained work in mammals; that is, on the average about 2.76 log. decades above the standard poikilotherm line, corresponding to an increase of on the average about 575 times over the basal metabolism represented by the line. It is characteristic, then, for this group that both the average and maximal flight metabolism exceed the basal metabolism, or even any value of resting metabolism, by a much higher figure, than maximal sustained work in the homoiotherms exceeds their basal metabolism (about 575 times over basal metabolism against 20 times). And the level of the maximal flight metabolism of these insects is apparently at the same allometric level as the metabolism of maximal sustained work or maximal flight metabolism in homoiotherms, though the poikilothermal insects have to start at a much lower body temperature and basal or resting metabolism level than the homoiotherms. In the homoiotherms during maximal sustained work the body temperature is known to rise (e. g. to 39—40° C. in man according to Hohwü Christensen (1931) and M. Nielsen (1938)); and this is the case in the larger insects too. According to **Dotterweich** (1928), **Oosthuizen** (1939), and **Krogh** and **Zeuthen** (1941) as a preliminary to flight the wing muscles of at least some insects must usually be heated by vibrations to above 30° C, and for instance in *Vanessa* a high rate of flight can be attained only when the wing muscles have been heated above 35° C. **Krogh** and **Zeuthen** suggest that a definite relationship may exist between temperature and the maximal work of which a muscle is capable. In flight the body temperature is then likely to be still somewhat higher and to approximate that of homoiotherms.

The values of maximal insect flight metabolism in fig. 11 were obtained at air temperatures varying from 15° to 30° C. In larger Hymenoptera (*Apis, Bombus, Vespa,* but not typically in *Polistes*) during flight at environmental temperatures of 15°—37° or 22°—37° C. **Sotavalta** (1954 b) found values of thoracic temperatures scattering considerably about or near those of homoiotherms and rising somewhat with environmental temperature, yet, at least in the three first mentioned *Hymenoptera,* with a pronounced tendency towards smaller average or maximal differences between thoracic and environmental temperature at the higher environmental temperatures. Under the experimental conditions adopted by **Weis-Fogh** (1956, pp. 492 and 497) the increase in thoracic temperature of *Schistocerca gregaria* during normal flight at 30° C. was 6.8° C., and any alterations in air temperature was thought to produce a similar alteration in thoracic temperature. Oddly enough normal flight and thus presumably energy metabolism was uninfluenced by alterations in air temperature between 25° and 35° C., so a check of thoracic temperature at different air temperatures would have been interesting. It is not known to what extent similar conditions exist in the other insects in question, and it seems difficult if at all justifiable to correct their maximal flight metabolism for air temperature.

The other group (small *Diptera*) has an increase of maximal or average flight metabolism (measured at air temperatures of 15—25° C., average 18° C.) over resting or basal metabolism which is much nearer in magnitude to the increase in the metabolism of maximal sustained work over standard (basal) metabolism in homoiotherms.

The lower difference between flight metabolism and resting or standard metabolism of the second group cannot be due to the somewhat (4° C.) lower average of air temperatures. For the same, or within 1½° C. the same, air temperatures as in the second group prevail in 5 of the species of the first group. The difference of 4° C. between the average air temperatures is also much too small, through a possibly ensuing equal difference in body temperature, to account for the difference in vertical distance from the standard line. It would require a Q_{10} of 32. Probably the small species of *Diptera* are not able to maintain any significant temperature differences at all. The relatively lower flight metabolism in the second group may appear to be somehow associated with differences in the power output required for flight in the small flocculent *Diptera* (fruit flies and gnats) and the heavier first group (blowfly, horse flies, bee, butterflies and locust).

Until the body temperature of flying smaller insects is better known we must leave open the question whether the correspondence between the maximal metabolism measured in the first group of larger insects in question at air temperatures of 19—30° and the extrapolated line for maximal sustained homoiothermal metabolism may be associated with the correspondence in body temperature during sustained maximal work in these insects and homoiotherms.

Krogh and **Weis-Fogh** (1951, p. 356) and **Weis-Fogh** (1952 b, p. 2) point out that *Drosophila* and *Schistocerca* have the same maximal flight metabolism per unit weight; the same, by the way, as the pigeon. A line connecting the 3 respective points in fig. 11 would incline 45 ° to the abscissa axis corresponding to $n = 1$. According to **Sotavalta** (1954 a) the corresponding n for fuel consumption per unit weight of some other flying insects is 1.4; and, in agreement with his quotation of **Maynard-Smith** (1953), for geometrically similar animals in general, 1.2. Actually, as may be seen from fig. 11 of the present paper, a straight line drawn by eye-fitting between the points of gravitation of the two groups of points for smaller and larger insects, with or without the deviating *Schistocerca,* would not be incompatible with $n = 1.2—1.3$, but the pigeon point could hardly comply.

The cost of aerial transport per unit weight of conventional small or large monoplanes and helicopters is about the same (about 400—500 Cal./kg/hour) as that of the flying blowfly and bee; that is, 4 times that of *Drosophila, Schistocerca* and the pigeon (calculated from Weis-Fogh, 1952a, table 3 on p. 345). These values would thus in terms of Cal. per hour per flying insect or plane body fall on another line inclined 45° to the abscissa axis in fig. 11 at a 0.6 log. decades higher level. (For jet transporters or fighters the figures are still 3—4 times higher). This correspondences in flight metabolism per unit weight at different weights suggests that the close coincidence of the values of flight metabolism of larger insects and even hummingbirds and pigeon with the line representing maximal metabolism for man and horses may be a mere chance coincidence. But is it really? A sort of theoretical correction to equal air speeds might perhaps throw light on the question, which, however, we must leave at that for the present.

The apparently somewhat lower level of the flight metabolism of *Schistocerca* compared with the other species of the first group may probably be correlated with the fact that in contrast to at least some of the other insects in question (incl. *Drosophila,* blowfly and bee) it utilizes fat and not carbohydrates as the predominant fuel thereby enabling the endurance necessary for long-range migrations (Weis-Fogh, 1952 a, pp. 342 ff.).

We must conclude from this chapter that *the energy metabolism required for maximal sustained work in homoiotherms and apparently insects down to the size of a blowfly is proportional to the same fractional power of the body weight as their standard (basal) metabolism,* and this maximal metabolism is at the same allometric level in homoiotherms and these insects, though their levels of standard metabolism are very different.

Maximal flight metabolism within the insects as a group is perhaps more nearly proportional to the body weight, or to a power of the body weight of about 1.2—1.3. If this latter power should apply also to birds it would be difficult to reconcile with the position of the bird points in fig. 11.

10.

ENERGY METABOLISM OF HOMOIOTHERMS AT SUBNORMAL BODY TEMPERATURES

Is energy metabolism at subnormal body temperatures in homoiotherms (torpidity, hibernation) proportional to the same fractional power of the body weight as the standard metabolism? At night when they do not take food, the temperature of the adult (but not of the young) hummingbirds normally drops to a lower level, the birds entering into a stage of torpidity. At environmental temperatures of 22—24° C. (body temperature not measured) the metabolism was found by Pearson (1950) to be about 13 times—when corrected to 20° by Krogh's curve (1916, p. 96) as in fig. 11, 17 times—lower than the "resting" level, i. e. as seen from fig. 11 not far from corresponding to the fall in standard metabolism of a curarized dog at 20° or the resting metabolism of bats at 26° (from Morrison, 1948, p. 288) as corrected to 20° C. in fig. 11: that is at 20° C. 0.4—0.8 decade of the logarithmic ordinate scale.

This confirms for the lowest homoiothermal body weights the fact found by Krogh (1916, p. 146) and Benedict (1932) that the difference in metabolism between poikilothermal and homoiothermal animals is considerably greater, in the cases mentioned about 4—10 times greater, than the difference in metabolism merely due to differences in body temperature.

Kayser (1950, pp. 373—374) measured the energy metabolism of 14 hibernating bats, insectivores and rodents in deep lethargy, belonging to 7 species varying in size from a pipistrel of 7.4 g to a marmot of 2.7 kg. The variation in energy metabolism in these animals, as long as they remained in lethargy, corresponded largely with Krogh's curve ($Q_{5^\circ-10^\circ} = 2.5-3.5$). When corrected to 20° C. (as in fig. 12) these measurements (made at 4.3°—10.1° C.) are seen to fall but 0.00—0.35 log. decade above the poikilotherm standard line (on the average 0.08 log. decade in the lower half of their weight range; 0.28, in the higher half; 0.21, for the whole range). The values thus obtained on lethargic bats fall considerably below the resting metabolism of bats corrected to the same temperature in fig. 11. This is presumably because the latter values were "taken from runs with food but in which the animal was completely inactive during the day" (MORRISON, 1948, p. 287), whereas the lethargic bats must have been really starving, hibernating animals. The values of energy metabolism of largely the same species of hibernating mammals after awakening corrected from temperatures of 22°—29.6° C. to 39° by means of a combination of KROGH's curve and table XV reproduced by KROGH (1916, p. 93) from VELTEN (1880) are seen in fig. 12 to fall some tenths of a log. decade above the homoiotherm standard line at 39°, presumably because the muscular activity was not reduced to a minimum. KROGH's curve (as long as acclimatizations have not set in) holds approximately (Q_{10} = about 2—3 from 30°—10° C.) both at homoiotherm, poikilotherm, and lethargic "homoiotherm" hibernation levels. The difference between homoiotherm and poikilotherm metabolism levels at 39° and 20° C., respectively, (vertical distance between the two respective lines in fig. 12) would require a Q_{10} = about 6; between homoiotherm and average lethargic "homoiotherm" hibernation levels, a Q_{10} = about 4.6. A similar high Q_{10} would be required to account for the more than 20 times greater oxygen consumption in a marmot which is awake at a rectal temperature of 36.5° C. than in a hibernating marmot with a rectal temperature of 10° C. as found by NAGAI (from KROGH, 1916, p. 126, or EISENTRAUT, 1956, p. 59). Apparently, therefore, the hibernating mammals in lethargy have reduced their metabolism to poikilotherm level by means other than the mere temperature reduction.

In KAYSER's experiments the respiratory quotient of lethargic and awakening hibernating animals was that of fat combustion. According to KAYSER (1940; cf. also EISENTRAUT, 1956, pp. 60—61) the abnormally low or varying respiratory quotients of lethargic or awakening hibernating animals found by earlier authors (cf. KROGH, 1916, pp. 126—130) are fallacious, and were produced by changes in the concentration of carbon dioxide of the inhaled air or by changes in temperature, e. g. during awakening.

It will be seen that in fig. 11 the values of metabolism of bats in torpidity and in fig. 12 the values of metabolism in lethargic hibernating mammals may, with allowance for the dispersion, well be compatible with parallelism to the poikilotherm standard line, so that *probably also at these levels n is about 0.75.*

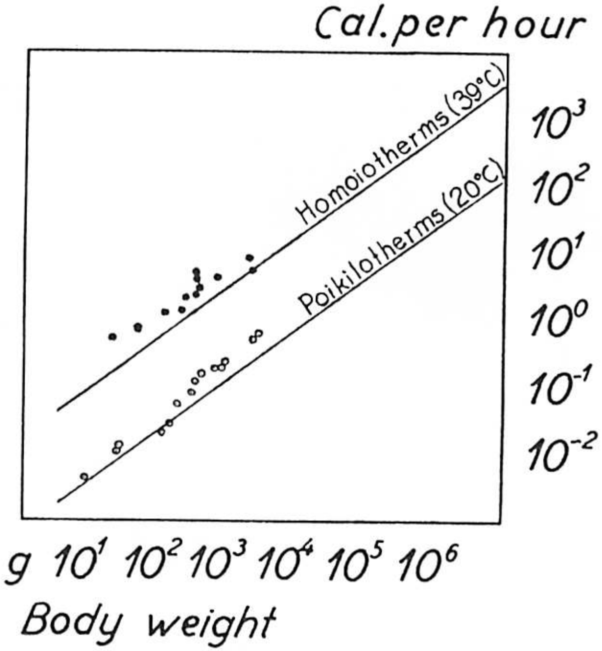

Fig. 12.

The temperature-corrected energy metabolism of hibernating mammals in lethargy (open circles) and after awakening (closed circles) from data of KAYSER (1950, pp. 369 and 373). The two straight lines represent the relation of standard energy metabolism to body weight in homoiotherms at body temperatures of 39° C. and poikilotherms at 20° C. (cf. fig. 2).

11.

THE EVOLUTION OF ENERGY METABOLISM

The idea of a *general* increase in body size in the course of evolution is old. It is sometimes called COPE's law; (for references see NEWELL, 1949, who however, omits to mention such earlier proponents of the idea as LAMARCK (1815, pp. 181—185), BRONN (1858, pp. 479—481), FÜRBRINGER (1888, pp. 991—995) and GAUDRY (1896); see also RENSCH (1954, pp. 218 ff.)). The opposite trend in special cases, e. g. in insular forms (HOOIJER, 1949), does not disprove the general trend.

Following up this idea HEMMINGSEN (1950, pp. 26—46) illustrated by calculations that the energy metabolism of plants, fishes and mammals could not have evolved in proportion to body size, because the increase in external and internal surfaces responsible for food absorption and heat dissipation could not keep pace with the increasing body weight. If metabolism increased in proportion to body weight, for instance from the size of a rat to the size of a rhinoceros, the latter would have to maintain a surface temperature of about that of boiling water to get rid of the heat produced. Trees would have been in a similar quandary if metabolism had increased in proportion to plant weight from bacteria to trees.

The idea that the evolution of energy metabolism is a function of the phyletic increase in body weight was especially elaborated by ZEUTHEN (1953) for the whole animal kingdom. Diagrams in which log. metabolism is plotted against log. body weight from the smallest unicellular organisms to the largest metazoans (such as figs. 1—2 by HEMMINGSEN, 1950; fig. 1 by ZEUTHEN, 1953; and fig. 2 of this paper) were taken to represent surveys of the phylogenetic evolution of the respiratory metabolism with increasing body sizes. ZEUTHEN's explanations of the evolution of the afore-mentioned 3 phases (cf. chapter 3) will be discussed in the following chapters.

12.

CELL SURFACE AND THE EVOLUTION OF ENERGY METABOLISM

Is energy metabolism proportional to cell surface? From his approximative determination of the slope (0.7) of the line relating unicellular metabolism to cell weight (cf. chapter 1) ZEUTHEN (1953, p. 9) concludes that among unicellular organisms (phase 1; cf. chapter 3) metabolism rose with about the same power (⅔) of the body weight as the cell surface, so he admits that cellular surfaces may in some way have been limiting for evolution in those organisms, with the result that metabolism per unit weight was very low in the larger *Protozoa*. He suggests that the *Metazoa* were the evolutionary answer to this situation: In metazoans total cell surface grows more or less in proportion to the body weight, not with the body surface, so by uniting cells and still maintaining the proportionality of metabolism to some cellular surface, the smallest metazoans kept up a body growth phase during which they suffered a very slight decrease in metabolism per unit weight (phase 2).

No documentation has been given that the cell numbers of the small metazoans in phase 2 rise gradually from unicellularity to the 40 mg limit. But evidently the theory presumes that this was how phase 2 originated; and we shall presume so in our discussion.

As shown in chapters 2—3 of this paper unicellular metabolism does not rise with the ⅔ power, but with at least very nearly the ¾ (0.75) power of the body weight. Will this necessarily vitiate ZEUTHEN's argument?

First we will read from fig. 2 that the size and metabolism of some unicellular organisms have continued to evolve e. g. into infusorians and giant amoebae in continuation of phase 1, still after some smaller cells have begun to unite to form the smallest metazoans (represented in fig. 2 by pairs of short horizontal lines: marine larvae and soil nematodes). Within a certain range of weights there will thus exist metazoans and unicellular organisms of equal body weight, the former with a higher metabolism than the latter. Larger unicellular organisms are known than the 0.1 mg amoebae representing the upper end of phase 1 in figs. 1—2, and it will be natural to expect and tentatively assume their metabolism to be represented by an extrapolation of the unicellular line.

If the metabolism of a small multicellular animal in, or at the end of, phase 2 has increased in proportion to its aggregate cell surface, it must exceed the metabolism of a unicellular organism of equal body weight, in which the metabolism has also increased proportional to cell surface, just as many times as its aggregate cell surface exceeds the surface of the unicellular organism. Let us disregard for a moment that *n* is not in unicellular organisms 0.67, corresponding to proportionality of metabolism to body or cell surface, but 0.75. We know that the metabolism of a unicellular organism of equal weight to the multicellular animal in question has in actual fact followed the unicellular line and will be so much lower than a metazoic poikilotherm of equal weight as is indicated by the vertical difference between the actual metabolism of the animal and the unicellular line. Let us assume that the multicellular organism is at the beginning of phase 3. As shown in chapter 3 the vertical difference between phase 1 and 3 is 0.91 ± 0.13 log. decade. Let us, however, further suppose to facilitate calculation, that the vertical difference in question is 1.0 log. decade. This figure falls within the standard deviation of 0.91. The aggregate cell surface of such an animal would then be 10 times the surface of a unicellular organism of equal weight. It is easy to calculate that the number of spherical or cubical cells which have an aggregate surface 10 times that of a sphere or cube of a volume equalling their aggregate volume is $10^3 = 1000$.

To calculate the number x of equally small cells into which a large cell must be divided in order to increase the total cell surface a times we have:

Surface of a cell = $k \cdot \text{vol}^{2/3}$ (for a cube $k = 6$; for a sphere, 4.83)
V_l = Volume of the large cell, V_s = Volume of one of the small cells.

$$\text{Naturally } \frac{V_l}{V_s} = x, \text{ and } V_s = \frac{V_l}{x}$$

$$x \cdot k \cdot V_s^{2/3} = x \cdot k \left(\frac{V_l}{x}\right)^{2/3} = a \cdot k \cdot V_l^{2/3}$$

$$x \cdot k \cdot V_l^{2/3} \cdot \frac{1}{x^{2/3}} = a \cdot k \cdot V_l^{2/3}$$

$$\frac{x}{\sqrt[3]{x^2}} = a$$

$$\frac{x^3}{x^2} = a^3$$

$$x = a^3$$

Since k cancels out, evidently the shape of the cells need not be spherical or cubical, if only k is the same in the large and in the small cells.

Cell numbers appear to be best known in the small animals with cell constancy, especially the rotifers. A rotifer of 0.1 mg, i. e. of the size of a large unicellular organism, has just about 1000 cells (*Hydatina senta* has 959 cells, for instance, according to MARTINI, 1912; see also WESENBERG-LUND, 1937, pp. 205 and 208, or 1939, p. 200). With a metabolism like that of a marine larva at the upper end of phase 2 such a rotifer might thus apparently fit ZEUTHEN's assumption with some approximation.

However, though phase 3 has already started at 0.1 mg or less, 0.1 mg is not at the upper end of phase 2, where higher cell numbers may be likely to occur. We shall see that this is borne out by another argument.

It is easy to prove graphically that the vertical distance of 1 log. decade between the unicellular and the poikilotherm lines (both lines with $n = 0.75$) requires for a line connecting them to have $n = 1$ a range of 4 log. decades; and for it to have $n = 0.95$, nearly 5 decades. This corresponds neatly to the actual weight range of 4—5 decades of phase 2 (0.1 μg—40 mg). A vertical distance of 0.91 (± 0.13) log. decades, as numerically found requires correspondingly for $n = 1$, three; and for $n = 0.95$, nearly four decades; that is, a somewhat less satisfactory correspondence.

However, the 1000 cells found above to be required at poikilotherm level for a difference in cell surface between unicellular and poikilotherm level at equal body weights to correspond to 1.0 log. decade, will require phase 2 to start 3 log. decades earlier at the body weight corresponding to the weight of one of the 1000 cells.

But could not the vertical distance be virtually greater than 1.0 so as to really require more than 1000 cells and thus be compatible with an earlier start of phase 3? Well, for the start of phase 2 to occur five decades earlier, 10^5 cells would have to be the cell number; and since 10^5 cells have an aggregate surface which exceeds that of one cell of equal volume 46.5 times ($\sqrt[3]{10^5} = 46.5$) the vertical distance between the two lines should be log. 46.5 = 1.67. For a 4 decades earlier start the figure is 1.33 (log. $\sqrt[3]{10^4}$). But the differences between both these figures and 0.91 ± 0.13 are statistically highly significant. So we are stuck.

If the over-all n had been 0.67, $n = 1$ for phase 2 would require it to start 3 decades earlier, as also then required by the vertical distance of 1.0 log. decade between the lines. Substitution of $n = 0.95$ for $n = 1$, and/or 0.91 for 1.0 as the vertical distance, would require 2.7—3.6 decades. These possibilities correspond to the actual 4—5 decades no more than $n = 0.67$ to actual fact.

In other words: *The difference between the aggregate cell surface of a metazoic animal and the surface of a unicellular organism of the same body weight cannot possibly correspond both to log. 0.91 ± 0.15 and at the same time to a range of 4 or 5 log. decades of phase 2.* And phase 2 *does* require 4—5 decades when $n = 0.95$—1.00, as also actually found.

The necessary 4—5 decades with unicellularity at their beginning incur (cf. the rotifer example) that at the end of phase 2 cell numbers are likely to be nearer to 10^4—10^5 than to 10^3; that is, the aggregate cell surface of a metazoic animal at that point should exceed that of a unicellular organism of the same body weight more than its metabolism exceeds that of the unicellular organism. Evidently, proportionality of metabolism to cell surface through phase 2 receives no support from this.

Now, in testing ZEUTHEN's proposition we have been arguing against our own better conscience, for we know from chapter 2 that cell metabolism, at least in unicellular organisms, is not proportional to cell surface, that is to cell weight$^{0.67}$, but to cell weight$^{0.75}$. The difference between 0.67 and 0.75, which we disregarded above, is not negligible. It corresponds, for instance, for the abscissa range of 5 log. decades, at the highest end of the range to a vertical difference of 0.4 log. decades, that is to a 2.5 times higher ordinate value for $n = 0.75$ than for $n = 0.67$.

Could the reason for the discrepancies be that cell surface is proportional to the 0.75 power rather than to the 0.67 power of cell weight?

If we imagine that some spherical bacterium at the lower end of the unicellular weight range of 8 log. decades grows in size throughout this range, its surface will increase in proportion to the 0.67 power of the cell weight if spherical shape is retained. If its surface were to increase in proportion to the 0.75 power of cell weight it would at the upper end of the range exceed spherical surface at the same weight corresponding to a log. difference of 6.000 − 5.333 = 0.667 ($0.75 = \frac{6}{8}$; $0.67 = \frac{5.333}{8}$) of which the antilog. is 4.642. But there is no evidence that the cell surface of infusorians or amoebae is 4.6 times that of a sphere of equal volume. Unicellular (approximately spherical) surface is evidently much closer to proportionality with the 0.67 power than with the 0.75 power (cf. chapter 7).

Now, it need not necessarily be simply cell surface alone, but as well "some cellular surface" such as surfaces of nucleus, of septa in mitochondria (as site of enzymes responsible for oxydation), of the membranes in the Golgi apparatus, of the membranes in the ground substance of the cytoplasma, or of other cellular elements which may be responsible for the surface-determined metabolism of the unicellular organisms and for the maintenance of "the proportionality to some cellular surface" during phase 2. If so, such cellular surfaces should be proportional to the 0.75 power of the body weight, that is, they should become relatively more developed with increasing cell sizes. ZEUTHEN's argument might be altered correspondingly and perhaps still explain phase 2 as outlined because total cellular surfaces would in the *Metazoa* still be "more or less proportional to body weight".

If, then, instead of considering the actual cell surface which is proportional to the ⅔ power of volume or weight, we substitute the ¾ power for the ⅔ power and thus assume the metabolically active surfaces in the cells to be proportional to the same power of the body weight as unicellular metabolism, the discrepancies almost disappear, or are at least considerably reduced.

Substituting ¾ for ⅔ in the above equations we obtain:

$$\frac{x}{\sqrt[4]{x^3}} = a$$

$$\frac{x^4}{x^3} = a^4$$

$$x = a^4$$

Thus, on this assumption 10^4 cells instead of 10^3 possess an active aggregate surface which exceeds that of a unicellular organism of equal weight 10 times; phase 2 should start 4 decades earlier at the weight of one of the 10^4 cells, and 4 decades is still what is required for a line with $n = 1$ to connect the unicellular and poikilotherm lines. The difference from the 4—5 decades over which phase 2 is supposed actually to extend may not be crucial in view of the uncertainty of the determination of the n of phase 2 and the position of its ends. As a necessary check of the theory it would be of considerable interest to know whether cell numbers of the small metazoans actually rise from about unicellularity at the lower end of phase 2, to about 10^4 at the transition to phase 3.

The above mentioned rotifer cell numbers of about 10^3 cells at 0.1 mg body weight might be compatible with 10^4 at 1 mg in other species of small metazoans and thus not be incompatible with a transition to phase 3 at about 1 mg.

While the theory may thus agree with the actual organism sizes, if cell surfaces are assumed to be proportional to the 0.75 power of the cell weight, it does not explain why phase 2 evolved before phase 1 stopped, and especially not why it stopped where it now meets phase 3.

If protistans began to unite to form small metazoans already at the body weights where phase 2 starts (below 1 μg) this could not be because sphere surface became too small for sufficient oxygen to pass through; for all animals weighing less than 1 mg can be sufficiently supplied with oxygen throughout (cf. chapter 8, and ZEUTHEN, 1953, p. 9, col. 1). According to ZEUTHEN (1953, p. 9, col. 2) the possibility cannot be entirely ignored that this critical limit at 1 mg may explain why phase 2 changes into phase 3. It seems plain, however, that the same explanation cannot possibly be applied both to the beginning and the end of phase 2. It seems awkward to the theory that the low protozoan metabolism per unit weight, to which according to ZEUTHEN's idea the *Metazoa* were the evolutionary answer, is actually lowered still further throughout phase 1 up to 10^4 times the cell sizes at which phase 2 starts. The low metabolism per cell or unit weight as such, is remedied by the supposed evolutionary answer only in as much as it is prevented from falling, for it is actually maintained (if 0.95 is the correct n, even slightly lowered) throughout phase 2; but then again it is even lowered still further continually throughout phase 3.

Let us try a different viewpoint: When spherical unicellular organisms or eggs have reached the size (presumably about 0.5—1 mg) at which cell surface has become too small relative to volume for sufficient oxygen to pass through, any deviations from spherical shape resulting in an increase in body surface and any increase of the internal convection at the surface, e. g. through vascularization or mere circulation of body fluids at the surface will make it possible for a metazoic animal *of the same size* to have a considerably larger metabolism. This may be the main reason why metabolism was raised to the level of the present poikilotherm line, through phase 2 or otherwise (cellular differentiation of multinuclear protistans?). Also in the further evolution of phase 3, as shown in chapter 8, the difference from extrapolated unicellular metabolism may be assumed to have been maintained by such qualitative and quantitative differences in respiratory surfaces.

Obviously the idea of ZEUTHEN that phase 2 arose by addition of cells, is not compatible with the idea of HADŽI (cf. chapter 3) that the metazoans evolved through cellularization of some imagined multinucleate infusorians into organisms much like acoelous turbellarians and not through union of single cells.

It is perhaps relevant in this connection that there is actually a tendency for just the above mentioned small-sized groups with cell constancy to consist of syncytia rather than of well defined cells; and also that the giant amoeba *Chaos chaos* is multinucleate. If metabolism is proportional to cell surface, syncytial metazoans and multinuclear protistans of equal weight should have the same energy metabolism.

We shall now leave the small metazoans in which $n = 0.95$—1.00 and see whether the concept of proportionality of metabolism to cell surface can be applied to the larger metazoans in which $n = 0.75$.

Not only rotifers and some other smaller poikilotherms e. g. dicyemides, tardigrades, trematodes, nematodes, acanthocephales, appendicularians and larvae of ascidians (MARTINI, 1924; LEVI, 1925, pp. 144—45), but also higher invertebrates, such as for instance certain insect larvae (TRAGER, 1935; ABERCROMBIE, 1936) have absolute or partial cell constancy and accordingly grow only or in part, notably ganglion and muscle cells, by enlargement of the cells, instead of by cell division; e. g. in *Oxyuris* linearly from 30 μ up to 6 mm (from WESENBERG-LUND, 1937, p. 277, or 1939, p. 267), i. e. 200 times.

Even in vertebrates a certain degree of cell constancy obtains in permanent tissues such as the nervous and especially the skeletal and heart muscular system, whereas the cell sizes are much less dependent on body size in less permanent tissues such as epithelial glandular and connective tissues (cf. THOMPSON, 1917, p. 37, and RENSCH, 1954, pp. 163—165 and 225—226). Thus, the proportions between the cross section area of certain muscle fibres in a whale and a mouse have been found to be 100 : 0.9; in bull and rat 10 : 1, in man and rat 15 : 1 (from LEVI, 1925, pp. 192—193).

If metabolism per unit cell surface were maintained not only in the smallest metazoans between 0.1 μg and 40 mg, as suggested by ZEUTHEN, but throughout the metazoic poikilotherm range, some degree of cell constancy would be required to explain that n is lower than 1.0. Absolute cell constancy would of course lead to $n = 0.67$.

Applying this argument to limited weight ranges DAVISON (1955 and 1956) has adduced evidence to explain the n values found by him in frogs (0.67) and crayfish (0.76) by absolute and partial constancy, respectively, of the number of muscle fibres. Even within limited groups as these it is an oversimplification to regard the organism as a bundle of muscle fibres, as admitted by DAVISON himself (1955, p. 418). And the caution against attaching much importance to short range n values should perhaps be repeated here (cf. chapter 4, esp. fig. 9), the more so as no standard deviation of the n values in question were published by DAVISON, so that they may not even differ significantly.

Already RUBNER (1913, pp. 253—254) made calculations to show that cell size has nothing to do with metabolism of mammals. If we would try with our present knowledge of the over-all $n = 0.75$ to expand the assumption of proportionality of metabolism to cell surface to the whole organismal range, we meet serious difficulties. For one thing, unicellular cell surface proper should then be proportional to weight$^{0.75}$; and as shown above, it is not.

As shown above the number of cells required to unite for a rise in cell surface to be obtained corresponding to the rise in metabolism of about 1 log. decade (10 times) from unicellular level to metazoic poikilothermal level is about 1000. With proportionality of metabolism to cell surface, this cell number would have to be kept constant all through the poikilotherm range if n were 0.67. With $n = 0.75$, as actually found, an increase from 1000 to only 100000 correspondingly larger cells would be required through the weight range of about 8 log. decades up to about the size of an alligator.

As shown above the difference in ordinates at the upper end of a weight range of 8 log. decades between proportionality to the 0.75 and the 0.67 power of the body weight amounts to 4.642 times. With $n = 0.67$ there would still be 1000, though correspondingly larger, cells at the upper end of the 8 log. decades. To increase the surface of each of these large cells 4.642 times, each must be divided into 4.642^3 correspondingly smaller cells; and $4.642^3 = 100$.

If in these considerations we substitute for actual cell surface as proportional to weight$^{2/3}$ the above discussed hypothetical cell surfaces proportional to weight$^{3/4}$, we find that an increase from 10^4 cells to $10^4 \times 4.642^4 = 4.642$ million (4.642×10^6) cells would be required through the weight range in question. Calculations show that they would at the largest body size measure 2.5—3 mm linearly.

The aggregate cell number of adult man who weighs about the same as an alligator is allegedly (e. g. Broman, 1925; Hesse, 1935; Pilkington, 1953; Boas and Thomsen, 1953, p. 38; cf. Rubner, 1913, p. 251) of the order 10^{14-15} (created through approximately 47—50 cell divisions). A rough estimate gives with the well-known 5 millions red blood corpuscles per mm^3 of 5 l human blood 25×10^{12} cells. Assuming average cell size for the red blood corpuscles of 7 μ diameter, 50 % blood cell volume, and 65 l body volume, this gives 7.5×10^{14} body cells. The uncertainty of this estimate is very great. Cell constancy is known, for instance, within certain limits of heart sizes in man (Linzbach, 1950) and is to be assumed to a certain degree also for skeletal muscle fibres and nervous tissue (Levi, 1925, pp. 143 and 192—194). But still it is of course out of the question that any poikilotherm of the size of an alligator could consist of only 10^{5-7} cells all with linear measures of 2.5—3 mm.

It would not be easy to decide whether the concept of metabolism being proportional to cell surface could be applied to the whole poikilotherm range if only certain metabolically active tissues were considered. Assuming active cell surfaces to be proportional to the ¾ power of poikilotherm cell weight or volume there should then be at the 100 kg body weight 464 times more such cells than at 1 mg body weight, but they should be 216000 times larger by volume, that is 60 times by linear measures. We have already quoted an example of even larger size differences in existing cells. But no evidence has been adduced that any tissues common to 1 mg and 100 kg poikilotherms satisfy these or similar conditions.

It is relevant in this connection that Ellenby (1953) found no statistically significant difference in the rates of oxygen consumption in diploid and triploid prepupae of *Drosophila melanogaster* Meigen, though at equal body weights cell size and consequently aggregate cell surface differed. It must be admitted, however, that when taken at its face value the metabolism was actually lower in the triploid individuals, which have larger cells and consequently a smaller aggregate cell surface; and the

magnitude of the standard deviation does not exclude the possibility of a still larger difference. Especially his fig. 2 suggests a difference.

Even if identity of the powers of the body weight to which metabolism and muscle fibre surface or other cell surfaces are proportional, might explain *how,* it would not explain *why* the actual value of n is established.

We shall attempt a partial explanation at the end of the last chapter.

13.

RECAPITULATION IN ONTOGENY OF THE EVOLUTION OF ENERGY METABOLISM

Zeuthen (1953, fig. 4) has adduced some examples to show that the evolution of energy metabolism is recapitulated in ontogeny through the three phases (cf. chapter 3): 1) n lower than 1.0 as in unicellular organisms, 2) n equal to or very nearly equal to 1.0 as in marine larvae and soil nematodes at body weights between 0.1 μg and 40 mg, and 3) n again lower than 1.0 but at a higher level as in poikilothermal metazoans.

However, the weight range over which what is interpreted as the second phase, extends in the single examples given, is not coincident with the weight range 0.1 μg—40 mg but varies considerably within the total range 0.1 μg—70 g. The third phase is represented in some cases by such a low n (0.3 in *Asterias,* 0.6 in *Artemia,* 0.15 in *Rana,* 0.4 in the rat) that a fourth phase would be necessary to comply with the n values ordinarily found in adult metazoans. For instance, for some frog species between 0.1—100 g n was certainly not found to be 0.15 but nearer to 4—5 times this value (about 0.67: Davison, 1955, pp. 410—12), and for rats above 100 g n is certainly not 0.4 but nearer to double this value (e. g. Hemmingsen, 1934, with references). As regards *Asterias* Zeuthen himself in an earlier work (1947, pp. 83 and 107) suspected the low n in question to be due to dependence on the oxygen tension. Especially for the example representing *Artemia* a statistical test is lacking to prove that *n* actually varies at all during ontogeny. If not 3 lines with different slopes had been drawn graphically (fitted by eye) through the points, there would hardly have been anything to suggest that one slope might not fit the whole lot of points, as actually found by Bertalanffy and Krywienczyk (1953, p. 108) for that species. A similar doubt is felt for the three-phasic curve drawn for *Rana* between 0.1—100 g, especially in view of the results of Davison just cited. This may not necessarily mean that the metabolism is not three-phasic, merely that the presentation is unconvincing. Quotations by Davison (*loc. cit.*, p. 417) might as well be interpreted as representing 4 phases from cleavage of egg to adult. As to *Mytilus* the lower *n* of the alleged phase 1 is based on two measurements at the lowest end of the phase, which according to Zeuthen's own statement (1947, pp. 94—95 and fig. 28 on p. 96) must be suspected to be too high (increase in respiration after fertilization, vivid swimming). If they are lowered the phase becomes doubtful. And as to phase 3 which is based on more quiet individuals there seems to be the source of error that the animals get more quiet with increasing body weight which will lead to an apparent lowering of the *n* value. Perhaps also here with allowance for the source of errors mentioned a uniform slope might fit the whole range of measurements, especially if some points between 1 and 10 μg from the original material (1947, fig. 28) were not omitted in the example. Additional examples mentioned by Zeuthen (1955, p. 470) are on closer study equally unconvincing.

Later assertions (Zeuthen, 1955, p. 470) of three-phasic curves for earlier measurements on *Nassa reticulata* and *Littorina littorea* (Zeuthen, 1947, pp. 90 and 91) and of $n = 0.4$—0.5 for immature and 1.0 for mature individuals of a nematode and an oligochaete (measurements by Overgaard Nielsen) carry no more conviction. In a log. O_2-log. body weight diagram of the measurements by Overgaard Nielsen (1949, p. 93) there is nothing to disprove an intermediate *n* for the whole range, let alone to suggest a statistically significant difference between immature and mature worms. No statistical tests have been applied.

A critical accumulation of more convincing examples is necessary before the idea of ontogenetic recapitulation of metabolism evolution can be accepted as a general idea.

What seems best established in the three-phase concept is the weight-proportional metabolism in foetal life for which in the rat Zeuthen draws no phase 1 but a prolonged phase 2 from the egg below 1 μg to a body weight of nearly 70 g.

Zeuthen suggests that the high level of homoiotherm metabolism may have been reached through an extension of the ontogenetic phase 2 from the poikilotherm level of metabolism—in the rat this would mean from the level of egg metabolism—similar to the jump from unicellular level to poikilotherm level through the phylogenetic phase 2. Reasons for correlating this jump with the considerable increases in respiratory surfaces were given in chapter 6.

14.

ORTHOGENESIS OR ORTHOSELECTION?

Is the constancy and identity of n (= 0.75) in 1) unicellular organisms, 2) plants and poikilothermal, and 3) homoiothermal animals, non-adaptive (due to allometric "orthogenesis") or adaptive (due to allometric orthoselection)? Zeuthen (1953, p. 10) concludes that "evolution within large poikilothermic and within homoiothermic animals took place on the basis of established relationships between metabolism and body size, which were already acquired in animals growing beyond certain small sizes, and ......have been strongly held ever since", and (p.11) that "once such relations were acquired they were largely non-adaptive". He thinks that "the basal metabolism is adapted to the needs of a species to a lesser extent than the species are adapted to the metabolism derived according to the size and to the phylogenetic history of their whole group" (p. 10).

This view is equivalent to the concept of "Relative Growth" (heterogony, allometry, heteroauxesis, of Huxley, Teissier, Needham, etc.) as an explanation of the similar trend in the evolution of certain characters during phyletic increase in size (e. g. horns in titanotheres and antlers of deer, etc.). In the relation under consideration the less substantial "metabolism" might then be replaced by "the sum of respiratory enzymes, and metabolites". Speaking of one of the numerous instances of "Relative Growth", the linear relation between log. of length of face and log. of length of skull in both extinct and recent horses, SIMPSON (1944, pp. 5—6) finds that it amounts almost to a proven fact that the relative sizes of the two variates in question are genetically related or have proportions resulting from a single genetic rate determinant. Such non-adaptive allometric trends in evolution undoubtedly explain much of what is termed orthogenesis (cf. also HUXLEY, 1942, 1945, pp. 534 ff., and RENSCH, 1954, pp. 231 ff.).

In the course of evolution as outlined by ZEUTHEN there would thus three times have been an establishment of a genetically fixed proportionality, on all three occasions to about the same, or, as the present paper postulates, identically the same fractional power of the body weight: at the beginnings of phases 1 and 3 of the three-phased protistan-plant-poikilotherm-curve and at the beginning of homoiothermal evolution, the latter two occasions being, so to speak, re-establishments.

If, however, as argued by ZEUTHEN, on the first of these three occasions the metabolism-weight-relation was genetically fixed —or acquired in ZEUTHEN's words—as an adaptation to "cellular surfaces which may in some way have been limiting for evolution in these organisms", it seems illogical to deny that also on the occasions of its two later re-establishments its genetical fixation may have been brought about as adaptations, at least partly, to some surface functions. Important surfaces, such as gill surface (PRICE, 1931, for a fish; GRAY, 1957, for crabs) and muscle fibre surface (DAVISON, 1955, 1956, for frogs and crayfish) are proportional to a fractional power of the body weight close to the n of metabolism found by the authors themselves or others for the respective animal or animal group.

As mentioned in chapter 11 external or internal surfaces are limiting factors for the evolution of metabolism with growing sizes, as regards food absorption and heat dissipation. Thus, for instance, it was shown for heat dissipation through the body surface, that limitations occur not only when small animals are supposed to grow to the sizes of hypothetical giants with retention of the metabolism per unit weight (rat-rhinoceros), but already in the case of a 100 g rat growing to about only 338 g (HEMMINGSEN, 1950, pp. 40—46).

It seems in fact unlikely that the whole process of metabolism evolution should have been dependent on the establishment already at the smallest microscopic sizes of unicellular organisms of an allometric relation which proved to be so fortunate that it permitted a variation of metabolism sufficiently close with the body surface to prevent surface processes such as absorption from the intestine, heat dissipation through the surface, or cross section functions such as blood flow from becoming limiting in the large metazoans.

When we realize that any animal growing in size cannot keep up its energy metabolism per unit body weight because its surface functions set such limits that the metabolism must be adapted to them, there is no reason to believe that the relations resulting from such adaptations were established once and for all already in animals growing beyond certain small sizes. It seems much more likely that during the evolution of the metabolism-weight-relation an adaptation of the metabolism—the basal perhaps through the maximal—to the structural necessities has constantly taken place, not least to the surface functions, and thus not only so as to be genetically fixed by selection of mutations or gene-combinations at the beginning of the courses of evolution represented by the three straight lines with $n = 0.75$, but so as to be genetically fixed by similar means (selection) at any specific body size during their whole course of evolution. This would be then what is sometimes called orthoselection (PLATE, 1913, p. 511); that is, selection promoting the continuance of an adaptive trend.

Within all three ranges with the over-all $n = 0.75$, n values differing considerably from 0.75 have been found within narrower weight ranges (for the poikilotherm range exemplified in fig. 9). Some of them may not differ significantly from 0.75. Others may deviate from 0.75 because comparable standard conditions were not established. Still others may be virtually different from 0.75, in certain groups or during ontogenesis. As clearly exemplified in fig. 9 none of the short range lines with such deviating slopes continue over more than a few log. weight decades.

This suggests that the relations are not fixed *a priori* but that *with changing body weight a selective influence may have been operative having eliminated all mutants that would produce organisms with a metabolism deviating too much from that adapted to the average normal life functions at the particular body size.*

In human medical practice deviations of more than only about 20 % from the normal energy standard metabolism, as determined on the basis of age, height and weight are taken to be strongly suggestive of a pathological condition. Such and higher deviations—no doubt often occurring as hereditary Mendelian segregations of mutational origin—will have no survival value.

Suggestive are also instances quoted by Brody (1945, fig. 13.9 on p. 372) and Zeuthen (1953, pp. 7—8 and fig. 5) of a tendency in some species for the log. metab.-log. weight curve to branch off from the main curve as soon as a species approaches its maximum size; for the cessation of growth might depend on the deviation of the metabolism from the main line having become too large.

Also other instances of allometric relations are known which are more readily interpreted as results of orthoselection than as non-adaptive growth correlations. It was pointed out by Newell (1949, pp. 104—105; quoting personal communication by Simpson) that the allometric curve produced by plotting diameter of limb bone against linear dimensions of the body of land vertebrates must be the result of selection of mutations. With increasing size, limb bones must become relatively (as well as absolutely) more massive because body weight increases as the cube, bone strength as the square of linear increase. Large animals without a proper relation between limb and body size would not survive.

Similar cases in which selection has produced for the trans-specific growth allometry an *n* different from those of individual ontogentic growth allometries are mentioned by Rensch (1954, p. 235). For instance, growth allometry of intestines relative to body size of homoiotherms is negative ontogenetically, but positive phylogenetically, larger animals having relatively larger intestines (Rensch, 1954, p. 157), and though growth allometry of flight muscles of *Diptera* is positive ontogenetically, it is negative phylogenetically (Partmann, 1948). Growth allometry of wing length relative to total body length of some *Tipulidae* is negative intraspecifically; in others it is positive (Hemmingsen and Birger Jensen, unpublished). In flying animals taken as a whole (fly to stork) it is positive (Günther and Guerra, 1957).

Also Kleiber who was among the first to establish the inter-specific metabolism-weight allometry for homoiotherms (1932) considers it a result of natural selection (1947, p. 538): "In natural selection those animals prove to be better fit whose rate of oxygen consumption is regulated so as to permit the more efficient temperature regulation as well as the more efficient transport of oxygen and nutrients." To von Döbeln (1956, p. 45) it appears doubtful how this thesis can apply to standard conditions because only during the period of sleep do the conditions in nature approach those existing under laboratory standard conditions; that is, fasting and complete muscular relaxation. It must be plain, however, that also the metabolism during sleep, 1/3—1/2 of the life time of many animals,—or even in torpidity or lethargy—must possess survival value in the sense that it must comply with the structural and physiological needs of the organism. Furthermore, we saw in chapters 9—10 that to all appearances *n* is 0.75 not only for standard but also for maximal energy metabolism in homoiotherms, and for torpidity and lethargy metabolism in hibernating mammals, so it seems that Kleiber's thesis may be applicable to any level of metabolism.

No matter whether the evolution of energy metabolism has been adaptive or non-adaptive, a riddle remains in either case: The energy metabolism is proportional to the 0.75 power and not to the 0.67 power of the body weight, as one would expect if only surface functions alone had been limiting.

The attempts at an explanation so far put forward by various authors apply to higher animals or shorter weight ranges (cf. Hemmingsen, 1950, p. 47; and also the theory of Davison as discussed above) and are irrelevant as far as unicellular organisms are concerned. Quite obviously an explanation must cover all the allometric levels in question. In the present state of matters this is a burning issue.

Apparently the only explanation which fits both unicellular and multicellular organisms, seems to be that in the course of evolution of sizes there has been constantly a tendency for energy metabolism to increase in proportion to size. But limitations set e. g. by surface functions have forced it by constant selection to increase much more in proportion to surface than to size, without, however, thereby necessitating a complete abolition of the tendency to proportionality to size. This tendency is thus still represented by the difference between 0.67 and 0.75.

A combination of a tendency to phyletic increase in size together with a tendency for metabolism to be proportional to body weight will necessarily favour selection of extra external or internal surface increments with rising size, in compensation of the decrease of surface per unit volume with increasing volume, and may thus have been one of the driving forces in the evolution of such surfaces.

At each major jump in allometric metabolism level, that is from unicellular to multicellular level and from poikilotherm to homoiotherm level, the tendency towards proportionality to body weight has overridden the limitations set by the surfaces at the existing level of organization, largely by evolving more efficient or larger surfaces.

Evidence of the struggle between size proportionality and surface proportionality, leading to extra surface increases, may perhaps be seen in the phylogenetically positive growth allometry of intestines and inner intestinal surface relative to body size (larger animals have relatively large intestines; see e. g. Partmann, 1948, for *Diptera* and Rensch, 1954) and in the extension in certain fish larvae of the intestinal canal outside the body proper into a long thread-like appendage (cf. Hemmingsen, 1950, p. 27), perhaps also in the preponderance of short range *n* values that exceed the over-all *n* of 0.75 (cf. chapter 4).

However, while the hypothesis in point explains why *n* is much nearer to 0.67 than to 1.00 it leaves unexplained why just exactly the difference between 0.75 and 0.67 turns out as a resultant from the hypothetical struggle between size proportionality and surface proportionality.

15.

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16.

SUMMARY

The temperature-corrected basal (standard) metabolism of unicellular organisms is proportional to the same fractional power (0.75 ± 0.015) of the body (cell) weight as that of multicellular plants and poikilothermal and homoiothermal metazoans, yet at a lower allometric level. (Fig. 1, p. 12).

Within the range of body weights of approximately 1 μg—1 mg the energy metabolism of small metazoans (marine larvae) as measured by Zeuthen is higher than that of unicellular multinucleate organisms, lower than that of insect eggs, and as found by Zeuthen proportional to a higher power (nearly 1.00) of the body weight. Accordingly, the corresponding line representing the relation between log. metabolism and body weight of these small metazoans, rises (below 1 μg) from the "unicellular line" before this ends (at 0.1 mg) and reaches the "metazoic poikilotherm line" (according to Zeuthen at 40 mg) after this begins (at 10 μg or below). Fig. 2, p. 16).

The straight lines representing the relation of log. Cal. to log. body weight intra- or interspecifically within shorter ranges of body weights in many different groups of poikilothermal animals, have been plotted in a log. Cal.-log. body weight diagram together with the over-all standard "poikilotherm line" which has a slope representing for poikilotherms proportionality of log. Cal. to the fractional power 0.75 of body weight. It is then seen that the short range lines which do not coincide with the standard line, are distributed about it, falling either somewhat above or below or cutting it, the extreme upper or lower ends of such lines tending to fall approximately in (imaginary) lines parallel to the standard line. The evolutionary significance of this is evidently that no value of the fractional power of body weight except 0.75 can be maintained over any wider range of body weights. Lower and higher slopes are eliminated by selection. (Figs. 3—9, pp. 24—30).

The theories of BERTALANFFY (on metabolic types and growth types) and LUDWIG (on metabolic types and type of respiratory apparatus) are discussed.

Though ontogenetically body surface area tends to vary with a fractional power of body weight which is lower than ⅔, this power is to all practical purposes equal to ⅔ when the whole range of vertebrates is considered; and at any body weights, the body surface area is on an average about twice the surface area of a sphere of equal volume. (Fig. 10, p. 42).

The surface areas of beech trees (without leaves and roots) exceed the surface areas of hypothetical spherical unicellular organisms extrapolated to the same sizes (that is, spheres with volumes equal to those of beech trees) about as much as the energy metabolism of beech trees exceeds unicellular metabolism at the same temperature (20° C.) extrapolated to the same size.

The energy metabolism of poikilotherms at any certain size above 1 mg is about 8.1 times higher than that obtained for a hypothetical unicellular organism of the same size by extrapolation. This higher level is not effectuated primarily by increase of area of respiratory surfaces in excess of body surface, but in some (insect eggs) by unknown factors, in others by increased internal convection, vascularization of skin or of lung and gill surfaces. Yet in some, not least tracheates, some fishes and reptiles the development of internal respiratory surfaces plays a major part. The body + respiratory surfaces in some poikilotherms surveyed exceed the surfaces of spheres of equal volume by figures (2—26) which are of the same order of magnitude as 8.1.

The lung surface of man appears to exceed the surface area of a hypothetical spherical unicellular organism extrapolated to the size of man (that is, a sphere with the volume of man) about as much as his temperature-corrected standard metabolism exceeds unicellular standard metabolism at the same temperature extrapolated to his size.

This is taken to suggest that the increase of internal respiratory area plays a major role in the evolution of poikilotherms into homoiotherms. Both the difference between the metabolism of unicellular organisms and poikilotherms (and plants), as calculated by extrapolations to equal body weight, and the difference between poikilotherms and homoiotherms of equal body weights are taken to be closely associated with qualitative and quantitative differences in respiratory surfaces.

The metabolism during maximal flight or maximal sustained work in the homoiotherms dealt with is proportional to the same fractional power (0.75) of the body weight as the standard metabolism and exceeds the latter about 20 times. (Fig. 11, p. 63).

The maximal flight metabolism in insects above the size of a blowfly may or may not be proportional to the same power (0.75) of the body weight as standard poikilothermal metabolism at 20° C., but it exceeds the latter about 575 times and falls about an extrapolation of the maximal homoiotherm metabolism. It is suspected that correspondence in body temperature of homoiotherms and these insects during flight may account for this. The flight metabolism of smaller *Diptera* differs less extremely from resting or standard metabolism, and is per unit body weight similar to that of the larger insects and the pigeon.

Also at torpidity levels (e. g. of bats) and at the still lower lethargy levels of hibernating mammals approaching that of poikilotherms at the same temperature, the energy metabolism is probably at least approximately proportional to the same power (0.75) as standard (basal) metabolism. (Fig. 12, p. 71).

In agreement with the idea of a widespread phyletic increase in body size the relation between energy metabolism and body weight is taken with **Zeuthen** to illustrate the evolution of energy metabolism from the lowest unicellular sizes to those of giant metazoans.

Theories of proportionality of metabolism to cell surface in protistans and small metazoans (**Zeuthen**) and in some poikilotherms (**Davison**) and of recapitulation in ontogeny of the evolution of energy metabolism (**Zeuthen**) are discussed.

Reasons are given for believing that the metabolism-body-weight-allometries with identical n ($= 0.75$) within unicellular organisms, plants, poikilothermal and homoiothermal animals are adaptive and have evolved by orthoselection, resulting perhaps from a struggle between proportionality of metabolism to body weight and proportionality to surface functions.

17.

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