lich heftige Kämpfe mit den zahlreichen *laevinodis*-Kolonien unseres Gartens zu bestehen; sie trugen dabei wiederholt Brut der letzteren (auch Puppen) in ihr Nest. Im nächsten Jahre sah ich unter den *rubida* auch einige Exemplare der viel kleineren *laevinodis* aus den Eingangslöchern des Nestes kommen. — Es wäre wünschbar, die Sache experimentell nachzuprüfen.

Further Explanatory Remarks Concerning the Normal Rate of Growth of an Individual and its Biochemical Significance.

By T. Brailsford Robertson.

(From the Rudolph Spreckels Physiological Laboratory of the University of California.)

In a recent article[1]) Moeser has called in question the correctness of my representation[2]) of the autocatalytic character of the growth-process. The chief objections which he raises are the following:

A. According to my formula the maximum velocity of growth (= yearly, daily or hourly increment) occurs in the middle of the growth-cycle. Moeser points out that this is, in actual experience, frequently not the case.

B. My formula, according to Moeser, represents growth purely as a function of time. He points out that it is also a function of temperature, light, moisture etc. Since these factors are not without effect upon growth, therefore, Moeser argues, it is not correct to speak of growth as a simple autocatalytic process.

I will deal with these objections separately:

A. As examples of the fact that the maximum rate of growth frequently does not occur in the middle of a cycle, Moeser cites measurements made by Sachs of the daily increment in the length of a root of *Vicia faba*, of the elongation of three internodes of *Dahlia variabilis* and of the elongation of four internodes of *Fritillaria imperialis*.

In this connection it appears necessary to point out:

a) that increments of length are very unsafe measures of increment in mass, since the diameter of the body measured may alter as well as the length, and, moreover, even if the diameter remains constant, the specific gravity of the substance composing the body measured may also alter from time to time. Now chemical reaction-formulae deal solely with the relation of mass to time or

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1) W. Moeser. Biolog. Centralbl., Bd. XXXII (1912), p. 365.

2) T. Brailsford Robertson. Arch. f. Entwicklungsmech., Bd. XXV (1908), p. 581, Bd. XXVI (1908), p. 108. Biolog. Centralbl., Bd. XXX (1910), p. 316.

temperature or mass, and consequently the autocatalytic formula of growth can only legitimately be applied to the growth of mass.

b) Since, as Moeser very justly points out, temperature, moisture, and a number of other factors have an influence upon growth, and we usually possess little certainty all that of these factors are maintained constant during the growth of a single individual, it is safer, in order to eliminate fluctuating variations due to these uncontrolled variables, to measure and average the growth of a very large number of individuals, rather than to depend as Moeser does, upon measurements made upon a single individual.

c) In order to avoid assuming that the maximum increment in growth occurs at the middle of a growth-cycle (i. e. when the total growth due to the cycle is half completed) Moeser suggests the following modification of my formula.

The differential equation which expresses the progress of an autocatalytic (monomolecular) reaction is the following:

$$\frac{dt}{dt} = Kx(A - x) \quad \ldots \ldots \quad (1)$$

in which x is the mass which has undergone transformation (= growth) at time t and A is the final mass which has undergone transformation at the end of the reaction (i. e. the total growth at the end of the growth-cycle).

Integrating, we obtain:

$$\ln \frac{x}{A - x} = KAt + C \quad \ldots \ldots \quad (2)$$

where C is the constant of integration.

In my derivation of the growth formula I proceeded as follows: Since the value of C must be the same for all values of x let us make $x = {}^1/_2 A$ and let t_1 be the corresponding value of t, then from equation (2) we have:

$$KAt_1 + C = o \quad \ldots \ldots \quad (3)$$

hence:

$$C = -KAt_1 \quad \ldots \ldots \quad (4)$$

and equation (2) becomes:

$$\ln \frac{x}{A - x} = KA(t - t_1) \quad \ldots \ldots \quad (5)$$

Moeser, however, proceeds from equation (2) as follows:

When $t = o$ let $x = v$, then when $t = o$ we have:

$$C = \ln \frac{v}{A - v} \quad \ldots \ldots \quad (6)$$

hence (2) becomes[3]):

$$\ln \frac{(A - V)x}{V(A - x)} = KA(t - t_1) \quad \ldots \ldots \quad (7)$$

3) For the constant A, Moeser employs the symbol V.

Moeser thinks that this equation is superior to my equation (5) because, he believes, it avoids the assumption that $\frac{dt}{dt}$ (= daily increment) is a maximum when growth is half completed ($x = \frac{1}{2}A$). In this belief he is mistaken, however, as the following considerations show:

Differentiating equation (7) we obtain:

$$\frac{dx}{dt} = Kx(A - x) \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (8)$$

which is identical with equation (1).

Differentiating again we obtain:

$$\frac{d^2x}{dt^2} = KA - 2Kx \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (9)$$

hence $\frac{d^2x}{dt^2}$ is zero when $x = \frac{1}{2}A$, and for that and all values of x, $\frac{d^3x}{dt^3}$ is negative, hence $\frac{dx}{dt}$ is a maximum when $x = \frac{1}{2}A$[4]).

Consequently Moeser's equation involves, just as much as mine does, the assumption that the rate of growth is a maximum when the growth-cycle is half completed. Now it is to be recollected that, especially when we rely upon observations upon the growth of a single individual, any single measurement may chance to be erroneous, and if we incorporate into our equation such a measurement our equation will also be erroneous. In employing my equation it is possible to eliminate this source of error to the greatest possible extent, for K and t_1 are determined, not from any single observation but from all of the observations by the method of least squares. By employing this method the + errors attaching to certain observations are cancelled by the — errors attaching to others and the constants thus computed, as all physicists know, are much more nearly ideally correct that constants computed from single observations. In employing Moeser's equation, however, we are forced to rely absolutely upon the accuracy of a single observation, namely, the measurement of the length, volume or weight when $t = o$, and then, if this observation should chance to be erroneous (owing to the intrusion of adventitious variables such as fluctuations of temperature etc.) the whole equation will share in the error and the experimental results may not fit the equation at all owing to a single experimental error.

Moeser states that „Die Robertson'sche Interpretation der autokatalytischen Formel ist direkt falsch. Daher ist es nicht wunderbar, dass seine Zuwachswerte manchmal um die Hälfte von

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4) Cf. J. Todhunter „Differential Culculus" 7th Edn. London 1875, Chapter 13.

den wirklichen abweichen." This statement contains two inaccuracies. In the first place my interpretation of the autocatalytic formula is, as we have seen, correct and identical with Moeser's while my employment of it is accurate in principle and Moeser's is not. In the second place in all cases in which I have stated that the autocatalytic formula certainly applies the deviations between theory and experiment never exceed 20 % and are in almost every instance much less than this. This is especially true when the data are derived from the average of a large number of individual measurements. The large deviations to which Moeser refers occur in cases to which, as I have expressly pointed out in each of the articles to which I have referred, the autocatalytic formula does not apply. In fact I refer to these deviations as direct proof that the formula does not apply. It appears necessary once more to reiterate my statement that the autocatalytic growth-formula does not apply in the following instances:

1. To the decrease of weight which occurs in senile decay, from which Loeb[6]) and I have argued that the processes underlying senile decay are essentially different from those which underlie growth.

2. To the growth of the Mineral Content of plants. This has recently been confirmed by Chodat and Monnier[2]) who have shown that it is due to the fact that at certain periods in the growth of plants there is a „negative Migration" of mineral constituents from the plant into the soil.

In passing I wish to correct yet a third mis-statement made by Moeser. He asserts (p. 370), without citing any article, that I have employed two autocatalytic curves to represent the complete curve of muscular contraction, the one representing the ascending portion of the curve, the other the descending portion of the curve. I have never done so and in no publication have I attempted to apply the autocatalytic formula to the curve of muscular contraction. I have, it is true, ventured to assert that autocatalytic processes underlie muscular contraction[7]), but I cited, in support of this view, not the form of the curve of muscular contraction, but the fact that muscular contraction is rendered more energetic by perfusing the muscle with a weak solution of the products of muscular activity, and less energetic by perfusing it with a stronger

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5) J. Loeb. „Die chemische Entwicklungserregung des tierischen Eies". Berlin 1909, p. 246.

6) R. Chodat and A. Monnier. Arch. d. Sciences physiques et naturelles. Soc. de physique et d'histoire naturelle de Genève. 4me Ser. tome 33, p. 101 (1912).

7) T. Brailsford Robertson. "On the Biochemical Relationship between the 'Staircase' phenomenon and Fatigue". Festband der Biochem. Zeitschr. f. H. T. Hamburger, 1908, p. 287.

solution of the same products. I have expressly refrained from attempting to apply the autocatalytic formula to the curve of muscular contraction because I am of the opinion that the time-relations in muscular contraction are determined by changes of capillarity and by the elasticity of the muscle-elements rather than by the chemical reactions which underlie and cause these changes[8]). It must be recollected, yet again, that the autocatalytic formula expresses a relationship between mass and time and that before attempting to apply it to a relationship between length and time we must first ascertain that the observed changes in length are directly proportional to changes in the mass of some chemical product. Now we have no proof whatever that during the course of a single muscular contraction the shortening of the muscle is directly proportional to the mass of carbohydrate which is transformed into CO_2 and H_2O or other products. Until we possess such proofs, any attempt to apply the autocatalytic formula to curves of muscular contraction is of very doubtful utility. In applying the formula to growth, on the contrary, we have in the weight of the animal or plant a direct measure of the mass of the products of the chemical reactions underlying the process. The application of the formula to growth in weight is therefore rational.

B. Moeser, as I have stated, raises the further objection that the autocatalytic reaction-formula expresses only a relation between mass and time and fails to incorporate the influence of temperature, moisture, etc. It is for this reason, he asserts, that the deviations between the autorcatalytic curve and the empirical curve occur. I do not question that this is the case, but it may be pointed out that it is also the case in all chemical reactions. In ascertaining the relationship between mass and time in a chemical transformation we endeavor to keep such factors as temperature, pressure, etc. constant. If the temperature varies, the velocity of the reaction varies, and, in fact Karl Peter and I[9]) have utilised the fact that growth is accelerated by a rise of temperature in support of the view that the velocity of growth is determined by the velocity of a chemical reaction[10]). But because an autocatalytic chemical reaction is accelerated by a rise of temperature, it does not cease to be an autocatalysed chemical reaction and to display the characteristic time-relations of an autocatalysed reaction at a

8) T. Brailsford Robertson: "Remarks on the Theory of Protoplasmic Movement and Excitation". Quarterly Jour. of Exper. Physiol. 2 (1909), p. 303. Cf. also T. Bernstein. Arch. f. d. ges. Physiol. 122 (1908), p. 129.

9) K. Peter. Arch. f. Entwicklungsmech., Bd. 20 (1906), p. 130.

10) T. Brailsford Robertson. Arch. f. Entwicklungsmech.. Bd. 25 (1908), p. 581.

given constant temperature. In order to obtain a reliable comparison between the empirical growth curve and the autocatalytic curve, we must so far as possible exclude such adventitions variables either by taking the average of a very large number of observations, or by keeping the conditions of temperature, moisture, supply of nutrition, etc. under which the organism is growing as strictly constant as possible.

Dreitausend und dreihundert Generationen von Paramaecium ohne Konjugation oder künstliche Reizung.

Von Prof. Lorande Loss Woodruff, Ph. D.
(Aus dem Sheffield Biologischen Laboratorium der Yale Universität, New Haven, Conn., U. S. A.)

Die einzelligen Organismen bieten eine natürliche Methode dar, dem Problem der Befruchtung näher zu kommen; die Durchmusterung der in einer Reihe sorgfältig ausgeführter experimenteller Studien von verschiedenen Forschern an diesen Formen gewonnenen Tatsachen zeigt, dass die wichtigste Aufgabe der Konjugation bei den Protozoen die Erfüllung eines unausbleiblichen periodischen physiologischen Bedürfnisses der lebendigen Substanz ist, die eine Erneuerung der Lebenskraft der Zelle zur Folge hat. Diese „dynamische“ Ansicht der Befruchtung hat sich allmählich eine herrschende Stelle erobert, obwohl sie der Ansicht, dass die Befruchtung, die mit einer Amphimixis endet, in irgendeiner Weise mit dem Phänomen der Variation verbunden oder ein Prozess ist, wodurch einige Formen veränderten äußeren Umständen widerstehen können, weder widerspricht, noch mit ihr übereinstimmt.

Die vorliegende Abhandlung zeigt kurz die Resultate eines intensiven Studiums einer von einem bekannten Stamm hergekommenen Rasse von *Paramaecium aurelia* in bezug auf das Problem des protoplasmatischen Alterns und die Funktion der Konjugation. Ich habe die bis zum September 1910 gewonnenen Resultate schon publiziert[1]) und mit Rücksicht auf die genauen Einzelheiten der Kultur und die allgemeine Diskussion der verschiedenen Phasen der Arbeit verweise ich auf meine frühere Abhandlungen.

Diese Kultur wurde am 1. Mai 1907 mit einem „wilden“ aus einem im Laboratorium stehenden Aquarium isolierten *Paramaecium aurelia* angefangen. Dieses Individuum wurde in etwa fünf Tropfen Kulturmedium auf einem vertieften Objektträger aufgestellt und als das Tier sich in vier Individuen geteilt hatte, wurden diese vier je eines auf einem Objektträger isoliert, um die vier Linien

1) Arch. f. Protistenkunde, Bd. 21.