

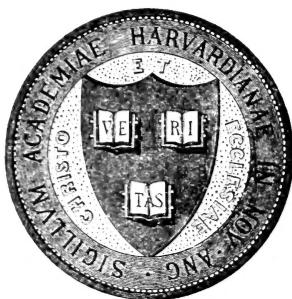
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*Somatic modifications.*

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# An Experimental Study of Somatic Modifications and their Reappearance in the Offspring

by

**Francis B. Sumner**

With 11 figures in text and 3 plates

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# An Experimental Study of Somatic Modifications and their Reappearance in the Offspring.

By

**Francis B. Sumner**

(Woods Hole, Mass., U. S. A.).

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With 11 figures in text and tables XVI—XVIII.

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Eingegangen am 3. März 1910.

For several years past the present writer has studied the effects of differing temperature conditions upon the growth of the white mouse. In a recent paper<sup>1)</sup> some of these effects have been discussed rather fully. It has there been shown that the length of certain peripheral parts of the body (tail, foot and ear) is greater in individuals which have been reared in a warm room than in ones reared in a cold room. As regards the tail, the modification was found to be very striking, the mean length of this organ for the two sets of individuals differing in one experiment by more than 30 per cent. In the case of the foot, the difference was less pronounced, but its reality was evident in every experiment. The ear, on the other hand, appeared to respond but feebly to temperature conditions<sup>2)</sup>. From determinations of the quantity of hair in two of these contrasted lots of mice, it was shown to be probable that this likewise was affected by sufficiently great differences of temperature. The extreme laboriousness of these latter determinations has, however, rendered it impossible thus far to deal with a sufficiently great number of individuals to satisfy the demands of statistical theory.

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<sup>1)</sup> Journal of Experimental Zoology. August 1909.

<sup>2)</sup> In my earlier paper, indeed, I expressed doubt as to the significance of such small differences as I did detect in the case of this organ. Further observations have, however, lessened these doubts.



I have already dwelt upon the significant fact that these artificially produced differences are just such as have long been known to distinguish northern from southern races of mammals. This fact will be taken by some as evidence that these differences in nature are likewise 'ontogenetic' or acquired independently by each individual. Conversely, the neo-Lamarckian will perhaps argue — and with equal right — that here we have evidence that natural varieties and species have resulted from the accumulated effects of external conditions, since the reality of such effects has been palpably demonstrated by the present experiments<sup>1</sup>). Neither conclusion is of course warranted until we have convincing evidence for or against the transmissibility of this class of modifications. It has accordingly been my chief motive throughout the course of these experiments to obtain evidence of this sort. And it is the object of the present paper to report such data as I have thus far obtained<sup>2</sup>).

I trust that no apology is necessary for the presentation of results which have been derived from a single generation of offspring, comprizing only a few hundred individuals. I need only point out to the reader that this meagre showing is the fruit of monotonous drudgery<sup>3</sup>) occupying most of my spare time for over three years, during which period my best energies were unavoidably devoted to a quite different task. Without special facilities (and none were at my disposal) it was obviously impossible to obtain the necessary differences of temperature except during the winter months. If one experiment failed, it was necessary to wait until the following winter before I could begin anew. Indeed, it was not until the close of the third winter that I obtained a generation of offspring which fulfilled the requirements of the test<sup>4</sup>). And unfortunately it was not possible, even in this case, for me to keep these animals long enough for further breeding. They were all killed at the age of about 3½ months,

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1) Op. cit. p. 152.

2) A preliminary account of these data was published in the *American Naturalist*. January 1910.

3) Any one who has had experience with animal breeding knows that the mere daily care of several hundred mice requires not a little time, especially when one is unassisted. Even this labor has been trifling, however, in comparison with that required for the measurements and the subsequent computations.

4) I. e., which contained a large enough number of healthy animals born nearly or quite simultaneously.

and thus the experiment was brought to a close. It is not intended, however that the matter shall rest here.

In order to fairly test the heritability of somatic modifications, individually acquired, the following conditions should, I believe, be realized: 1) We must select for experiment such an organism and such a physical agency that the latter may modify the former without directly influencing the germ-cells. 2) We must discover readily measurable, *quantitative* changes in the parent generation before we can hope to test the reappearance of such changes in the offspring.

Most of the past experiments in this field have been rendered inconclusive by a failure to conform to the first of these conditions. Thus the congenital effects of temperature and humidity upon insects, which have been described by STANDFUSS<sup>1)</sup>, FISCHER<sup>2)</sup>, TOWER<sup>3)</sup> and others, are equally well explained as the result of an immediate modification of the »germ-plasm« by the external stimulus itself. The same is true of the enduring effects of special feeding, cumulative from generation to generation, such as have been described by PICTET<sup>4)</sup> for *Lepidoptera* and by HOUSSAY<sup>5)</sup> for fowls. Indeed this postulate of a »direct effect upon the germ-plasm« has been freely used by WEISMANN and his followers as a cheap and easy way of disposing of most of the experimental evidence which has been brought forward in favor of the inheritance of acquired characters. But it scarcely seems applicable to any effects which may be found to result from the action of temperature upon a mammal. For differences of external temperature, *as such*, manifestly cannot reach the germ-cells of a warm blooded animal unless during the first few days after birth<sup>6)</sup>.

1) Zur Frage der Gestaltung und Vererbung auf Grund achtundzwanzig-jähriger Experimente. Leipzig 1902.

2) Allgemeine Zeitschrift für Entomologie. 6. 1901. 7. 1902.

3) An Investigation of Evolution in Chrysomelid Beetles of the Genus *Leptinotarsa*. Carnegie Institution. 1906. p. 320. pl. 30.

4) Mémoires de la Société de Physique et d'Histoire naturelle de Genève. 35. 1905.

5) Archives de Zoologie Expérimentale et Générale. 4<sup>e</sup> série. VI. 1907.

6) PEMBREY (Journal of Physiology. Vol. XVIII. 1905) found the body temperatures of adult mice to remain constant at widely different external temperatures. In the young, however (under ten days old), the internal temperature was found to vary with that of the atmosphere. These experiments should be repeated with the aid of more delicate instruments than ordinary mercurial thermometers. At present it is, of course, open to the Weismannian to contend 1) that very slight differences of internal temperature may actually be produced in the parents and may be responsible for any effect upon the succeeding

As regards the second of the above stated conditions which should be fulfilled by the experimenter, it is obvious that in the present instance I have produced readily measurable, quantitative changes in the parent generation. It would appear scarcely necessary to urge that a modification must first be manifested by the parents in order that it may be transmitted to the offspring. Yet we read of one investigator who watched for a reduction in the size of the wings of flies which had been prevented from flight for more than 40 generations. It is difficult to understand how the length of an insect's wing could be increased or decreased by use during the life of the individual; and it is therefore scarcely surprising that such an effect was not found to be cumulative.

If »acquired characters« are in reality transmitted, we should not in a given case expect that more than a small fraction of a parental modification would reappear in the first generation of offspring. For this reason it is plain that we have more to hope for from a comparison of averages based upon the measurements of large masses of individuals than from a search for *qualitative* differences of a sort which are apparent to the eye. Yet with a few exceptions, past experimenters in this field have dealt with modifications of color, or of physiological reactions, such as do not lend themselves readily to quantitative treatment. Ever so slight measurable changes, if sufficiently constant, would be of far greater significance than occasional manifestations, however striking; for the latter are always open to the interpretation of being »mutations«, examples of »reversion« or the like, which are purely accidental as regards the conditions of the experiment.

Having discovered suitable modifications in the parent generation, there are theoretically two methods by which we may attack the problem in hand. We may either 1) raise the offspring of the experimental and control<sup>1)</sup> lots under identical conditions, or 2) we may raise the offspring of the modified parents under the same conditions as were employed to effect the original modifications. In the first case, we should compare the two sets of animals having differ-

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generation; or 2) that in any case the germ-plasm may be influenced during those early days of life before the animal has become strictly homoiothermic.

<sup>1)</sup> For the sake of simplicity I have here assumed that one lot was merely a »control« lot, i. e. one exposed to normal or indifferent conditions. In my own experiments, however, I have chosen conditions with a view to modifying both sets of individuals in opposite directions.



ent parentage. Assuming a given modification of the value  $x$ , and supposing that  $\frac{1}{n}$  represents the proportional part of this to be transmitted, the offspring of the two lots would be found to differ by the quantity  $\frac{x}{n}$ . If the second of these methods were employed, we should compare the second generation with the parent generation, the two being measured at the same age. Assuming as before that the parents had been modified to the extent  $x$ , the offspring, according to hypothesis, would be found to be modified to the extent  $x + \frac{x}{n}$ , i. e., the effect of the conditions would have been cumulative.

Now, as a matter of fact, I have attempted both of these tests upon rather a large scale; but I have not yet found the second one to be practicable, owing to the difficulty, without special facilities, of repeating precisely the same temperature conditions during the lives of two successive generations<sup>1)</sup>. But, the first of these tests finally proved to be practicable, and has yielded the results which are dealt with on the ensuing pages.

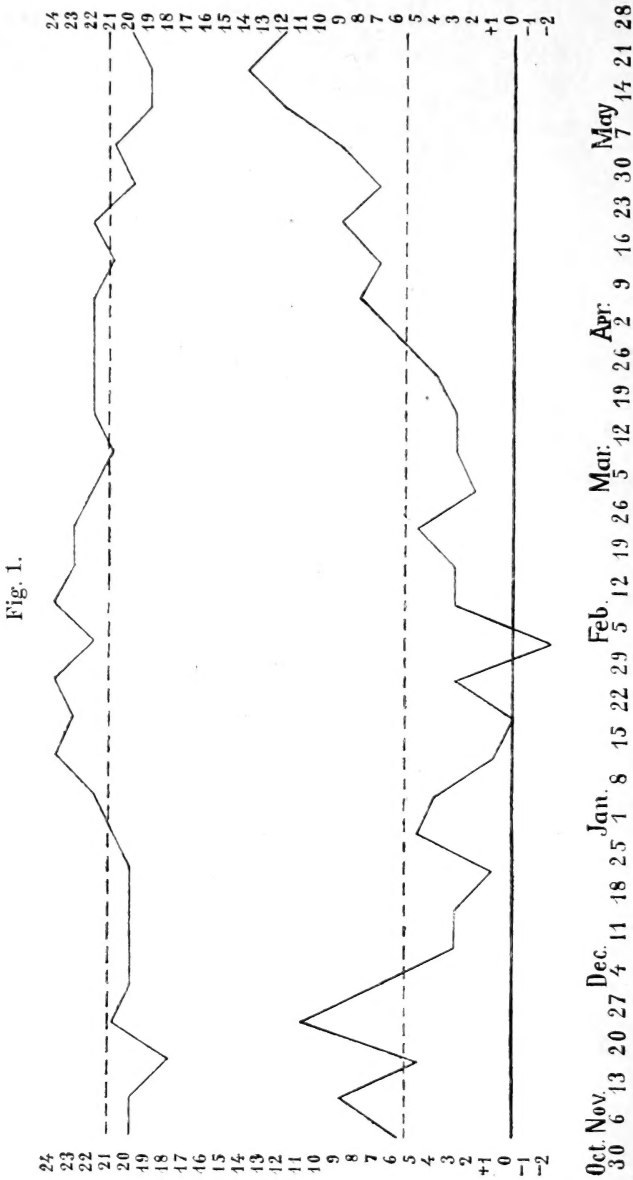
The methods which I have employed in dealing with the parent mice have been described in detail in my paper of 1909, so that little attention need be devoted to them at present. The parent generation (i. e. that immediately subjected to the experimental conditions) which is here to be considered is the one which I have discussed on pp. 139—144 of the paper cited, under the heading »Series of 1908—1909«. At the date of writing that account, however, these mice had not yet reached maturity. The temperature conditions to which they were subjected from the commencement of life<sup>2)</sup> until some days before the birth of their last brood of offspring are represented in Fig. 1 of the present paper. The mean temperatures<sup>3)</sup> of the warm and cold rooms respectively throughout this entire period were 21.27° and 5.57° C. respectively. For the period prior to the date of pairing (May 2), the mean difference was somewhat greater than this, viz. 16.8° C. Since the curves shown in the chart are based upon weekly averages, the extremes of temperature are of course eliminated. The

1) See foot-note on p. 324 and 325 below.

2) Sometimes commencing with the day of birth, sometimes a few days after this, in many cases before birth i. e. during the pregnancy of the mother.

3) I am indebted to my wife for the tedious work of compiling these data from the thermograph sheets.

average daily range was  $11.2^{\circ}$  for the warm room and  $6.2^{\circ}$  for the cold room. The mean relative humidity, during the first four months



Curves showing temperature conditions in the warm and cold rooms during the life of the parent generation of mice. Each is based upon weekly averages, computed from thermograph records. The dotted lines indicate the mean temperatures for the two rooms.

of the experiment was roughly 40 per cent for the warm room and 75 per cent for the cold room. This factor, as well as temperature

proper, may therefore have played a part in the results produced. For present purposes, however, it matters little whether one or both of these factors was concerned.

Each entire brood of mice with its mother<sup>1)</sup>, was transferred as soon as it was received from the dealer to one or the other of these experimental rooms. No selection was exercised in thus disposing of the mice, the broods being chosen at random<sup>2)</sup>.

In all 98 mice, representing 22 broods, survived to the age of 42 days in the warm room; 88 mice, representing 23 broods surviving to this age in the cold room. During the ensuing months there were, as commonly happens, a considerable number of deaths. At the time of the final pairing (May 2) 39 warm-room females and 34 cold-room females were still living. The males, with the exception of those which were selected for breeding purposes<sup>3)</sup>, had previously been killed.

The following table from my early work (1909, p. 138) summarizes the results of the measurements made upon these mice at the age of six weeks. The diagram (Fig. 2) shows the differences in tail length between the warm-room and cold-room individuals (both sexes), these being divided into groups according to weight.

Series of 1908—1909 (parents): Weight and tail length at six weeks.

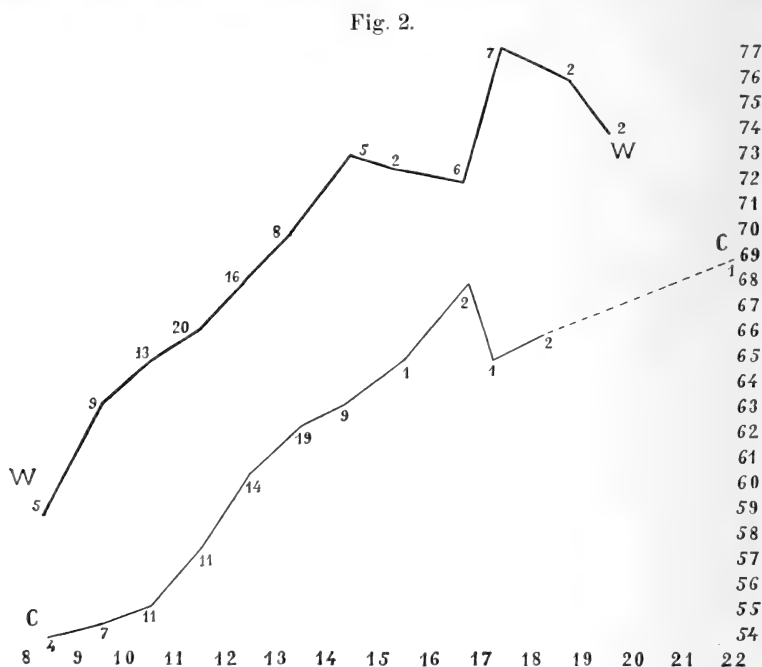
	Weight				Tail length			
	Males		Females		Males		Females	
	Warm (55)	Cold (50)	Warm (43)	Cold (38)	Warm (53)	Cold (47)	Warm (42)	Cold (35)
Mean . . . . .	12.604	13.180	12.663	11.889	67.19	60.11	68.95	59.49
	± 0.238	± 0.241	± 0.217	± 0.195	± 0.55	± 0.51	± 0.48	± 0.53
Standard deviation	3.119	2.522	2.107	1.783	5.98	5.20	4.61	4.63
	± 0.201	± 0.170	± 0.153	± 0.138	± 0.39	± 0.36	± 0.34	± 0.37

<sup>1)</sup> In a large proportion of cases before birth (see above).

<sup>2)</sup> It would doubtless have been a somewhat more scientific method of procedure to divide each litter into two portions, for the warm and cold rooms respectively, thus ensuring the presence, in these two rooms, of mice having the same parentage. This indeed had been done in the series of the preceding year, but such a procedure naturally involved considerable difficulties. I have therefore acted upon the supposition that the use of a sufficiently large number of broods would minimize the possibility that the two contrasted lots differed appreciably in their mean hereditary constitution.

<sup>3)</sup> The principle of selection was as follows: that male was chosen from

Unfortunately, only the weight and tail length of these mice were determined at the age of 6 weeks. At this time I did not realize that the foot and ear of a living mouse might readily be measured if the latter were etherized. The modification of foot-length and (with less certainty) of ear-length has already been demonstrated, however, for other lots of mice. Moreover, in the case of one set, comprizing over two hundred individuals, foot and ear measurements were made at the age of six weeks. The results of these latter measurements have



Curves showing tail length of parent mice at the age of 42 days. The upper line (W) represents the condition in the warm-room animals; the lower line (C) representing the condition in the cold-room animals. Abscissas denote weight in grams; ordinates denote tail length in millimeters. The figures along the curves represent the number of individuals in each size-group.

been plotted in graphic form (Figs. 3 and 4)<sup>1)</sup> and will be of interest by way of comparison with the curves (Figs. 6 and 7) which have

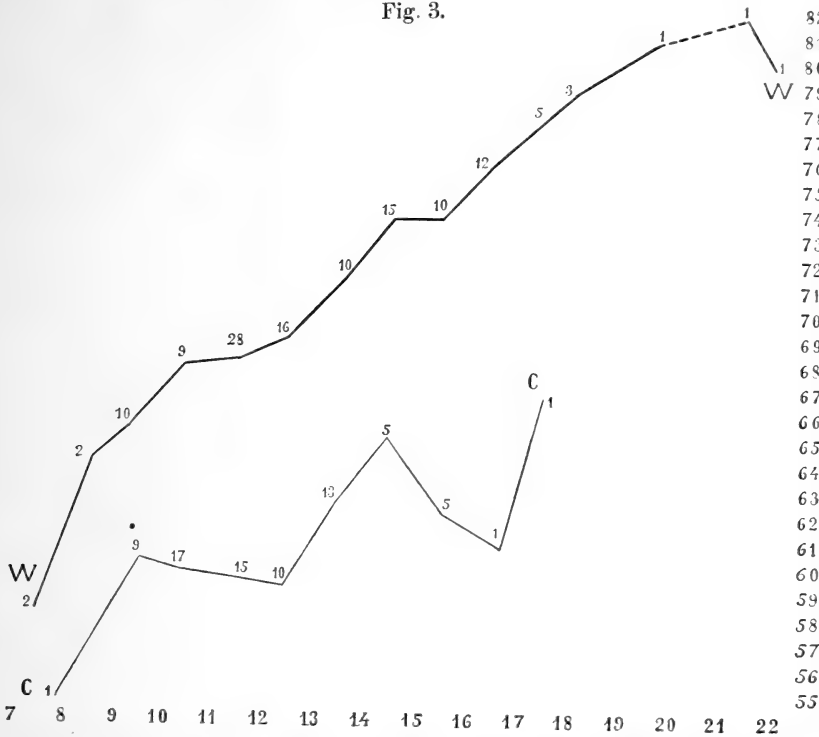
each brood which in weight approached most nearly the mean of the entire lot (>warm< or >cold<). Each male used for breeding was derived from a different brood.

<sup>1)</sup> This lot of mice comprized 80 cold-room and 129 warm-room individuals. They were the first offspring of the same parent brood as that just referred to, i. e. the parents of the generation to be discussed below. Since they were likewise subjected to considerable temperature differences, a possible cumula-

been constructed for the later offspring of the same parents. These latter curves are based upon measurements made at the same age (6 weeks), but they do not, like the foregoing, represent differences produced during the individual lifetime.

The relative modifiability of tail, foot and ear are clearly shown in the present diagrams (3 and 4), though it must be borne in mind

Fig. 3.



Curves representing tail length, at 42 days, of another lot of mice (first offspring of those represented in Fig. 2), which have been subjected to similar differences of temperature. For further explanation, see preceding figure.

that the scale for the two last characters is five times as great as that for the tail.

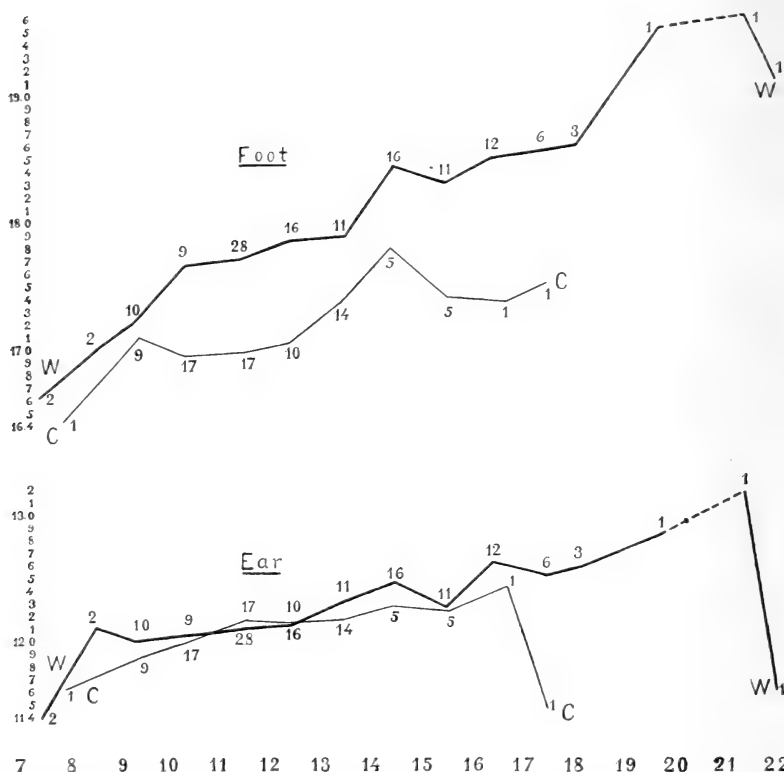
ative effect was sought for. Reference to the temperature chart (Fig. 1) shows us, however, that after the middle of March, when these second-generation mice were born, the temperature differences between the two rooms diminished rapidly. Thus the offspring were subjected to decidedly smaller differences than were the parents; and under these circumstances we could hardly hope to discover any cumulative effect. As a matter of fact, the figures, though inconclusive, are favorable, rather than contradictory, to the hypothesis of transmission. They will not, however, be presented here.



The parent mice, after they had been exposed to these temperature extremes for about six months, were paired for a second time on May 2, 1909. The resulting offspring are those to which attention will henceforth be devoted in this paper.

The demands of our problem would have been realized more

Fig. 4.

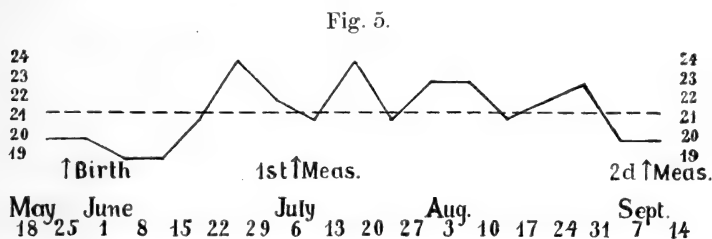


Foot and ear length of same mice as those represented in Fig. 3. Note that the vertical scale is five times as great as in the preceding figure.

completely had the two contrasted sets of parent mice been transferred to a common room before pairing. Unfortunately this was not done<sup>1</sup>). Indeed the females were not removed to such a room until each was

<sup>1</sup> My failure to do so was the result of deliberate intention. At the time of pairing this lot, I had in hand another lot of modified individuals which I expected to pair later under temperature conditions which should be identical for the two sets of parents. I should thus be able to perform both of these experiments, and further restrict the possibilities of interpretation. Circumstances prevented the fulfilment of this plan.

discovered to be pregnant. The discovery was made, on the average, about five days before the birth of the young, i. e. about two weeks after the actual commencement of pregnancy. Thus some indirect influence of the external temperature conditions upon the developing fetus is at least conceivable. Such a possibility will be considered later. At present I shall merely point out that at the time of the pairing (May 2) the differences in temperature between the two rooms had diminished greatly (Fig. 1) and that they continued to diminish rapidly. The average difference from May 2 to May 29 (when the last of the parent mice were brought into a common room) was only  $7.6^{\circ}\text{C}$ ., as compared with a difference of  $16.8^{\circ}$  during the preceding period. Furthermore, the mean date of the *commencement of pregnancy* was not May 2, but some days later.



Curve showing temperature conditions to which the offspring of the modified parents were subjected from birth up to the time of the last measurements. For further explanation see Fig. 1.

From the time when pregnancy became apparent, the two sets of mothers were kept in the same room and under conditions which were indetical for all, so far as care could make them so. Unequal temperature conditions were particularly guarded against. The cages containing the two contrasted sets of animals were kept close together upon alternate shelves, and this arrangement was continued throughout the first six weeks of the life of the young.

The temperature conditions to which the offspring were exposed are represented graphically in Fig. 5. The mean temperature for the entire period was  $21.4^{\circ}\text{C}$ . That from the mean date of birth (May 25) to the mean date of the first measurements (July 6) was  $20.8^{\circ}$ ; to the mean date of the second measurements (Sept. 8) it was  $21.4^{\circ}$ .

In all, about 182 living<sup>1)</sup> mice were born by the warm-room mothers; about 172 by the cold-room mothers. Of these, 141 offspring

<sup>1)</sup> A considerable number of still-born young are always to be reckoned with.

of the warm-room parents, belonging to 33 litters, and 145 offspring of cold-room parents, belonging to 30 litters, survived to the age of six weeks, when the first measurements were made. There was thus a somewhat greater mortality among the warm-room descendants, a tendency which was manifested even more strongly during the subsequent history of the animals.

Since the atmosphere in which these mice were reared underwent considerable changes of temperature from day to day and from week to week, depending upon climatic conditions, it was of course important that the animals should commence their lives at nearly or quite the same time, in order that they might all be subjected to conditions as nearly identical as possible throughout their history.

It is fortunate, therefore, that the mean date of birth differed in the two contrasted lots by only half a day. The extreme dates were May 21 and June 6 for the cold-room descendants, and May 22 and June 7 for the warm-room descendants. Furthermore, nearly 80 per cent of the former lot were born within a period of 5 days (May 21 to 25, inclusive); while 85 per cent of the latter lot were born within an equal interval (May 22 to 26, inclusive). Thus it will be impossible to ascribe any constant differences which may be discovered between these two lots of mice to differences in the external conditions to which they had been subjected during their own lifetime.

The young were measured first at the age of 42 days<sup>1</sup>). In order that the ear and foot length might be measured accurately at this time, the mice were rendered insensible by ether. The linear measurements were taken with a graduated sliding caliper, indicating tenths of a millimeter. In the case of the foot and ear, two measurements were made of each, the mean figure being employed in the computations<sup>2</sup>). The caliper scale was at all times invisible to me until the instrument was finally adjusted. This practice of course diminished the chances of unconscious bias in making the measurements. Further precautions were taken at the time of making the second series of determinations at the age of 3<sup>1</sup>/<sub>2</sub> months (see below).

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<sup>1</sup> In a small proportion of each lot the age was 43 days; in a yet smaller number it was 41 days.

<sup>2</sup> The average difference between the first and second reading of the caliper was 0.19 mm for the foot and 0.12 mm for the ear. Assuming that the value sought lay between the two readings of the instrument, it will be seen that the average error for foot and ear equals in each case about half the mean difference which was found to obtain between the two contrasted lots of mice.

From this earlier series of measurements the following gross averages were obtained:

	Weight (grams)	Tail (mm)	Foot (mm)	Ear (mm)
Cold-room descendants . . . .	10.897	71.04	17.833	12.434
Warm-room descendants . . . .	10.631	71.19	17.960	12.536

It will be seen at once that, although the offspring of the warm-room mice average slightly less in weight, they have slightly longer tails, feet and ears than the offspring of the cold-room mice. These differences are exactly such as were noted, on a larger scale, in the parent generation. But such gross averages do not, in themselves mean very much. In each of the contrasted lots were comprized individuals of widely different size (the extremes were 6.5 and 19.3 grams). Our material, therefore is not at all homogeneous.

Accordingly I have divided the animals into groups, each comprising individuals of approximately the same weight. These groups have further been subdivided according to sex, the averages for the males and the females being determined separately. Herewith are appended in tabular form the results of such an analysis (Table A).

Considering first the averages for the two contrasted sets of individuals within each size group as a whole (i. e. the sexes being combined), it will be seen that there are 11 groups in which such a comparison between warm-room and cold-room descendants is possible. The mean tail length for the former animals is greater in eight of these eleven cases (exceptions starred); the mean foot length is greater in nine of the eleven cases; while the mean ear length is greater in nine cases and equal in one case. Let us consider the likelihood that such results have been obtained through »chance«, i. e. that they are the result of a multitude of independent causes having no relation to the conditions of the experiment.

Our method of procedure is the same as that employed in determining the probability that a given number of »heads« or »tails« shall be thrown in the course of tossing a coin<sup>1)</sup>. We here resort to the well-known formula of the binomial theorem:  $(a + b)^n = a^n + na^{n-1}b + \frac{n(n-1)}{2}a^{n-2}b^2 + \frac{n(n-1)(n-2)}{2.3}a^{n-3}b^3 + \dots$  etc.

<sup>1)</sup> Apology is perhaps due for this excursion unto elementary mathematics. It is safe to say, however, that most of us allow our knowledge of even such elementary principles as these to lapse through years of disuse.

Now in any given throw, the chance for either a »head« or a »tail« is of course 1 out of 2. Our binomial thus becomes

$$\left(\frac{1}{2} + \frac{1}{2}\right)^n.$$

This, upon expansion and simplification, resolves it self into:

$$\left(\frac{1}{2}\right)^n + n\left(\frac{1}{2}\right)^{n-1} + \frac{n(n-1)}{2}\left(\frac{1}{2}\right)^{n-2} + \frac{n(n-1)(n-2)}{6}\left(\frac{1}{2}\right)^{n-3}, \text{ etc.}$$

As a concrete illustration, suppose that the number of throws:  $(n) = 4$ , then our equation becomes:

$$\left(\frac{1}{2} + \frac{1}{2}\right)^4 = \frac{1}{16} + \frac{4}{16} + \frac{6}{16} + \frac{4}{16} + \frac{1}{16}.$$

The successive coefficients (1, 4, 6, 4 and 1) represent respectively the chances that we shall throw 4 heads, 3 heads + 1 tail, 2 heads + 2 tails, 1 head + 3 tails, and 4 tails<sup>1)</sup>.

If, instead of 4 trials, we should take 11 trials, the chances of our throwing heads every time would be 1 in 2048; the chances of throwing 10 heads and 1 tail would be 11 in 2048; those of throwing 9 heads and 2 tails would be 55 in 2048, etc. What, now, are the chances that we shall obtain *as large a proportion of heads* as 9 out of 11? To find this we determine the collective chances for 11, 10 and 9 heads, i. e.  $\frac{1 + 11 + 55}{2048}$ , or  $\frac{67}{2048}$ , or approximately  $\frac{1}{30}$ .

The same figure represents the chances that in as large a majority of our size-groups as 9 out of 11 the mean figure for a given character shall be greater in the warm-room descendants.

		Figure larger for Warm-room descendants	Figure larger for Cold-room descendants	Figures equal.	Chances
Sexes com- bined	Tail . . . . .	8	3	—	$\frac{1}{9}$
	Foot . . . . .	9	2	—	$\frac{1}{30}$
	Ear . . . . .	9	1	1	$\frac{1}{32}$
	All three characters	26	6	1	$\frac{1}{2435}$
Sexes separ- ately	Tail . . . . .	14	5	—	$\frac{1}{63}$
	Foot . . . . .	16	3	—	$\frac{1}{452}$
	Ear . . . . .	13	5	1	$\frac{1}{17}$
	All three characters	43	13	1	$\frac{1}{19902}$

<sup>1)</sup> This may readily be verified by anyone who cares to figure out the number of possible combinations of H and T in four consecutive throws. We have H + H + H + H, H + H + H + T, etc. etc. It will be found that 16 such combinations are possible.



A table has been prepared (preceding page) showing the likelihood of the ›accidental‹ occurrence of such majorities for each of the characters singly and for all of them combined<sup>1</sup>). It will be seen that the cumulative improbability of the occurrence of all these majorities in the same direction is very high indeed, being about one in 2,400 in the case of the figures for the sexes combined. When we consider the sex-groups separately, it will be seen that the chances for the purely ›accidental‹ occurrence of such majorities are even slighter. Those for the preponderance of the ›warm‹ figure in 43 cases out of 57 (with one case of equality) are but a little over one in 20,000.

It must here be granted that those figures which express the cumulative improbability of a similar preponderance being manifested in all three of the characters measured are subject to one important qualification. They are accurate only upon the assumption that these characters vary quite independently of one another. In reality, there is probably a certain degree of correlation, the extent of which has not been determined. This correlation would, of course, considerably increase the chances here stated. But in any case they would remain so slight that in most of the practical affairs of life we should reject them as not worth considering.

The fact is worth noting that it is among the females that the preponderance of the ›warm‹ over the ›cold‹ figures is shown with the greatest approach to unanimity. For example we find among the 57 pairs of figures which admit of a comparison between two averages for the same sex, the following distribution of cases:

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<sup>1</sup>) It will be found that these figures differ throughout from those given in my preliminary paper in the *American Naturalist* (Jan. 1910). In most cases the probabilities here stated are just half as great as those which I had previously allowed. My earlier figures indicated the probabilities for the occurrence of such majorities in *either direction*. We are, however, only concerned with the probabilities for a preponderance in *one direction*, i. e. in favor of the warm-descendants.

Another source of discrepancy between the present figures and the earlier ones results from the treatment of those cases in which the two averages for a given character are equal. In the present computations, I have divided each instance of equality between the plus and minus groups. For example, to take the case of the ear measurements in the accompanying table (first-part), I have regarded the ›warm‹ figure as being larger in  $9\frac{1}{2}$  of the size-groups, smaller in  $1\frac{1}{2}$  of these. The probability given is the mean of the figures for 9 out of 11 and 10 out of 11. This seems a fairer procedure than that of throwing the case of equality out of consideration as I had earlier done.

	»Warm« figure larger	»Warm« figure smaller	The two equal
Males . . . . .	21	9	0
Females . . . . .	22	4	1

The same difference between the sexes in this respect is shown even more forcibly by the figures derived from the later measurements.

Thus far we have treated these groups as of equal value in our computations. From our table it will be seen, however, that the groups differ greatly in respect to the number of individuals comprized, and in respect to the magnitude of the differences shown. I have computed the probable errors of the averages for those seven size-groups which are large enough to make this worth while<sup>1</sup>). Taking into account the three characters (tail, foot and ear) for the seven groups, we have, accordingly, twenty-one probable errors for each of the contrasted sets (»warm« and »cold«). By a little figuring it may be shown that in twelve of these 21 cases the difference between the two contrasted averages is two<sup>2</sup>) or more times as great as the probable error of that difference; in one case the difference is over three times its probable error, and in three cases it is over four times its probable error. Furthermore, it is important to note that in none of the exceptional cases (i. e. those in which the cold-room descendants have *longer* peripheral parts) is the difference between the averages as high as two times its probable error<sup>3</sup>). The significance of these facts will be appreciated by anyone familiar with statistical methods.

Diagrams (Figures 6 and 7) have been constructed permitting of a comparison between the two contrasted sets of mice, with respect to the mean length of tail, foot and ear, for each of the size groups. The insignificance of the differences in the exceptional groups as compared with those conforming to the rule, is still further emphasized by these diagrams.

The question naturally arises: How do these differences between the warm-room and cold-room descendants compare in amount with the differences which were shown by the parents as a direct result of the

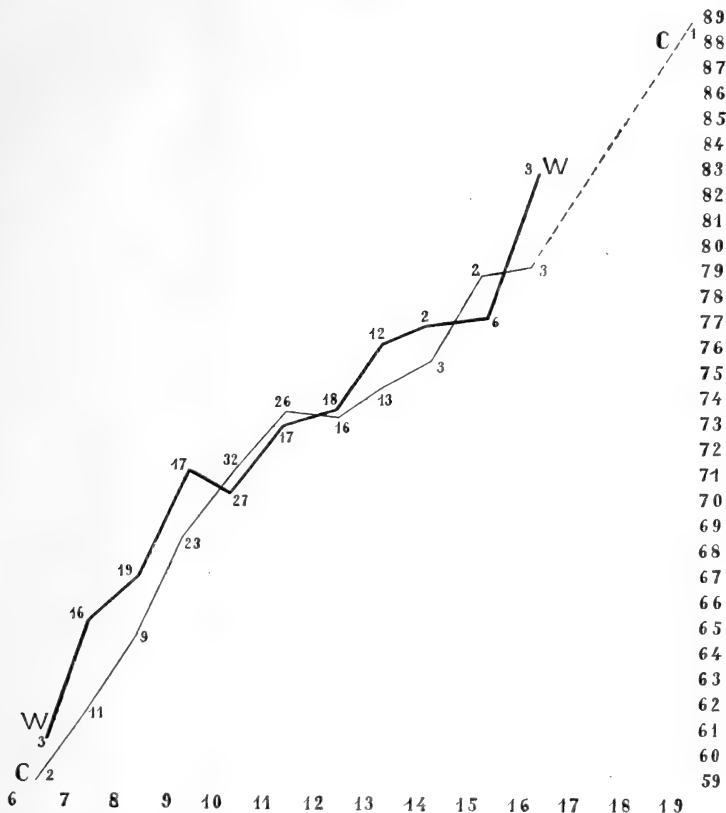
<sup>1</sup>) I. e. those in which both sets (»warm« and »cold«) consist of ten or more individuals apiece (in one exceptional case, one set contains only nine).

<sup>2</sup>) Here including one case in which it was *very nearly* twice as great.

<sup>3</sup>) In one case it is practically equal, in another it is considerably less.

external conditions to which they had been subjected? Unfortunately, the data necessary for a satisfactory answer to this question are not at hand, since, in the case of the parents of this particular lot, only the weight and tail length were determined at the age of six weeks<sup>1)</sup>. We may, however, make this comparison in respect to tail length.

Fig. 6.



Curves showing tail length, at 42 days, of the offspring of modified parents, reared under conditions identical for all. The heavy line (W) represents the condition in the offspring of warm-room parents, the lighter line (C) representing the condition in the offspring of cold-room parents. Abscissas denote weight in grams; ordinates denote tail length in millimeters. The figures along the curves denote the number of individuals in each size-group.

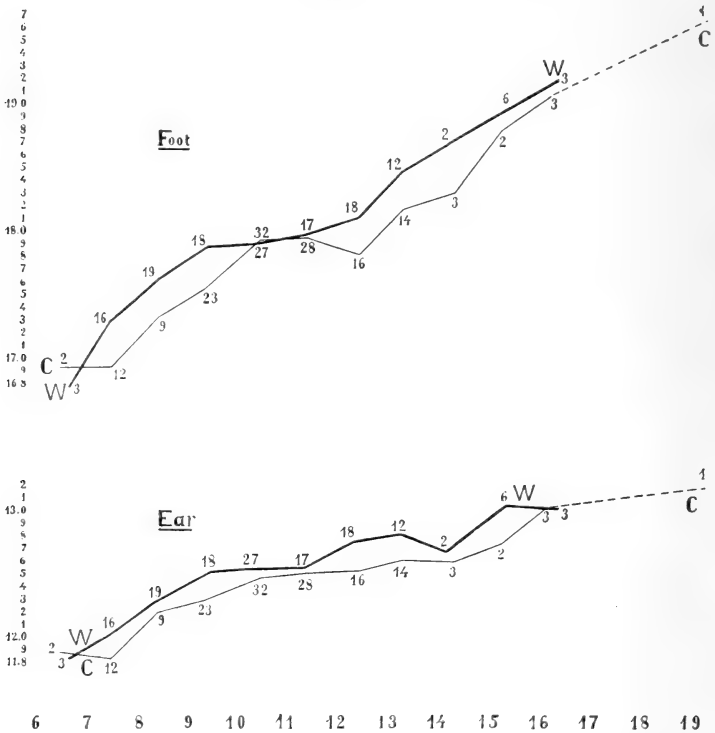
An inspection of Figures 2 and 6 shows at once that this difference has very much diminished in the second generation.

It will likewise be instructive to compare the the *mean* differences shown by parents and offspring in respect to this character.

<sup>1)</sup> See above.

To determine the extent of these differences, we shall consider, not the differences between the gross averages, for reasons already stated, but the average difference between the »warm« and the »cold« figure within each size-group. The mean difference in tail length, as thus computed, shown by the parent generation at the age of six weeks, was 8.195 mm, that shown by the offspring being 1.264. Thus the latter figure is a little over 15 per cent of the former.

Fig. 7.



Showing foot and ear length of same mice as those represented in Fig. 6. Note that vertical scale is five times as great as in preceding figure. For further explanation, see the latter.

As regards foot and ear length, we may profitably compare the generation with which we are dealing here with the first offspring of the same parents. These first offspring, it will be recalled, were subjected to temperature differences similar to (though not as great as) those to which the parents had been exposed. An instructive comparison may therefore be made between the curves (Figs. 3 and 4) for these mice which had themselves been directly modified and

the curves (Figs. 6 and 7) for mice whose parents alone had been modified.

We may likewise compare the figures expressing the mean differences, computed according to the principle just stated:

	Mice directly modified <sup>1)</sup>	Offspring of modified individuals
Tail . . . . .	9.710	1.264
Foot . . . . .	0.7138	0.1890
Ear . . . . .	0.2021	0.1281

Comparing these two sets of figures, we find that the difference in tail length is 13 per cent as great in the second case as in the first; the difference in foot-length is 26 per cent as great, while the difference in ear length is 63 per cent as great! These figures are not offered as expressing, with even a rough degree of approximation, the proportional part of these parental modifications which is handed on to the offspring — even granting that it is *handed on* in any strict sense of the words. The relative magnitude of the three percentages is particularly surprising, in view of the fact that the tail is the organ which responds most decidedly to the temperature differences, while the ear has been shown to be the least affected. It might be argued that the very plasticity of a part, which makes it so responsive to outside influences, might render it correspondingly ill-adapted to retaining such impressions permanently<sup>2)</sup>. Such speculations would be decidedly premature, however.

As already stated another set of measurements was made with this same lot of mice when they reached the age of about 3½ months. By that time the numbers had been considerably reduced by death<sup>3)</sup>.

<sup>1)</sup> Comment may be made in passing upon the fact that in this lot the difference in tail-length is over 1.5 mm greater than in the case of the parents, despite the fact that the temperature differences had been much greater for the latter. I will not lay much emphasis on this circumstance, however, since it has been shown in my earlier paper (1909) that different lots of mice may respond to a very different extent to substantially the same differences of temperature.

<sup>2)</sup> It may be pertinent to point out, likewise, that the tail is far more variable than either the foot or the ear.

<sup>3)</sup> A certain proportion had succumbed under the influence of the ether. at the time of the 42-day measurements. Commencing with about July 1, I was prevented by other duties from giving proper attention to the animals. They were kept in a limited number of cages, and over-crowding was doubtless responsible for many deaths.



There were at the later date 114 of the cold-room descendants, and only 84 of the warm-room descendants. The survivors all appeared to be in good health, however, and few or no deaths had occurred during the few weeks immediately preceding these measurements.

At the time of the first series of measurements, each mouse had been measured upon arriving at a certain age (42 days). The later series, on the contrary, were made during a period of one week (September 5—11), and without reference to the age of the individual mice<sup>1</sup>). An approximately equal proportion of warm-room and cold-room descendants were, however, measured each day of this period. It was determined later that the mean age of the two sets of individuals at the time of these second measurements was in each case almost exactly the same, i. e. about 105 days. The youngest mouse was 90 days old, the oldest being 113 days old. These extremes were exceptional, however, for 76 per cent of the cold-room descendants were between the ages of 103 and 110 days, while 87 per cent of the warm-room descendants were between the ages of 103 and 109 days.

In order to exclude the possible influence of suggestion or unconscious bias in determining these rather delicate caliper measurements, I adopted at this time the plan of keeping myself in ignorance as to the parentage of each mouse until the latter had been measured. The animals were put into separate small cages, each bearing an identification mark upon the bottom. These cages were then »shuffled« by one of my colleagues in the laboratory.

The mice were killed at the time of these latter measurements. For this reason it was possible to determine another character — body length — with accuracy. This is not feasible with living animals, even when etherized.

The gross averages for the two contrasted sets of individuals are presented herewith:

	Weight	Body length	Tail	Foot	Ear
Cold-room descendants (114)	18.56	86.703	81.162	17.8960	13.3386
Warm-room descendants (84)	19.45	87.683	82.732	18.1427	13.5143

<sup>1</sup>) The latter — identified by marks, to be sure — had been mingled together in a few large cages, and it would have required much labor to pick out, each day, those which had arrived at the age desired.

It will be seen at a glance that the mean length of tail, foot and ear is, as was previously the case, greater for the warm-room descendants than for the cold-room descendants. But the differences between these gross averages signify even less here than in the case of the earlier figures, since the two contrasted lots now differ quite appreciably in their mean size. The warm-room descendants are heavier on the average by more than a gram, while their average body length is nearly one millimeter greater. For this reason it is even more important that our animals should be divided into groups according to size. I have, accordingly, grouped the mice in two different ways: 1) according to weight, as was done previously, and 2) according to body length. The latter method of grouping seems a much fairer one than the first, for it seems likely that the length of the appendages is correlated primarily with body length and only incidentally with weight. The latter, of course, depends in large degree upon the nutritive condition of the animal, amount of adipose tissue, etc. The single weight-groups, it may be added, contained individuals which differed from one another by as much as 4 or 5 mm of body length.

To consider the second of these methods first, the animals were divided into groups, within each of which the individuals differed by less than one millimeter in length. The appended table (B) permits of a comparison of warm-room and cold-room descendants within each of these size-groups, for each sex separately, and for the two sexes combined.

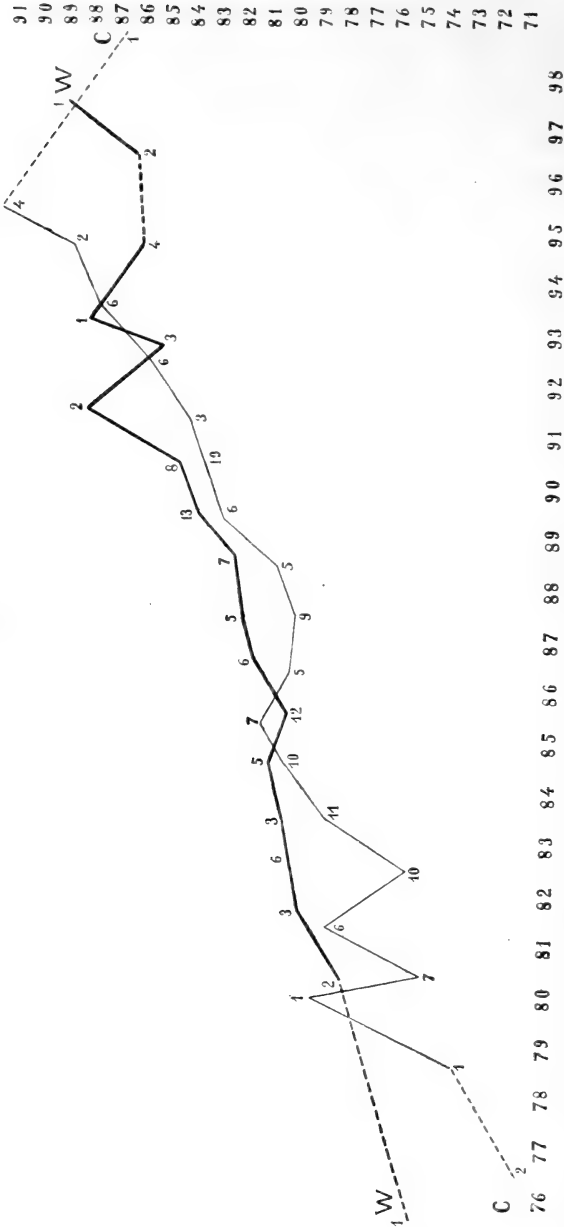
Considering the averages for the two sexes combined, we find that in the 15 size-groups which admit of such a comparison, the »warm« figures for tail, foot and ear length are larger than the »cold« figures in 12, 11 and 10 cases respectively. The chances for the accidental occurrence of such majorities are approximately 1 in 57, 1 in 17, and 1 in 7, respectively. But we have the cumulative testimony of all three of these characters, pointing in the same direction. The chances that the »warm« figure shall thus be greater in 33 out of the 45 cases are only 1 in 814<sup>1)</sup>.

If we deal with the sexes separately, we find 21 groups within which comparison is possible between the warm-room and cold-room descendants, or 63 pairs of averages, when the three characters are considered. In 40 of these the »warm« figure is larger than the

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<sup>1)</sup> Leaving out of account correlation between these characters (see above).

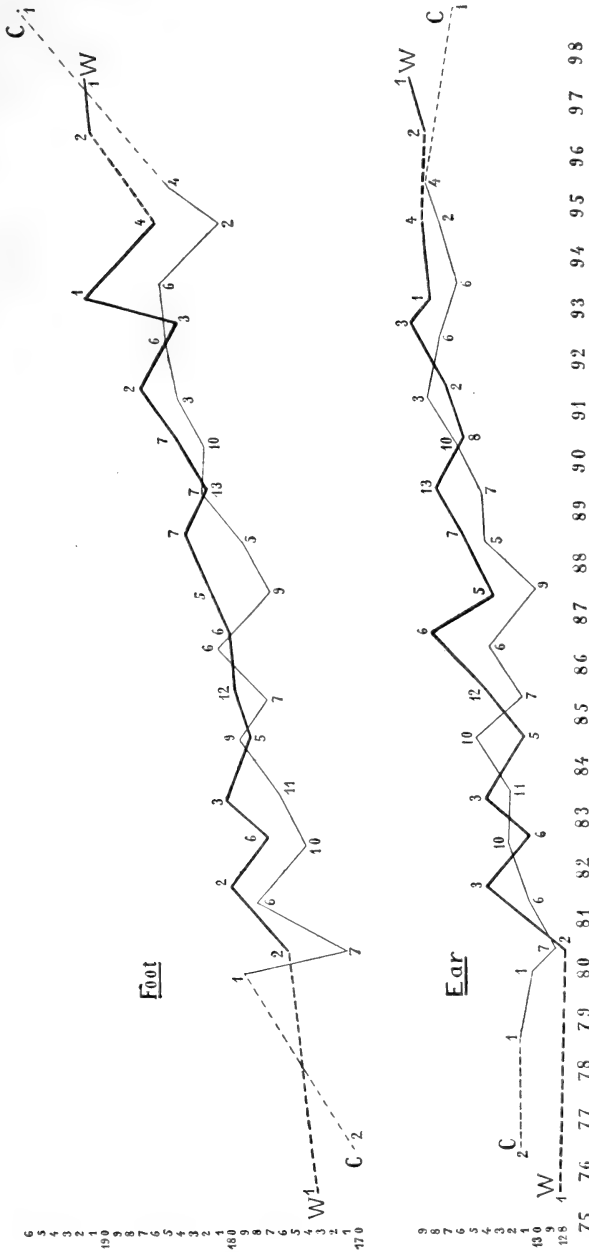
Fig. 8.



Tail length of same generation of offspring as the foregoing, measured at the age of 3 1/2 months; here divided into groups according to body length. Abscissas denote body length in millimeters; ordinates denote tail length in millimeters. For further explanation, see Fig. 6.

»cold« figure; in 22 cases it is smaller, while in a single case the two figures are equal. The probabilities for such a state of affairs may be computed by the reader if he chooses. The author does not at present care to devote himself further to this pastime. As was

Fig. 9.



Foot and ear length of same generation of offspring, likewise at the age of 3 1/2 months. (See legend under Fig. 8.)

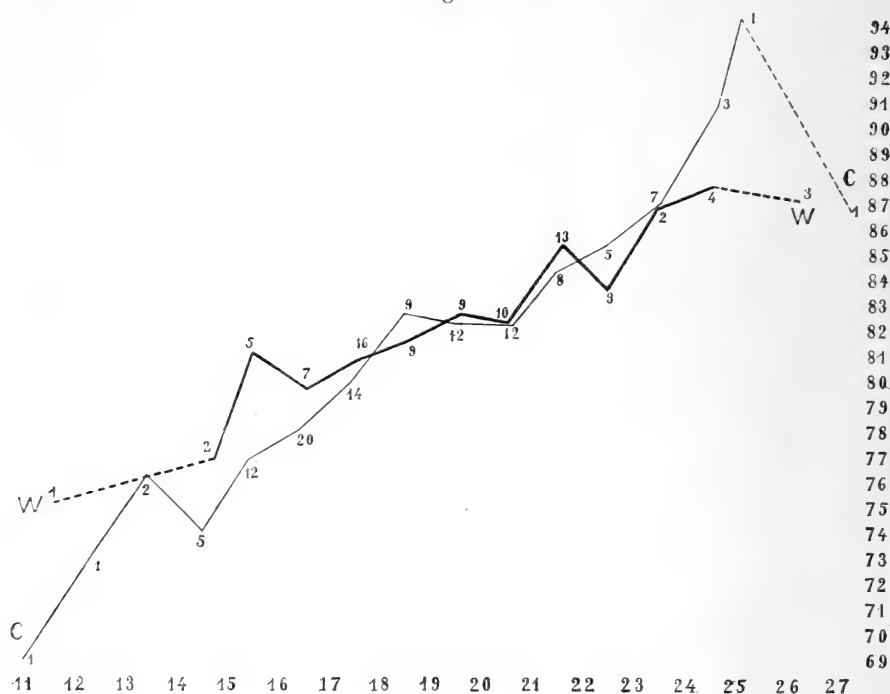
the case with the earlier measurements, the females show a much closer approach to unanimity in this tendency than the males. Among the former there are 19 positive cases and 8 negative ones; among

the latter, 21 positive cases, 14 negative ones, and 1 case of equality.

The diagrams (Figs. 8 and 9) show these relations graphically, and demand no discussion. As regards the ear, the case can hardly be regarded as convincing.

In the next table (C) the averages for the weight-groups have been presented. In the 12 groups which admit of a comparison between

Fig. 10.



Tail length of the same generation of offspring, likewise at the age of  $3\frac{1}{2}$  months; here grouped according to weight.

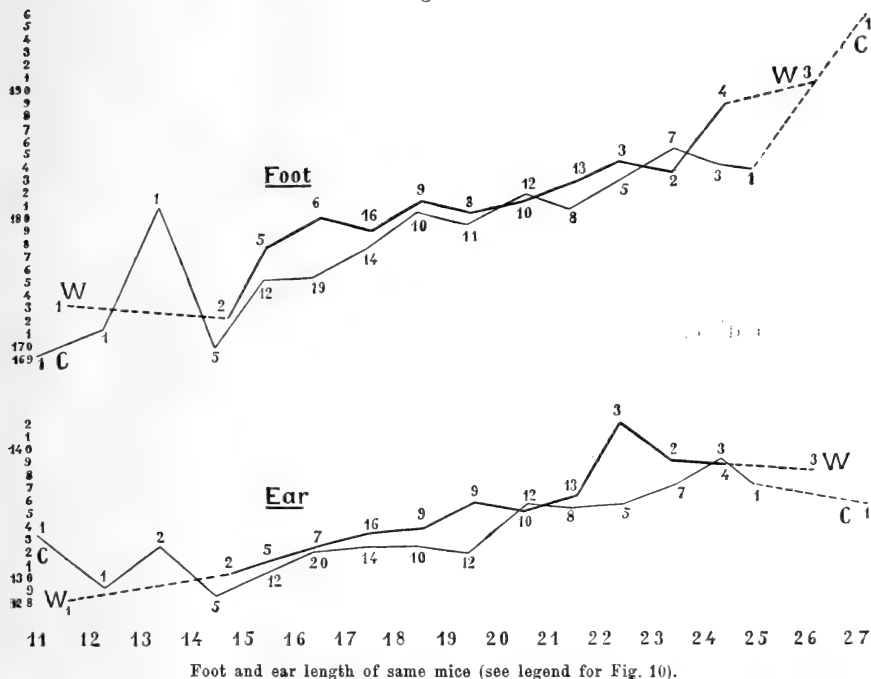
the averages for all individuals (sexes combined), the mean length of tail, foot and ear is larger in the warm-room descendants in 8, 10 and 9 cases respectively. The probabilities for these majorities are 1 in 5, 1 in 52 and 1 in 14 respectively. The chances that in 27 out of 36 cases (considering all three characters) the »warm« figure would be larger are only 1 in 508.

It must be granted, however, that when the sexes are considered separately, the figures are somewhat equivocal. There are 15 groups in which we may compare the »warm« and »cold« figure for mice



of the same weight and of the same sex. Taking into account the three characters under consideration, there are thus 45 pairs of contrasted figures to be reckoned with. The figure for the ›warm‹-room descendants is greater in 26 of these cases, smaller in 19. The preponderance is thus not large. Furthermore, for one character (foot length) there is an actual majority in favour of the cold-room descendants, i. e. there are only 7 cases in which the ›warm‹ figure is larger, 8 in which the ›cold‹ figure is larger. Indeed among the males alone, there are only 3 positive cases and 6 negative ones.

Fig. 11.



Foot and ear length of same mice (see legend for Fig. 10).

When all three of the characters are considered, the males show 12 positive cases to 15 negative ones, i. e. the ›cold‹ figures is larger in an actual majority of cases. For the females, however, the relations are quite different. We have 14 positive cases and 4 negative ones.

Thus, a consideration of this last table, taken by itself would not be very convincing, though it must be remembered that the general tendency of the figures, viewed as a whole, is distinctly in accordance with the results of the earlier analyses. As may be seen

at a glance, the curves (Figure 11) which are based upon the averages for the weight-groups (sexes combined) show that for foot and ear length, at least, the same relations obtain as were previously portrayed in Figs. 7 and 9.

It might indeed have been anticipated that the results derived from these later measurements would be less striking than those derived from the earlier ones<sup>1</sup>). To begin with, the number of individuals was considerably reduced, they varied somewhat in age, and the mean size of the two contrasted lots differed. Then too, we have to reckon with the principle of the »levelling down of initial differences«, concerning which I have had considerable to say in an earlier paper. And lastly, it is possible that unconscious bias in the use of the calipers may have somewhat exaggerated the differences shown in the earlier series of measurements, although caution was, of course, taken to avoid this.

### Summary and Conclusions.

1) Mice which were reared in a warm-room (about 21° C.) were found to differ considerably from those reared in a cold-room (about 5° C.) as regards the mean length of the tail, foot and ear. These organs were found to be longer in the former than in the latter set of individuals. (The two sets probably also differed from one another in respect to the amount of hair, though this does not concern us here.)

2) These same differences were found to be manifested by the *offspring* of the warm-room and the cold-room parents, although the animals belonging to this second generation were all reared together in a common room, and exposed to identical temperature conditions. In the experiment here considered, there were 141 of the warm-room descendants, 145 of the cold-room descendants.

3) These differences between the warm-room and cold-room descendants are revealed not only through a comparison of the gross averages for these three characters in the two contrasted sets of in-

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<sup>1</sup>) As a matter of fact, I had not yet analyzed the data from the earlier measurements at the time when the later ones were made, and at that time had no expectation that these interesting relations would be shown to exist. Indeed nothing was observed during the course of the measurements to justify such an expectation.

dividuals, but by a comparison between averages computed for each group when the mice have been divided into groups according to size, and when these groups have been still further subdivided according to sex. By calculations of probability it has been shown that the chances for the purely >accidental< occurrence of all these differences are very slight.

4) These differences among the offspring were manifested with fullest certainty in an earlier series of measurements, made at the age of six weeks. In a later series, made at the mean age of 3½ months, the same relations were found to exist, though to a less striking degree.

5) The differences were exhibited with a closer approach to unanimity by the females than by the males. It does not seem justifiable, however, to lay much stress upon this fact without further data.

I will freely grant that this reappearance of the parental differences in the two sets of offspring is open to a number of interpretations. Some of these have little to warrant them and may be disposed of briefly:

A. The differences in the offspring may have been due to >coincidence< or >accident<. The odds against such an occurrence have been shown to be high. Indeed the cumulative improbability that all these differences have been accidental is enormous.

B. They may have resulted unconsciously from a slight though constant biasing of the caliper measurements in favour of that result which was calculated to give the greatest personal satisfaction. This possibility has been excluded in the case of the second series of measurements.

C. Granting their genuineness, these differences may have been due to the immediate effect of temperature as such upon the germ-cells. Since, however, we are dealing with a warm-blooded animal, it would be necessary to assume either that such an effect was impressed upon the germ-cells during the first few days after birth, before the animal had become homoiothermic, or that slight and hitherto unmeasured differences in the internal temperature of the adults were sufficient to affect the germ-cells. In either case, the production of *parallel* modifications in parent and offspring would have to be accounted for.

D. These differences may be related to the circumstance that the difference in temperature conditions to which the parents were sub-

jected was continued (though to a qualified extent) during the earlier stages of pregnancy of the mothers. This interpretation is subject to the same objections as the preceding. It is obvious that in a warm-blooded animal the fetus could not be directly affected by differences of temperature *as such*. And, even if we grant some indirect influence upon the fetus, it would be curious indeed if the parental modifications should be so closely paralleled.

Deserving more serious consideration, we believe, are the following possible interpretations of these results:

E. The differences may have been due, not to any specific influence (hereditary or otherwise) which has affected the tail, foot or ear directly, but to some general constitutional difference in the offspring of the two sets of parents. In other words, these differences in the length of the peripheral parts may be *correlated* with some constitutional difference of a very general sort<sup>1</sup>). In this connection, it must be admitted that the offspring of the warm-room mice showed a very much higher mortality (40 per cent between the first and second measurements) than those of the cold-room mice (20 per cent). The former were likewise somewhat larger, on the average, when measured at the age of three months. Thus there did appear to exist some sort of a constitutional difference, at least as regards certain individuals. We should not be justified, however, in assuming any such difference in constitution between *surviving mice of equal size*, and these it was which have been compared in our tables. And in any case, we do not thus far have the least evidence that the length of these appendages is correlated with any such congenital differences in constitution.

F. An explanation closely similar to the last would be that the general stage of development in one lot of mice had been accelerated or retarded as compared with that of the other. We know that the ears and feet of young mice are relatively much larger than those of older ones. It might be contended, therefore, that the warm-room descendants were in a relatively more juvenile condition, as a result, perhaps, of an enfeeblement to which their parents had been subjected. This supposition is hardly in accord, however, with the fact

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<sup>1</sup>) HATAI (Journal of Comparative Neurology and Psychology. 1908) believes that he has demonstrated for white rats that underfeeding produces short tailed individuals. Since this conclusion appears to be based upon a consideration of only five underfed animals, it cannot be regarded as proven. On the other hand, there is nothing improbable about it.

that these warm-room descendants were no smaller than the cold-room descendants. Indeed they were larger at the time of the second measurements.

G. One of the alternatives considered above (C) might be offered in a modified form. It might be conceded that temperature *as such* could not affect either the fetus or the germ-cells to any appreciable extent. But it might, on the other hand, be contended that the effects of temperature, even upon the parent body itself, may not be direct, but may be due to the formation of specific chemical substances which, through the medium of the blood, may be supposed to simultaneously influence the body and the germ-cells. Such a hypothesis can neither be proved nor disproved in the present state of our knowledge, but it is perhaps the type of explanation which is calculated to appeal most strongly to the biologist of to day. It may be pointed out, however, that *if a mechanism exists whereby the germ-cells may be so influenced as to bring about a modification of the offspring parallel to that which was undergone by the parent, such a mechanism would be of exactly the same value for evolution as the »inheritance of acquired characters« in the old sense.* For heredity, however, the case would be somewhat different. We might still continue to talk about the »continuity of the germ-plasm«, though that expression would have been shorn of much of its meaning.

H. Finally, we have the view that the changes undergone by the parent body are themselves registered in some way in the germ-cells, so as to be repeated, in a certain measure, in the body of the offspring. The »classical« attempt to make this process intelligible is of course DARWIN'S hypothesis of »pangenesi«. Other views have been put forward recently<sup>1)</sup> which are scarcely to be distinguished from the preceding type of explanation (G).

In conclusion, the writer will express his qualified conviction that the truth is contained in one or both of the last two alternatives. It would not be profitable, however, to enter into any scholastic discussion of these various hypothesis. One after another of these alternatives must be excluded by carefully planned experiments, and it is the intention of the present writer to continue such experiments on a much greater scale in the near future.

Naples Zoological Station<sup>2)</sup>, Feb. 26, 1910.

<sup>1)</sup> E. g. the »hormone theory« of CUNNINGHAM (Archiv f. Entw.-Mech. 1908).

<sup>2)</sup> My hearty thanks are due to the director and staff of the station for facilitating the work of preparing this paper, particularly in placing at my

## Zusammenfassung und Folgerungen.

1) Es ergab sich, daß in einem warmen (etwa 21° C.) Raume aufgezogene Mäuse sich erheblich bezüglich ihrer mittleren Schwanz-, Fuß- und Ohrlänge von den im kalten (ungefähr 5° C.) erzogenen unterscheiden. Ich fand diese Organe länger bei dem ersten als bei dem zweiten Tiersatz. (Die zwei Sätze sind voneinander wahrscheinlich auch in bezug auf die Haarmenge unterschieden, doch geht uns dies hier nichts an.)

2) Ich fand, daß sich diese selben Unterschiede auch bei den *Nachkommen* der Warm- und Kaltraumeltern zeigten, obgleich die zu dieser zweiten Generation gehörigen Tiere alle zusammen in einem gemeinsamen Raume aufgezogen und identischen Temperaturverhältnissen ausgesetzt waren. Bei dem hier besprochenen Versuch kamen 141 von den Warmraum- und 145 von den Kaltraumnachkommen unter Beobachtung.

3) Diese Unterschiede zwischen den Warm- und Kaltraumnachkommen ergeben sich nicht bloß aus einem Vergleich des groben Durchschnitts der beiden gegensätzlichen Tiergesellschaften bezüglich der drei erwähnten Charaktere, sondern durch einen Vergleich zwischen Durchschnittswerten, die in *der* Weise für jede Gruppe aufgestellt sind, daß die Mäuse erst nach der Größe in Gruppen geteilt wurden, und dann diese Gruppen noch weiter in Unterabteilungen nach dem Geschlecht. Durch die Wahrscheinlichkeitsrechnung wurde gezeigt, daß die Chancen für ein lediglich zufälliges Vorkommen aller dieser Unterschiede sehr gering sind.

4) Diese Differenzen unter der Nachkommenschaft zeigten sich mit vollster Sicherheit bei einer frühzeitigen, im Alter von 6 Wochen vorgenommenen Serie von Messungen. Bei einer späteren, im mittleren Alter von 3½ Monaten angestellten Messungsreihe zeigte sich das Bestehen derselben Größenbeziehungen, doch in einem weniger frappanten Grade.

5) Die Differenzen wurden von den Weibchen mit einer größeren Annäherung an eine allgemeine Übereinstimmung zur Schau getragen, als von den Männchen. Immerhin erscheint es nicht gerechtfertigt, auf diesen Umstand ohne neue Tatsachen zu großes Gewicht zu legen.

Ich will gern zugeben, daß dieses Wiedererscheinen der elterlichen Verschiedenheiten zwischen den beiden Nachkommensätzen eine Anzahl verschiedener Erklärungen zuläßt. Für einige von ihnen lassen sich nur wenige Stützen finden, und diese sollen kurz abgetan werden:

A. Die Verschiedenheiten bei der Nachkommenschaft können auf »Koinzidenz« oder auf »Zufall« beruhen. Es wurde aber gezeigt, daß die Wahrscheinlichkeit sehr gegen ein derartiges Vorkommen spricht. In der Tat ergibt sich eine enorme Häufung der Unwahrscheinlichkeiten gegen die Auffassung, daß alle diese Differenzen rein zufällig sind.

B. Sie könnten unwissentlich von einer geringen, doch konstanten Beein-

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disposal the services of a draughtsman, who assisted in the preparation of the charts. The experiments upon which this paper is based were conducted at Woods Hole, partly in the Laboratory of the United States Bureau of Fisheries, partly in the Marine Biological Laboratory. My thanks are due to the director of the latter institution for placing at my disposal a small building in which my »cold-room« mice were reared during the experiments of the third year.

flussung der Kalibermessungen im Sinne desjenigen Ergebnisses herrühren, von dem man sich voraussichtlich die größte persönliche Befriedigung versprechen konnte. Diese Möglichkeit ist bei der zweiten Messungsreihe ausgeschlossen worden.

C. Gesteht man ihr wirkliches genuines Vorhandensein zu, so könnten diese Verschiedenheiten auf dem Einfluß der Temperatur unmittelbar als solchem auf die Keimzellen beruhen. Da wir es ja aber mit einem warmblütigen Tier zu tun haben, so müßte man da notwendigerweise annehmen, daß ein solcher Einfluß auf die Keimzellen während der ersten paar Tage nach der Geburt ausgeübt wurde, bevor das Tier noch homöotherm geworden war, oder, daß ganz geringe und bis jetzt noch nicht gemessene Differenzen in der Innentemperatur der erwachsenen Tiere zur Beeinflussung der Keimzellen hinreichten. In beiden Fällen wäre für die Entstehung *paralleler* Veränderungen bei Eltern und Nachkommen noch die Erklärung zu finden.

D. Diese Verschiedenheiten könnten mit dem Umstand in Beziehung gebracht werden, daß die Verschiedenheiten der Temperaturverhältnisse, denen die Eltern unterlagen, noch während der frühen Schwangerschaft der Mütter anhielten (allerdings in beschränkter Ausdehnung). Diese Erklärung unterliegt denselben Einwürfen wie die vorige. Es liegt auf der Hand, daß bei einem warmblütigen Tier der Fötus durch Temperaturdifferenzen *als solche* nicht beeinflusst werden kann. Und selbst wenn wir einen gewissen indirekten Einfluß auf den Fötus zugeben wollen, so wäre es doch sehr merkwürdig, wenn es dadurch zu so strikten Parallelveränderungen zu den mütterlichen kommen sollte.

Ernstlichere Erwägung verdienen, wie wir glauben, die folgenden Erklärungsversuche der vorliegenden Ergebnisse:

E. Die Verschiedenheiten können beruhen, nicht auf einer spezifischen Einwirkung (durch Erblichkeit oder anderswie), die den Schwanz, den Fuß, das Ohr direkt beeinflusst hatte, sondern in einer gewissen allgemeinen konstitutionellen Verschiedenheit der Nachkommen aus den zwei elterlichen Tiersätzen. Mit andern Worten: Diese Differenzen in der Länge der peripheren Teile könnten *in Correlation stehen* mit einer gewissen konstitutionellen Verschiedenheit sehr allgemeiner Art<sup>1)</sup>. In diesem Zusammenhange muß zugegeben werden, daß die Nachkommenschaft der Warmraum-Mäuse eine sehr viel höhere Mortalität zeigte (40% zwischen der ersten und zweiten Messung), als diejenige der Kaltraum-Mäuse (20%). Die ersteren waren außerdem im Durchschnitt etwas größer, als sie im Alter von 3 Monaten gemessen wurden. Also scheint da eine Art von konstitutioneller Verschiedenheit zu existieren, wenigstens soweit das gewisse Individuen angeht. Dennoch wären wir nicht berechtigt, zwischen *überlebenden Mäusen gleicher Größe* irgendeine derartige konstitutionelle Verschiedenheit anzunehmen, und nur solche wurden in unseren Tabellen verglichen. Und in jedem Falle haben wir insoweit nicht das geringste Zeichen dafür, daß die Länge dieser Anhänge mit irgend solchen congenitalen konstitutionellen Verschiedenheiten in Correlation steht.

<sup>1)</sup> HATAI (Journal of Comparative Neurology and Psychology. 1908) meint für die weiße Ratte gezeigt zu haben, daß unzulängliche Fütterung Individuen mit kurzen Schwänzen hervorbringt. Da dieser Schluß lediglich auf der Beobachtung von nur fünf unzulänglich gefütterten Tieren zu basieren scheint, so kann er nicht als bewiesen gelten. Andererseits liegt darin aber durchaus nichts unwahrscheinliches.

F. Eine der letzterwähnten ganz ähnliche Erklärung würde die sein, daß der allgemeine Entwicklungszustand bei dem einen Mäusesatz dem des andern gegenüber beschleunigt bzw. verzögert worden ist. Wir wissen, daß die Ohren und Füße von jungen Mäusen verhältnismäßig viel größer sind als die von alten. Es könnte daher behauptet werden, daß sich die Warmraumnachkommen in einem verhältnismäßig jugendlicheren Zustande befinden, vielleicht infolge einer Schwächung, die ihre Eltern erfuhren. Diese Annahme ist jedoch schwerlich mit der Tatsache in Übereinstimmung zu bringen, daß diese Warmraumnachkommen nicht kleiner als die Kaltraumnachkommen sind. In der Tat waren sie größer zur Zeit der zweiten Messung.

G. Eine von den oben (unter C.) betrachteten Alternativen könnte sich in veränderter Form darbieten: Man könnte zugeben, daß Temperatur *als solche* weder den Fötus noch die Keimzellen irgendwie affizieren kann. Es könnte aber anderseits behauptet werden, daß die Temperaturwirkungen sogar auf den elterlichen Körper selbst nicht direkte sein könnten, sondern auf der Bildung spezifischer chemischer Substanzen beruhen könnten, welche unter Vermittlung des Blutes gleichzeitig einen Einfluß auf den Körper und die Keimzellen haben könnten. Eine derartige Hypothese kann beim gegenwärtigen Stande unsres Wissens weder bewiesen noch widerlegt werden, — das ist aber vielleicht der Erklärungstypus, der darauf berechnet ist, die stärkste Anziehungskraft auf die heutigen Biologen auszuüben. Immerhin soll hervorgehoben werden, daß, wenn ein Mechanismus existiert, durch den die Keimzellen so beeinflusst werden können, daß sie eine Veränderung der Nachkommenschaft parallel zu den von den Eltern erlittenen Veränderungen hervorbringen, dieser Mechanismus für die Entwicklungslehre genau denselben Wert hätte, wie die »Vererbung erworbener Eigenschaften« im alten Sinne. Für die Erbllichkeit würde der Fall immerhin etwas anders liegen. Wir könnten immer noch fortfahren, von der »Kontinuität des Keimplasmas« zu reden, jedoch würde dieser Ausdruck viel von seiner Bedeutung eingebüßt haben.

H. Endlich haben wir noch die Ansicht, daß die vom elterlichen Körper erlittenen Veränderungen selbst auf irgendeine Weise in den Keimzellen registriert werden, so daß sie sich in einem gewissen Grade im Körper der Nachkommenschaft wiederholen. Der »klassische« Versuch, diesen Prozeß dem Verständnis näher zu bringen, ist natürlich DARWINS »Pangenesi«-Hypothese. Andre Ansichten sind neuerdings ausgesprochen worden, welche sich kaum von dem vorhergehenden Erklärungstypus (G.) unterscheiden<sup>1)</sup>.

Zum Schluß möchte Schreiber dieses seiner bedingten Überzeugung Ausdruck geben, daß die Wahrheit in einer oder in beiden von den letzten zwei Alternativen liegt. Es würde jedoch nicht viel nützen, in eine scholastische Diskussion dieser verschiedenen Hypothesen einzutreten. Eine nach der andern müssen diese Alternativen durch sorgfältig entworfene Versuche zur Erledigung kommen, und es ist die Absicht des Verfassers, derartige Versuche in nächster Zeit in einem viel größeren Maßstabe fortzusetzen.

(Übersetzt den 7./8. März 1910. **W. Gebhardt.**)

<sup>1)</sup> z. B. die »Hormonentheorie« von CUNNINGHAM (Archiv f. Entw.-Mech. 1908).



Table A.

Offspring of Cold-room and Warm-room Parents, measured at 42 days.

Size-group	Sex	Parentage	Number of individuals	Weight	Tail	Foot	Ear
6—6.9 grams	♂	Cold	1	6.60	60.00	17.100	11.750
		Warm					
	♀	Cold	2	6.55	59.00	16.950	11.900
		Warm	2	6.85	61.00	16.650*	11.900*
7—7.9 grams	♂	Cold	2	6.55	59.00	16.950	11.900
		Warm	3	6.77	60.67	16.800*	11.850*
	♀	Cold	3	7.57	62.67	17.217	12.317
		Warm	11	7.53	64.36	17.336	12.032*
8—8.9 grams	♂	Cold	9	7.57	61.62	16.867	11.694
		Warm	5	7.70	67.60	17.250	12.050
	Alto-gether	Cold	12	7.57	61.91 ± 0.79	16.954 ± 0.110	11.850 ± 0.076
		Warm	16	7.58	65.37 ± 0.51	17.319 ± 0.082	12.037 ± 0.047
9—9.9 grams	♂	Cold	3	8.50	66.00	17.617	12.283
		Warm	11	8.39	67.45	17.677	12.200*
	♀	Cold	6	8.52	64.17	17.225	12.183
		Warm	8	8.60	66.62	17.594	12.469
10—10.9 grams	♂	Cold	9	8.51	64.78 ± 1.23	17.356 ± 0.110	12.217 ± 0.054
		Warm	19	8.48	67.11 ± 0.45	17.642 ± 0.052	12.313 ± 0.054
	♀	Cold	8	9.32	69.25	17.544	12.381
		Warm	8	9.42	71.56	17.956	12.587
11—11.9 grams	♂	Cold	15	9.46	68.33	17.587	12.273
		Warm	10	9.57	70.90	17.865	12.490
	Alto-gether	Cold	23	9.41	68.65 ± 0.57	17.572 ± 0.069	12.311 ± 0.035
		Warm	18	9.51	71.29 ± 0.30	17.906 ± 0.041	12.533 ± 0.034
12—12.9 grams	♂	Cold	20	10.45	71.70	18.135	12.540
		Warm	10	10.32	68.80*	17.975*	12.505*
	♀	Cold	12	10.55	71.08	17.675	12.408
		Warm	17	10.34	71.35	17.906	12.591
13—13.9 grams	♂	Cold	32	10.51	71.47 ± 0.39	17.962 ± 0.069	12.491 ± 0.037
		Warm	27	10.33	70.41* ± 0.47	17.931* ± 0.050	12.559 ± 0.043
	♀	Cold	12	11.50	73.42	18.004	12.521
		Warm	8	11.37	73.12*	18.019	12.669
14—14.9 grams	♂	Cold	16	11.37	73.79	17.953	12.544
		Warm	9	11.38	73.00*	17.972	12.478*
	Alto-gether	Cold	28	11.42	73.62 ± 0.36	17.975 ± 0.063	12.534 ± 0.035
		Warm	17	11.38	73.06* ± 0.38	17.994 ± 0.057	12.568 ± 0.055
15—15.9 grams	♂	Cold	9	12.52	73.33	17.861	12.489
		Warm	10	12.32	72.80*	18.065	12.935
	♀	Cold	7	12.37	73.43	17.821	12.614
		Warm	8	12.49	74.75	18.194	12.594*
16—16.9 grams	♂	Cold	16	12.46	73.37 ± 0.66	17.844 ± 0.100	12.544 ± 0.065
		Warm	18	12.39	73.67 ± 0.42	18.122 ± 0.052	12.783 ± 0.053
	♀	Cold	8	13.30	74.37	18.087	12.656
		Warm	9	13.33	75.67	18.528	12.772
17—17.9 grams	♂	Cold	6	13.33	74.80	18.350	12.592
		Warm	3	13.27	78.33	18.433	13.050
	Alto-gether	Cold	14	13.31	74.54 ± 0.79	18.200 ± 0.094	12.629 ± 0.069
		Warm	12	13.32	76.33 ± 0.46	18.504 ± 0.052	12.842 ± 0.083
18—18.9 grams	♂	Cold	3	14.30	75.67	18.333	12.617
		Warm	1	14.30	76.00	19.000	12.900
	♀	Cold	1	14.10	78.00	18.450	12.500
		Alto-gether	Cold	3	14.30	75.67	18.333
19—19.9 grams	♂	Cold	2	14.20	77.00	18.725	12.700
		Warm					
	♀	Cold	1	15.30	80.00	19.300	13.000
		Warm	5	15.48	77.60*	19.040*	13.010
20—20.9 grams	♂	Cold	1	15.20	78.00	18.350	12.500
		Warm	1	15.00	76.00	18.800	13.350
	Alto-gether	Cold	2	15.25	79.00	18.825	12.750
		Warm	6	15.40	77.33*	19.000	13.067
21—21.9 grams	♂	Cold	3	16.20	79.33	19.100	13.050
		Warm	1	16.30	82.00	19.450	13.200
	♀	Cold	2	16.40	83.50	19.100	12.975
		Alto-gether	Cold	3	16.20	79.33	19.100
22—22.9 grams	♂	Cold	3	16.37	83.00	19.217	13.050*
		Warm	3	16.37	83.00	19.217	13.050*
	♀	Cold	1	19.30	89.00	19.700	13.200
		Alto-gether	Cold	1	19.30	89.00	19.700



Table B.  
Offspring of Cold-room and Warm-room Parents, measured at 3½ months.  
Grouped according to Body Length.

Size-group	Sex	Parentage	Number	Weight	Body length	Tail	Foot	Ear	Size-group	Sex	Parentage	Number	Weight	Body length	Tail	Foot	Ear
75-75.9 mm	♂	Cold Warm	1	11.60	75.600	75.400	17.350	12.850	86-86.9 mm	♂	Cold Warm	4	18.35	86.337	79.312	17.725	13.287
	♀	Cold Warm								♀	Cold Warm	2	17.95	86.400	84.850	18.800	13.500
	Alto-gether	Cold Warm	1	11.60	75.600	75.400	17.350	12.850		Alto-gether	Cold Warm	6	18.22 18.30	86.358 86.650	80.420 81.867	18.083 17.983*	13.358 13.808
76-76.9 mm	♂	Cold Warm							87-87.9 mm	♂	Cold Warm	5	19.44	87.420	79.430	17.650	13.020
	♀	Cold Warm	2	11.65	76.475	71.200	17.050	13.150		♀	Cold Warm	4	17.45	87.525	81.125	17.700	12.962
	Alto-gether	Cold Warm	2	11.65	76.475	71.200	17.050	13.150		Alto-gether	Cold Warm	9	18.56 18.66	87.467 87.380	80.183 82.270	17.672 18.110	12.994 13.320
78-78.9 mm	♂	Cold Warm							88-88.9 mm	♂	Cold Warm	5	20.70	88.430	80.880	17.880	13.390
	♀	Cold Warm	1	13.70	78.600	73.750	—	13.150		♀	Cold Warm	4	20.22	88.725	81.337	18.237	13.487
	Alto-gether	Cold Warm	1	13.70	78.600	73.750	—	13.150		Alto-gether	Cold Warm	3	18.73	88.483	84.283	18.433	13.667
79-79.9 mm	♂	Cold Warm							89-89.9 mm	♂	Cold Warm	6	20.18	89.400	82.270	18.200	13.400
	♀	Cold Warm	1	15.50	79.950	79.450	17.900	13.050		♀	Cold Warm	1	19.60	89.200	86.900	18.150	13.500
	Alto-gether	Cold Warm	1	15.50	79.950	79.450	17.900	13.050		Alto-gether	Cold Warm	2	21.65	89.575	86.200*	18.750	14.075
80-80.9 mm	♂	Cold Warm	1	16.20	80.550	81.250	18.000	12.850	90-90.9 mm	♂	Cold Warm	10	20.53	90.325	83.740	18.180	13.595
	♀	Cold Warm	7	15.20	80.393	75.157	17.107	12.871		♀	Cold Warm	7	20.83	90.536	84.729	18.342	13.421*
	Alto-gether	Cold Warm	7	15.20 15.45	80.393 80.350	75.157 78.275	17.107 17.550	12.871 12.800*		Alto-gether	Cold Warm	10	20.53 21.01	90.325 90.469	83.740 84.819	18.180 18.379	13.595 13.550*
81-81.9 mm	♂	Cold Warm	1	16.80	81.950	75.800	—	13.600	91-91.9 mm	♂	Cold Warm	3	21.63	91.267	84.350	18.383	13.833
	♀	Cold Warm	6	15.67	81.342	78.933	17.800	13.067		♀	Cold Warm	1	20.60	91.190	85.350	18.550	13.450*
	Alto-gether	Cold Warm	6	15.67 15.90	81.342 81.683	78.933 79.950	17.800 18.000	13.067 13.400		Alto-gether	Cold Warm	1	21.80	91.900	91.550	18.800	13.900
82-82.9 mm	♂	Cold Warm	2	14.25	82.425	76.200	17.700	13.125	92-92.9 mm	♂	Cold Warm	6	22.33	92.408	85.925	18.475	13.733
	♀	Cold Warm	8	15.80	82.494	75.631	17.337	13.250		♀	Cold Warm	3	23.37	92.767	85.533*	18.383*	13.950
	Alto-gether	Cold Warm	10	15.49 16.08	82.480 82.658	75.745 80.333	17.410 17.700	13.225 13.067*		Alto-gether	Cold Warm	6	22.33 23.37	92.408 92.767	85.925 85.533*	18.475 18.383*	13.733 13.950
83-83.9 mm	♂	Cold Warm	3	17.10	83.717	78.250	17.800	13.150	93-93.9 mm	♂	Cold Warm	6	22.67	93.492	87.958	18.517	13.592
	♀	Cold Warm	8	16.79	83.419	79.200	17.550	13.212		♀	Cold Warm	1	24.30	93.250	88.350	19.100	13.800
	Alto-gether	Cold Warm	11	16.87 16.53	83.500 83.417	78.941 80.617	17.618 18.033	13.195 13.400		Alto-gether	Cold Warm	6	22.67 24.30	93.492 93.250	87.958 88.350	18.517 19.100	13.592 13.800
84-84.9 mm	♂	Cold Warm	2	16.20	84.650	79.375	18.175	13.475	94-94.9 mm	♂	Cold Warm	2	23.25	94.700	89.025	18.050	13.725
	♀	Cold Warm	8	16.79	84.519	80.887	17.843	13.469		♀	Cold Warm	4	23.67	94.700	86.325*	18.550	13.850
	Alto-gether	Cold Warm	10	16.67 17.96	84.545 84.590	80.585 81.150	17.917 17.830*	13.470 13.100*		Alto-gether	Cold Warm	2	23.25 23.67	94.700 94.700	89.025 86.325*	18.050 18.550	13.725 13.850
85-85.9 mm	♂	Cold Warm	1	18.70	85.800	81.400	17.550	12.950	95 mm and over	All males	Cold Warm	4	24.30	95.462	91.812	18.450	13.837
	♀	Cold Warm	6	17.67	85.275	81.558	17.733	13.133			Cold Warm	2	26.25	96.475	86.500	19.050	13.825
	Alto-gether	Cold Warm	7	17.81	85.350	81.536	17.707	13.107			Cold Warm	1	26.00	97.550	89.250	19.100	13.950
			12	18.00	85.546	80.537*	17.946	13.400			Cold Warm	1	27.20	98.900	87.000	19.600	13.600



Table C.

Offspring of Cold-room and Warm-room Parents, measured at 3½ months.  
Grouped according to Weight.

Size-group	Sex	Parentage	Number	Weight	Body length	Tail	Foot	Ear	Size-group	Sex	Parentage	Number	Weight	Body length	Tail	Foot	Ear	
11—11.9 grams	♂	Cold Warm	1	11.60	75.600	75.400	17.350	12.850	20—20.9 grams	♂	Cold Warm	12	20.57	90.337	82.421	18.200	13.600	
	♀	Cold Warm	1	11.00	76.500	69.200	16.950	13.350		♀	Cold Warm	10	20.47	89.615	82.520	18.135*	13.540*	
	Alto-gether	Cold Warm	1	11.00	76.500	69.200	16.950	13.350		Alto-gether	Cold Warm	12	20.57	90.337	82.421	18.200	13.600	
			1	11.60	75.600	75.400	17.350	12.850*				10	20.47	89.615	82.520	18.135*	13.540*	
12—12.9 grams	♂	Cold Warm							21—21.9 grams	♂	Cold Warm	8	21.40	91.519	84.531	18.081	13.575	
	♀	Cold Warm	1	12.30	76.450	73.200	17.150	12.950		♀	Cold Warm	11	21.55	90.159	84.600	18.200	13.605	
	Alto-gether	Cold Warm	1	12.30	76.450	73.200	17.150	12.950		Alto-gether	Cold Warm	2	21.55	90.750	90.650	18.825	13.975	
											8	21.40	91.519	84.531	18.081	13.575		
											13	21.55	90.250	85.531	18.296	13.662		
13—13.9 grams	♂	Cold Warm	1	13.10	82.150	79.200	18.100	13.400	22—22.9 grams	♂	Cold Warm	5	22.42	91.620	85.570	18.320	13.590	
	♀	Cold Warm	1	13.70	78.600	73.750	—	13.150		♀	Cold Warm	1	22.90	94.800	83.450*	18.100*	14.150	
	Alto-gether	Cold Warm	2	13.40	80.375	76.475	18.100	13.275		Alto-gether	Cold Warm	2	22.15	89.775	84.050	18.625	14.275	
											5	22.42	91.620	85.570	18.320	13.590		
											3	22.40	91.450	83.850*	18.450	14.233		
14—14.9 grams	♂	Cold Warm							23—23.9 grams	♂	Cold Warm	7	23.44	93.107	87.200	18.550	13.743	
	♀	Cold Warm	5	14.50	80.720	74.250	17.020	12.880		♀	Cold Warm	2	23.40	93.775	87.075*	18.375*	13.925	
	Alto-gether	Cold Warm	2	14.75	81.075	77.125	17.250	13.050		Alto-gether	Cold Warm	7	23.44	93.107	87.200	18.550	13.743	
											2	23.40	93.775	87.075*	18.375*	13.925		
15—15.9 grams	♂	Cold Warm	2	15.25	83.025	73.825	17.300	13.000	24—24.9 grams	♂	Cold Warm	3	24.33	95.567	91.167	18.433	13.950	
	♀	Cold Warm	10	15.47	81.755	77.735	17.585	13.060		♀	Cold Warm	4	24.45	93.787	87.912*	18.900	13.900*	
	Alto-gether	Cold Warm	5	15.48	82.270	81.280	17.800	13.140		Alto-gether	Cold Warm	3	24.33	95.567	91.167	18.433	13.950	
											4	24.45	93.787	87.912*	18.900	13.900*		
16—16.9 grams	♂	Cold Warm	2	16.20	84.650	79.375	18.175	13.475	25—25.9 grams	♂	Cold Warm	1	25.00	95.100	94.550	18.400	13.750	
	♀	Cold Warm	2	16.50	81.250	78.525*	18.000*	13.225*		♀	Cold Warm							
	Alto-gether	Cold Warm	20	16.40	83.292	78.252	17.563	13.227		Alto-gether	Cold Warm	1	25.00	95.100	94.550	18.400	13.750	
											7	16.54	83.379	79.886	18.033	13.271		
17—17.9 grams	♂	Cold Warm	2	17.75	85.300	74.900	17.625	13.150	26—26.9 grams	♂	Cold Warm	3	26.17	96.833	87.417	19.067	13.867	
	♀	Cold Warm	6	17.67	85.583	77.892	17.600*	13.267		♀	Cold Warm							
	Alto-gether	Cold Warm	14	17.41	85.107	80.150	17.761	13.264		Alto-gether	Cold Warm	3	26.17	96.833	87.417	19.067	13.867	
											16	17.56	85.737	80.991	17.919	13.366		
18—18.9 grams	♂	Cold Warm	5	18.56	85.670	81.830	17.860	13.220	27—27.9 grams	♂	Cold Warm	1	27.20	98.900	87.000	19.600	13.600	
	♀	Cold Warm	1	18.80	84.900	81.550*	17.850*	12.950*		♀	Cold Warm							
	Alto-gether	Cold Warm	10	18.44	85.850	82.839	18.085	13.275		Alto-gether	Cold Warm	1	27.20	98.900	87.000	19.600	13.600	
											9	18.56	86.089	81.772*	18.156	13.394		
19—19.9 grams	♂	Cold Warm	11	19.41	88.318	82.035	17.950	13.191										
	♀	Cold Warm	5	19.52	88.440	82.460	18.012	13.440										
	Alto-gether	Cold Warm	12	19.42	88.392	82.477	17.967	13.217										
											4	19.62	86.725	83.362*	18.100*	13.825		
											9	19.57	87.678	82.861	18.056	13.611		



# Über die Zelle

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von

**Alfred Schaper**

weiland a. o. Professor der Anatomie und Entwicklungsgeschichte an der Universität zu Breslau

Nach dem Tode des Verfassers herausgegeben

von

**Wilhelm Roux**

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