CONCERNING THE HEREDITARY ADAPTATION OF ORGANISMS TO HIGHER TEMPERATURE.

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Since the time of Lamarck the theory of the adaptation of organisms to their environment and the inheritance of these adaptations has been a hotly debated question. The original theory considered that the organism responded to changes in environment in such a way as to become better fitted to it, and that these changes then became hereditary. In this form the theory is probably no longer accepted by the majority of students. There is also little doubt that structural adaptations of the individual organisms are not inheritable. A general discussion of this question is out of place here, and the reader is referred to Loeb and Conklin. It may be pointed out, however, that according to the accepted theory of Weismann in regard to the continuity of the germ plasm, it seems a priori improbable that any change in the individual could affect succeeding generations.

Morgan and his coworkers have shown that structural changes are continually arising in many forms, and that these changes or mutations are inherited according to Mendel's law. There seems no reason to suppose that physiological changes might not arise in the same way. If these physiological changes were such that the organism became better fitted to a new environment, we might expect to find adaptation under some conditions, although it would not be the direct result of the changed environment. Tower has reported

experiments which apparently showed some such result. In the bacteria and other unicellular organisms, there is no doubt that cultures may be adapted to very marked changes both in temperature and concentration of toxic substances. This is, however, analogous to the adaptation of an individual multicellular organism, and cannot be considered hereditary in the sense in which the word is used in regard to higher organisms. The individual cells of a bacterial culture bear the same relation to each other as the somatic cells of a single multicellular organism, and are not at all analogous to successive generations of individuals of multicellular organisms.

The experiments reported in this paper were made with aseptic cultures of *Drosophila*. These are especially favorable for such a study for the following reasons. (1) If kept free from microorganisms the results of any experiments made with them become quite regular. (2) They have a very short generation time, about 7 days at 30°. (3) Loeb and Wasteneys found that the individual *Drosophila* show the same marked adaptation to temperature as does *Fundulus*. In the case of the latter, Loeb and Wasteneys found that fish transferred suddenly from 10 to 35°C died in the course of 1 to 2 hours, whereas fish transferred first to 27° for 2 or 3 days and then put at 35° were able to live indefinitely at this temperature. The results with *Drosophila* showed equally striking individual adaptations. These experiments were partially repeated and confirmed in the course of the present work.

The relation of the rate of growth and of the duration of life of *Drosophila* to the temperature has been the subject of a previous paper from this laboratory. It was found in that work that the insects developed normally up to a temperature of 32.5°C. Above this temperature the pupal stage was injured and no further development took place; but the larval and imago stages could live at a temperature several degrees higher. It was also found that increasing the temperature from 10 to 27.5°C increased the rate of development of the larvae and pupae; but that between the temperatures of 27.5 and 32°C the rate decreased again; i.e., the larvae grow more slowly at
either 25 or 30° than they do at 27.5°. This secondary decrease in the rate at temperatures above 27.5° was compared with a similar decrease in the rate of enzyme action, and was ascribed to a similar cause; namely, injury and subsequent slowing up of the growth processes.

In all these experiments the eggs whose development was studied were produced by imagos which had been raised at temperatures of from 15–20°C. If there was any hereditary adaptation to higher temperature it would be expected that flies which had developed near the upper temperature limit would be able to produce eggs slightly more resistant to temperature (i.e. able to develop at a slightly higher temperature) than flies which had developed at a lower temperature. In order to test this assumption, cultures of imagos which had developed at 20 and 32° respectively were placed in incubators at 29, 32, and 33°. The development of the eggs produced by these imagos was then followed. The results are summarized in Table I.

It will be seen that those imagos which had developed at 20° and were then transferred to a temperature of 29 or 32° were able to produce eggs capable of developing into imagos at that temperature. The eggs produced at 33°, however, do not develop beyond the pupal stage. The imagos which had developed at 32° are unable to produce eggs capable of development into imagos at temperatures higher than 29°. The effect of raising Drosophila at high temperatures,

<table>
<thead>
<tr>
<th>Temperature at which parent imagos were raised, °C.</th>
<th>Temperature of development of succeeding (F₁) generation, °C.</th>
<th>Condition of succeeding (F₁) generation after days noted.</th>
</tr>
</thead>
<tbody>
<tr>
<td>32</td>
<td>29</td>
<td>&quot;        &quot;    &quot;    &quot;</td>
</tr>
<tr>
<td>20</td>
<td>32</td>
<td>&quot;        &quot;    &quot;    &quot;</td>
</tr>
<tr>
<td>32</td>
<td>32</td>
<td>&quot;        No larva.   No larva.   No larva.</td>
</tr>
<tr>
<td>20</td>
<td>33</td>
<td>&quot;        Larvae.  Pupa.  Pupa dead.</td>
</tr>
<tr>
<td>32</td>
<td>33</td>
<td>&quot;        No larva.   No larva.   No larva.</td>
</tr>
</tbody>
</table>
therefore, is to lower the upper temperature limit for the development of the succeeding generation and not to elevate it as would be expected if the adaptation to temperature was hereditary.

It might be objected that the results shown in Table I are not due to any difference either in the eggs or imago but merely to the fact that, in the case of the imagos raised at 20°, the eggs which are to give rise to the succeeding generation pass through the early stages of development within the female while at the lower temperature and so escape injury; while in the case of the cultures kept continuously at 32° the early stages of the eggs must necessarily be passed at this temperature and the eggs are thereby injured. If this was the case, only those eggs produced by the 20° culture immediately after being transferred to 32° should develop, and the ones produced later should fail to develop. This, however, is not so. Imagos raised at 20° and transferred to 32° can produce eggs, capable of developing at this temperature, for a week or 10 days after having been transferred from the lower temperature.

It was found that imagos, raised and kept permanently at a temperature of 30°, are unable to produce eggs capable of development at this temperature. If, however, they are removed from the 30° incubator within a week after emerging from the pupae and placed at a temperature of about 20°C. for 24 hours or longer, they become able to produce eggs capable of development at 30°C. when replaced at this temperature. Table II is a summary of an experiment illustrating this point. It is necessary to remove the imagos from the higher temperature within a week or 10 days after they have emerged from the pupae. If they are left longer at the higher temperature, the injury becomes permanent and they are no longer able to produce eggs capable of development at any temperature.

It is therefore not possible to raise more than one generation of *Drosophila* at a temperature of 29° or over unless the culture is removed to a lower temperature for at least 24 hours every generation. A culture has been continued at 30° by this method of intermittent

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8 This fact may seem surprising since the organism is a tropical form. The explanation is probably that the temperature even in the tropics does not stay continuously higher than 28 or 30° for more than a week or 10 days.
cooling for ten generations without any noticeable change in the upper temperature limit. A second culture was kept continuously at 28° for fifteen generations. In this case also there has been no noticeable change in the temperature limit; i.e., the organisms are still unable to grow for more than one generation at a continuous temperature of 29° or over.

**TABLE II.**

*Effect of Placing Cultures, Raised at 30°, at 22°C.*

<table>
<thead>
<tr>
<th>Days</th>
<th>Time during which (F1) cultures were left at 22°C.</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>0.25 hr.</td>
</tr>
<tr>
<td>------</td>
<td>-----------</td>
</tr>
<tr>
<td>3</td>
<td>Eggs, but no larvae.</td>
</tr>
<tr>
<td>5</td>
<td>Eggs, but no larvae.</td>
</tr>
<tr>
<td>10</td>
<td>Eggs, but no larvae.</td>
</tr>
</tbody>
</table>

**EXPERIMENTAL.**

*Temperature Control.*—The cultures were kept in water jacketed incubators regulated as described in another paper. 9

*Food.*—All cultures were fed on a sterilized suspension of yeast in water. The excess water was absorbed by cotton added to the flask, as described below.

*Method of Transferring Cultures, Etc.*—The insects were kept in 1 liter flat bottom Florence flasks having a side tube fused on as in a Pasteur flask. This side tube was closed with a rubber tube and glass plug, and the neck of the flask plugged with cotton. About 25 cc. of a thick suspension of yeast in water were

added to the flask, the excess water was absorbed by the addition of absorbent
cotton, and the flask sterilized. It is important to add sufficient cotton to absorb
the water as otherwise the insects stick to the side of the flask and are drowned.
In order to transfer the culture, the flask is connected to one containing the insects
by means of the side tubes, using the same technique as in handling a Pasteur
flask. The flies are then shaken from one flask to the other through the connect-
ing side tubes, the flasks disconnected, and the connecting tubes flamed and re-
plugged. In this way the organisms can be handled with as little danger of in-
fection as cultures of bacteria.

SUMMARY.

1. Imagos of Drosophila raised at temperatures of from 12–28.5°C. when placed at any temperature from 15–32.5°C. produce eggs which develop normally at these temperatures.

2. Imagos raised at temperatures of from 29–32.5° and then kept permanently within these temperatures produce eggs which do not develop.

3. Imagos raised at from 28.5–32.5°C. and then placed at temperatures of from 12–25°C. produce eggs which develop normally.

4. Imagos raised at from 28.5–32.5°C. placed at 15–25°C. for 24 hours or longer and then put back into a temperature of from 28.5–32.5°C., produce eggs which will develop at the latter temperature.

5. There is no evidence of any hereditary adaptation to higher temperatures.