METABOLISM DURING EMBRYONIC AND METAMORPHIC DEVELOPMENT OF INSECTS.

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PLATE 4.

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Insects, because of their abundance and wide variety in form and structure, have become more widely recognized in recent years as excellent material for the study of many physiological problems. Morphologists have intensively studied the developmental processes of insects, while relatively few physiologists have investigated such phenomena as histolysis and histogenesis occurring during pupal development. The most notable physiological work on these subjects seems to have been done by Farkas (6), Krogh (10), Tangl (13), and Weinland (14).

Weinland, as early as 1906, in his studies on *Calliphora vomitoria* (blow-fly), utilized the gaseous exchange of the organism as a basis for estimating the chemical changes occurring during histolysis and metamorphosis. He found that the larvae liberate ammonia, whereas in the pupae uric acid was produced. This clearly indicates, he states, a change in the chemical process in the development of the insect. His experiments with metabolism in general indicate a markedly low CO₂ output at the beginning or early stages of pupation, which is followed by a period of rest. In later stages, however, an increase in the gaseous exchange of the organism took place.

Tangl, in 1909, obtained results from metabolism experiments on *Bombyx mori* (silkworm) similar in many respects to those of Weinland. Extending his researches in other directions, however, and comparing his own results on the larvae and pupae of *Bombyx mori* with those obtained by Farkas on the embryonic development of the same form, Tangl was led to enunciate his energetic theory. This theory postulates that the amount of energy required in the process of embryonic development is greater and the rate of energy change more intense than is required for metamorphosis.
To the author it seems reasonable to suppose that the building and multiplication of cells from the relatively inert, non-living substance of the yolk, with its large store of unorganized material and infinitesimal amount of protoplasm, should require more energy than the process of reconstruction from histolytic products in metamorphosis, since this latter process is largely a matter of growth of imaginal tissues.

The histological investigations of Weismann (15) and others have shown that the larvae at birth possess two kinds of tissues, larval and imaginal. During embryonic and postembryonic development, larval tissues are dominant, whereas imaginal tissues are greatly retarded in their development. It is possible to conceive of the existence of such dominance as long as the larval tissues and organs are in a functioning condition. At the termination of the larval life, histolysis and disintegration of the larval tissues and organs seem to produce a condition favorable for the development and growth of the imaginal tissues.

The causes that initiate histolysis do not seem to be clear. Weinland, however, as stated above, has pointed out that during the larval life of Calliphora vomitoria ammonia is produced, whereas during pupal development uric acid is formed. This condition led Weinland to assume that the chemical changes thus produced are the most significant. Mathews (12), however, states that while in carnivorous animals the urine is acid in nature, in herbivorous animals the urine may be distinctly alkaline. Bishop (3) has recently found that an acid medium at the beginning of pupation is favorable to autolysis (in vitro) in bee larvae. Experiments performed by the author indicate that changes in pH from a neutral to an acid condition occur in the larval and pupal fluids of certain insects during histolysis and pupal development. Changes in pH from an acid to a neutral condition have also been observed to take place with some species from early to late embryonic development. During embryonic development, however, no histolysis occurs. The question, therefore, naturally arises, is the change from neutrality to acidity responsible for histolysis, or a result?

The object of the present paper is to describe the results from studies of the rates of respiratory metabolism and other phenomena during the embryonic and metamorphic development of certain insects.

**Material and Method.**

The material used consisted exclusively of insect eggs and pupae derived from different species of five orders.
The following species of insects were used.

- *Leptinotarsa decemlineata* Say (potato beetle).
- *Crioceris asparagi* L. (asparagus beetle).
- *Epilachna borealis* Fab. (squash ladybeetle).
- *Hippodamia convergens* Guer. (convergent ladybeetle).
- *Cotinis nitida* L. (green June beetle).
- *Popillia japonica* Newm. (Japanese beetle).
- *Ancylis comptana* Frohl. (strawberry leaf-roller).
- *Macrocentrus ancylicus* Rohw. (hymenopterous parasite).
- *Hylemyia cilicrura* Rond. (seed-corn maggot).
- *Anasa tristis* DeG. (squash bug).

That the respiratory exchange of an organism is one of the best criteria of metabolic activity seems to be an established fact. In the present experiments, therefore, the rates of metabolism as measured by the CO₂ output and the oxygen intake have been determined.

Two types of apparatus were found useful. First, the manometer described by Krogh (10) (Plate 4). This manometer has been slightly improved by Dr. Bodine of the University of Pennsylvania. The improvements consist in the elimination of all rubber connections, thus rendering the instrument especially reliable and accurate for metabolism experiments on insects. For detailed descriptions and methods of calculation of the results, the reader is referred to the original article by Krogh (10).

The second type of apparatus for measuring the rates of CO₂ output of small organisms is essentially the Haas colorimetric method as described by Jacobs (8). The type of standard and respiratory flask used with this method is of slight importance. Those devised by Dr. Bodine and used in these experiments were made of Nonsol or Pyrex glass.

Since normally no movements occur in eggs and pupae when properly handled, it was only basal metabolism that was recorded. In all metabolism experiments during embryonic development constant temperature conditions were maintained by using Krogh’s manometer immersed in a constant temperature water bath. During the course of any individual experiment temperatures were always maintained constant. The range of constant temperatures maintained during the course of the entire experiments was 21–24°C.
In following out the respiratory exchange during embryonic development, eggs known to have been recently deposited were selected and their weights obtained. Daily determinations of their CO₂ output up to the time of hatching were recorded. In following the metabolism during metamorphosis many single pupae were used and the same procedure followed as for the eggs, until the pupae emerged as adults.

The oxygen intake whether of eggs or pupae during development was recorded by means of the Krogh manometer. This apparatus may also be used in making CO₂ determinations as described by Krogh (10). It has many advantages in its favor over the apparatus described by Jacobs for CO₂ determinations, some of the outstanding features being the ease with which readings are made both of oxygen intake and CO₂ output during the entire period of development of eggs or pupae. Small objects, such as eggs or small pupae, may be left in the manometer during their entire period of development.

As a basis for comparison of the rates of metabolism of individual pupa or eggs, the data recorded in this paper were calculated to gm. CO₂ per gm. per hour and in cu. mm. of oxygen per gm. of organism per hour.

*Embryonic Development.*

During embryonic development an increase of living protoplasm occurs, followed by a continuous growth of tissues and organs. According to Weismann, in holometabolous insects, at the time the larval structures develop, imaginal buds originate as separate minute cellular masses. Such imaginal buds exist for each part of the future insect. Although Kulagin (11) states that the amount of chromatin in these cells is double that contained in the definitive cells from which they arose, the imaginal buds cannot be regarded as embryonic resting stages. During larval life their growth and development, however, is greatly retarded. The processes of metabolism that take place during embryonic development as observed in the following experiments are suggestive of such conditions.

First, a formative period occurs, during which metabolic activity seems to be very low. In all embryonic development, with a few exceptions to be noted later, this formative stage is very short. As
Figs. 1–4. Showing gm. CO₂ output per gaa. of organism per hour, during embryonic development. The brief formative period is indicated in Fig. 1, *Crioceris asparagi*; Fig. 2, *Hylemyia cilicura*; and in Fig. 3, *Leptinotarsa decemlineata* by the low CO₂ output during the 1st day of development. This is followed by a marked high rate of CO₂ output until hatching as is shown by the almost straight line curves. Fig. 4 shows the curve obtained during embryonic development of *Popillia japonica*, and indicates the extended formative period lasting for over 6 days.
the growth of tissues and organs proceeds a very rapid rise in rate of metabolism takes place.

In species that usually deposit their eggs on foliage, as with *Leptinotarsa decemlineata*, or, as the case may be with *Hylemyia ciliaris*, that deposit their eggs on the surface of the soil, the rates of metabolism during embryonic development follow definitely shaped curves as indicated in Figs. 1–3. An examination of these graphs shows that in nearly every instance the formative period may easily be recognized by the short stage during which metabolic activity is at its lowest. The growth curve that follows is almost a straight line, and indicates a much higher rate of metabolism.

Other species, as *Cotinis nitida*, possess the habit of depositing their eggs in the soil, usually at some depth below the surface. The formative period in such instances seems to be greatly extended, as shown in Figs. 4, 17, and 18 and may last for many days. The growth curve that follows is the same as in the previous cases cited and shows a much higher rate of metabolism. In general, the graphs depicting embryonic development for this and similar species, very closely resemble graphs obtained for pupal development as indicated further on.

**Prepupal Period and Histolysis.**

After the larvae of the different orders used in these experiments have attained full growth and have ceased feeding their behavior is quite different. Some, like *Leptinotarsa decemlineata* and *Crioceris asparagi*, enter the ground and construct cells in which to pupate. Figs. 5–10. Showing the rates of metabolism during prepupal and pupal development, in gm. CO₂ output per gm. per hour. Fig. 5 shows the metabolism during the prepupal period of *Leptinotarsa decemlineata*. The intense histolysis occurring during this period is indicated by the marked drop in CO₂ output lasting for several days. Figs. 6 and 7 show the CO₂ output and oxygen intake during both prepupal and pupal development of *Hippodamia convergens*. Fig. 8, *Hylemyia ciliaris* and Fig. 9, *Ancylis compta*, also indicate prepupal and pupal development. The first few days in each of these curves represent histolysis, followed by a general rise in the curves indicating pupal development. Fig. 10, *Popillia japonica*, shows histolysis during early pupal development followed by growth. Sex differences in the rate of metabolism are also very marked, males showing a higher rate.
With others, as *Ancylis comptana*, the larvae remain concealed in their retreats on the leaves before pupation. The larvae of *Hylemyia ciliicrura* and *Macrocentrus ancyliivora* construct puparia or cocoons in which they afterwards pupate. In all the examples cited, the larvae, after having prepared their pupal cells or cocoons, remain quiet for a time; the length of this prepupal period varies with the species. It is well known that histolysis first commences in the prepupal state. If, for example, we remove the larvae of *Leptinotharsa decemlineata* from their pupal cells as soon as these have been formed in the ground, and subject them to metabolism experiments during the prepupal period, we obtain a curve as shown in Fig. 5. This graph shows that during the first few days of the prepupal period a marked lowering of the rate of CO₂ output occurs. After a short time, usually a day or two, a gradual increase in the rate takes place as the pupa is forming.

Each organ which functions in the larva sooner or later disintegrates histolytically. The muscles degenerate first, followed by the alimentary tract and the salivary glands. The heart and central nervous system change only slightly, while the genital system is directly taken over by the adult. According to Korschelt and Heider (9) and Berlese (2) there is no sharp differentiation between larva, pupa, and adult, because parallel with the destruction is an upbuilding of organs. Although we note the abrupt changes that occur outwardly, the inner development is continuous. Metamorphic changes occur in the larvæ, but not so intensely as during histolysis in the prepupal and early pupal state.

This intensity of histolysis in prepupal larvæ is accompanied by very marked lowering in the CO₂ output, as indicated in Fig. 5. We shall have occasion to note later, during pupal development, that the process of growth of imaginal buds, in general, follows the same type of curve as obtained for embryonic development.

**Pupal Development.**

The characteristic process of metamorphosis is a growth, the growth of certain embryonic tissues, the imaginal buds. Organs are not built anew, but grow from the imaginal buds which have remained
Figs. 11–14. Show metabolism during pupal development in gm. CO₂ output per gm. per hour. Fig. 11, Leptinotarsa decemlineata; Fig. 12, Crioceris asparagi; Fig. 13, Macrocentrus ancyliivora; and Fig. 14, Ancyliis coptana. Note the absence of the intense histolysis that takes place in the preupal development as compared to Figs. 5–10. The above curves show growth and development and are comparable to embryonic development (see Figs. 1–4). A sex difference is also evident, especially in Leptinotarsa decemlineata, the male showing a higher rate of metabolism.
latent since their embryonic origin. A large growth of certain organs does occur, as for example in wings and appendages. Parallel with this growth notable changes occur in the heart and nervous system.

With the above distinction between histolysis and metamorphosis in mind, we should expect to find in metabolism experiments indications characteristic of the two processes. That such is the case is shown in Figs. 5-14.

The curves for rates of respiratory metabolism during pupal development fall into two groups. In the first group, Figs. 5-10 the curves first show a sharp decline and then a general upward trend. The decline is caused by the very low rates of CO₂ output during the first few days of histolysis, a concomitant of intense histolysis such as occurs in the prepupal state. The general rising of the curve after this initial low phase of metabolism accompanies metamorphosis, the growth of imaginal buds.

In the second group, Figs. 11-14, are records obtained from the pupae, excluding the intense histolytic process of the prepupal state. The striking characteristic of these curves is a general upward trend, indicating growth and development. In many respects these curves are similar to those for embryonic development. Marked differences in the formative period of growth exist in species during pupal development, just as they are found to exist during embryonic development.

The Energy Required in Embryonic and Metamorphic Development.

During the embryonic and metamorphic development, fat seems to be largely burned. The oxidation of fat must generate energy for development. The chemical processes concerned in the utilization of fat are not definitely known at present. According to Bayliss (1) and Mathews (12) the fats are first hydrolyzed before oxidizing, the fatty acids are then probably united to some substance which hastens their oxidation. The result of this oxidation is the liberation of a large amount of energy, carbon dioxide, and water. Since the egg contains a relatively larger amount of fat than does the pupa, we may expect the generation of energy to be greater during embryonic development.
To show the relative amounts of energy required during embryonic and pupal development, the total CO₂ output or oxygen intake per gm. per hour was calculated as averages; the results tabulated are shown in Tables I and II.

### TABLE I.
The Total CO₂ Output per Gm. per Hour during Embryonic and Metamorphic Development.

<table>
<thead>
<tr>
<th>Species</th>
<th>Egg CO₂ (g/h)</th>
<th>Pupa CO₂ (g/h)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Leptinotarsa decemlineata</em></td>
<td>0.00489</td>
<td>0.00343</td>
</tr>
<tr>
<td></td>
<td>± 0.00011</td>
<td>± 0.00015</td>
</tr>
<tr>
<td><em>Hylobius cilius</em></td>
<td>0.0123</td>
<td>± 0.0018</td>
</tr>
<tr>
<td></td>
<td>± 0.00012</td>
<td>± 0.0002</td>
</tr>
<tr>
<td><em>Popillia japonica</em></td>
<td>0.0018</td>
<td>± 0.0001</td>
</tr>
<tr>
<td></td>
<td>± 0.0001</td>
<td>± 0.0001</td>
</tr>
<tr>
<td><em>Epilachna borealis</em></td>
<td>0.0015</td>
<td>± 0.0001</td>
</tr>
<tr>
<td></td>
<td>± 0.0001</td>
<td>± 0.0001</td>
</tr>
</tbody>
</table>

### TABLE II.
The Total Oxygen Intake in Cu. Mm. per Gm. per Hour during Embryonic and Metamorphic Development.

<table>
<thead>
<tr>
<th>Species</th>
<th>Egg Oxygen (cu. mm/h)</th>
<th>Pupa Oxygen (cu. mm/h)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Leptinotarsa decemlineata</em></td>
<td>2,832 ± 62</td>
<td>1,270 ± 94</td>
</tr>
<tr>
<td></td>
<td>± 2,416 ± 49</td>
<td>± 1,902 ± 35</td>
</tr>
<tr>
<td><em>Hylobius cilius</em></td>
<td>2,705 ± 60</td>
<td>1,099 ± 80</td>
</tr>
<tr>
<td></td>
<td>± 2,229 ± 47</td>
<td>± 2,222 ± 21</td>
</tr>
<tr>
<td><em>Crioceris asparagi</em></td>
<td>2,222 ± 21</td>
<td>3,572 ± 33</td>
</tr>
<tr>
<td><em>Popillia japonica</em></td>
<td>1,175 ± 30</td>
<td></td>
</tr>
<tr>
<td></td>
<td>± 2,905 ± 24</td>
<td>± 3,572 ± 33</td>
</tr>
</tbody>
</table>

The tables indicate quite clearly that there are marked differences in metabolic rates between egg and pupa. Indeed, so great is this difference that with some species the rate during embryonic development is nearly treble that during metamorphosis. In some species egg incubation requires a much shorter time than pupal development. These results, show, therefore, an actually higher rate of metabolism for embryonic development than for metamorphosis. Tangl (13), it is interesting to note, compared the rates of embryonic development of *Bombyx mori* and the chick embryo and found the rates to be comparable.
Figs. 15-18. Showing the oxygen intake, the CO₂ output, and respiratory quotient during embryonic development. Fig. 15, Leptinotarsa decemlineata; Fig. 16, Anasa tristis; Fig. 17, Popillia japonica; Fig. 18, Cotinis nitida. The upper solid line curve in each figure represents the oxygen intake, the lower solid line curve the CO₂ output. The dotted line curve shows the respiratory quotient. Note the brief formative period as shown in Figs. 15 and 16, as compared to the more extended formative stage in Figs. 17 and 18. The former species deposit their eggs on foliage, the latter in the soil.
Respiratory Quotient.

Through the investigation of many workers it has been experimentally demonstrated that a low respiratory quotient indicates that the substances catabolized are chiefly fat and protein, and that a high quotient indicates the substances to be chiefly carbohydrates and protein.

Both Tangl and Weinland have obtained low respiratory quotients during metamorphosis of pupae, the daily quotients obtained by Weinland varying from 0.46 to 0.76. Similar strikingly low respiratory quotients were obtained by the author with daily variations ranging from 0.42 to 0.71, as shown in Figs. 15–18.

The embryonic development of *Anasa tristis* shows (Fig. 16) an initial respiratory quotient of 0.521, rising on the 3rd day to 0.732; the latter is practically maintained thereafter throughout development. In Fig. 15 referring to the embryonic development of *Leptinotarsa decemlineata* we have a similar condition, with a quotient ranging daily from 0.512 to 0.68. *Cotinis nitida* gives a much lower quotient during embryonic development, seldom rising above 0.524 and for several days even dropping to 0.413. A similar low respiratory quotient is found for *Popillia japonica*, but here it rises during the last few days of development to 0.732 (Figs. 17 and 18).

Many investigators have obtained low respiratory quotients with hibernating mammals such as the bat and marmot. Similar low quotients ranging from 0.41 to 0.71 have also been obtained by the author (unpublished data) for hibernating insects, while the active forms of the same species gave quotients ranging from 0.72 to 0.8. No satisfactory explanation has as yet been brought forward to explain the occurrence of a quotient lower than 0.7, although it is surmised that the substances oxidized are chiefly fat. Thus Bohr and Hasselbalch (4) believe that the variation in the quotient observed with the chick embryo is due to the decomposition of fat, not at one time, but in successive stages. This agrees with Bayliss, who holds that in the oxidation of fats there first occurs a splitting into fatty acids, followed by a quick oxidation of the lower fatty acids. Weinland is of the opinion that perhaps the oxygen intake is in some way held back in the organism. Bayliss also states that it can be shown by the increase of weight that oxygen is actually retained.
The Reaction of Body Fluids.

The pronounced changes in CO₂ output found during early and late embryonic development, prepupal and pupal changes, led to the assumption that perhaps changes in the pH of the body fluids were also taking place. It is not definitely proved as yet that we can correlate a low CO₂ output with an acid condition and, conversely, a high rate of CO₂ output with a neutral or slightly alkaline medium, for low rates of CO₂ output do not always seem to be associated with an acid medium. Bishop (3), however, is of the opinion that a change in pH and total acid content at the beginning of pupation in bee larvae produces a condition favorable to autolysis.

Experiments were made to test the reaction of the fluids of larvae, pupae, and eggs of the species recorded in this paper. The results obtained show marked changes in pH before pupation and during the last stages of pupal development. Owing to the extremely small amounts of fluid available in the material studied (not more than a drop or two can be obtained) the colorimetric spot-plate method was adopted. This method was found to give approximate results. The procedure was as follows: Drops of fluid obtained from the insect were diluted with a drop of pure water in a depression on the spot-plate and compared to equal size drops of standard buffer solutions, using one or more indicators to check a given result. When two indicators gave approximately the same pH, it was concluded to be the pH of the fluid in question. As indicators brom-thymol blue, brom-cresol purple, and phenol red were used. Determinations could be made in less than 10 seconds. Every precaution was used to insure uniform determinations. Any change in the reaction of the fluid must, therefore, be attributed to an actual change in its acidity or alkalinity.

In Table III the results are tabulated according to species. They reveal in some cases pronounced changes from a neutral to an acid reaction of the fluids at the termination of the larval period and in the early pupal stage. The acid condition, moreover, prevails throughout at least the first half of pupal development. Afterwards, usually at about the time the adults are ready to emerge, the pH changes again toward a neutral and, in some cases, to a slightly alkaline reaction.
As for changes from an acid to a neutral reaction during embryonic development, positive results could be obtained only in a few species, such as *Cotinis nitida*, *Hylemyia cilicrura*, and *Anasa tristis*. Other species, as *Leptinotarsa decemlineata*, showed very slight variations or none at all. Throughout all the stages of *Epilachna borealis*, a very marked acid reaction prevails. During the growth of *Anasa tristis* a very gradual change from an acid to neutral state occurs. In this species metamorphosis is incomplete.

All the species having complete metamorphosis except *Epilachna borealis* show distinct changes in pH—a change from neutral to acid reaction just previous to pupation, and from acid to neutral reaction as metamorphosis nears completion.

**TABLE III.**

<table>
<thead>
<tr>
<th>Species</th>
<th>Egg</th>
<th>Larva</th>
<th>Pupa</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Early</td>
<td>Late</td>
<td>Early</td>
</tr>
<tr>
<td><em>Leptinotarsa decemlineata</em></td>
<td>6.8</td>
<td>6.8</td>
<td>6.8</td>
</tr>
<tr>
<td><em>Cotinis nitida</em></td>
<td>7.1</td>
<td>7.1</td>
<td>7.1</td>
</tr>
<tr>
<td><em>Popillia japonica</em></td>
<td>5.9</td>
<td>5.9</td>
<td>5.9</td>
</tr>
<tr>
<td><em>Ancylois complexa</em></td>
<td>6.4</td>
<td>6.4</td>
<td>6.6</td>
</tr>
<tr>
<td><em>Pieris rapae</em></td>
<td>5.9</td>
<td>5.9</td>
<td>5.9</td>
</tr>
</tbody>
</table>

The destruction of larval tissues during histolysis has been described by many workers as due to phagocytes. Others, like Berlese, discard this theory entirely. Breed (5) found no evidence of phagocytes in the degeneration of larval muscle tissues of Coleoptera, and believes that histolysis is entirely a chemical process. Herbst (7) found that if sea water is deprived of its calcium, the blastomeres of sea urchin eggs fall apart; whereas if calcium is added, the cells cohere again. Bishop (3) is of the opinion that a change in metabolic equilibrium is the immediate cause of tissue autolysis, a more acid reaction acting as a contributing cause to the acceleration of the process. Whether an acid reaction is essential for histolysis is not definitely known.
SUMMARY.

1. For species of insects that deposit their eggs on foliage, as *Leptinotarsa decemlineata*, *Crioceris asparagi*, and *Anasa tristis*, the rates of metabolism as measured by the CO₂ output or the oxygen intake indicate, during embryonic development, a short formative period, followed by a very active extended growth. Those species that deposit their eggs in the soil, as *Cotinis nitida* and *Popillia japonica*, show that the formative period is greatly extended and the growth period similarly lengthened.

2. It has been shown from metabolism experiments that intensive histolysis occurs during the prepupal period and becomes less intensive during pupal development.

3. Metabolism experiments show a greater amount of energy change during embryonic development as compared to the energy developed during metamorphosis. This is shown by the greater CO₂ output and by the oxygen intake.

4. Low respiratory quotients, varying from 0.42 to 0.71, have been obtained during the embryonic and pupal development of insects, resembling similar low quotients obtained with hibernating forms.

5. Changes from a neutral to an acid reaction (pH 6.8 to 5.9) have been observed to take place in some species during prepupal and early pupal development. As metamorphosis is completed a converse change occurs (pH 5.9 to 6.8). Changes in pH from an acid to neutral reaction were also observed to take place in some species, as *Cotinis nitida* and *Hylemyia cilicrura*, during embryonic development.

The author desires to acknowledge his appreciation for the facilities extended him by the Department of Zoology of the University of Pennsylvania during these investigations; and particularly is he under deep obligation to Dr. J. H. Bodine for many helpful suggestions during the progress of the work.

BIBLIOGRAPHY.


EXPLANATION OF PLATE 4.

Fig. 1. Krogh's manometer, the apparatus used for determining the respiratory gas exchanges of insects during embryonic and metamorphic development.
(Fink: Metabolism of insects.)