THE RESPIRATION OF INSECTS THROUGH THE SKIN

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(With Seven Text-figures)

INTRODUCTION

The respiratory organ of the insects consists of a system of air-filled tubes, called the tracheae, which are in most cases in open connexion with the outside air through openings in the body wall, the spiracles. Renewal of oxygen in the tracheae takes place by diffusion, aided in the case of such large and active insects as dragonflies, grasshoppers and wasps by ventilatory movements of the body wall. Krogh (1920) has pointed out in a series of estimations and experiments that the amount of oxygen reaching the tissues by way of the tracheae through the spiracles by simple diffusion is sufficient for the requirements of the insects he was investigating.

But the factor of oxygen diffusion through the skin was omitted in Krogh's estimations and, strangely enough, has hardly ever been taken into account by students of insect respiration. Since the days of Malpighi and Réaumur, who showed that insects were killed by blocking the spiracles with drops of oil, it has always been accepted that occlusion of the spiracles stops respiration entirely and causes the death of the insect. There is no reason to doubt that the respiration of insects is gravely upset by blocking the spiracles. But it seems desirable to get information about the diffusion of oxygen through the skin and what proportion of the normal oxygen uptake can be attributed to such diffusion.

METHODS AND APPARATUS

All the experiments on respiration were performed on the modified Barcroft manometer, described by Dixon (1934, p. 8). The flasks used (Fig. 1) were similar to those of Dickens and Šimer (ibid. p. 62) with the exception that the side bulb containing the acid (*A*) was fitted into a ground joint in the body of the flask and could thus be rotated. The central portion containing the material under investigation (*B*) was also made detachable, with a ground joint (Fig. 1).

All experiments were run in a water bath which was kept at a constant temperature of 27° C., except where stated.

The following technique was adopted as standard in all experiments:

(1) *Respiration in air.* The insects are weighed to 0·1 mg. and placed in the "insect cup" (Fig. 1, *B*) and the flasks are assembled.

1 c.c. of 3*N* HCl is run into the side bulbs of both flasks (*A*), 0·6 c.c. of saturated $Ba(OH)_2$ is placed in the annular trough of each flask (*C*) and the whole apparatus is placed in the water bath for ½ hr. for equilibration.

In the earlier experiments air which had been freed from CO_2 was passed through both flasks before adding the baryta, but blank experiments showed this to be unnecessary, as the difference between the amounts of CO_2 in the flasks when full of atmospheric air was negligible.

During the equilibration period and throughout the experiment the respirometer is rocked at a constant speed of 60 complete shakings per minute. The

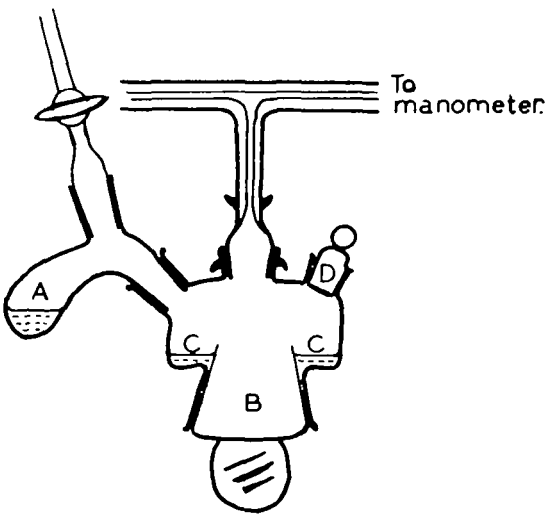

Fig. 1. Diagram of flask used for respiration experiments. Explanation of letters in text.

object of this is to prevent a crust of carbonate forming on the surface of the baryta, and, in the case of insects submerged in water, to assist the diffusion of gases into the water.

At the end of the equilibration period the mercury column is adjusted to a suitable level and the taps are shut. Readings of the oxygen uptake are taken every 15 min. for at least 1 hr.

When sufficient readings have been taken, the side bulbs containing acid are rotated, thereby mixing the acid with the baryta, and readings are taken every 5 min. It has been found that the CO_2 takes about 10 min. to come off, so allowance has to be made for the amount of oxygen that the insects have taken up in that period and also for the CO_2 that they have put out. In calculating the final CO_2 output the ½ hr. equilibration period has also to be allowed for. This introduces an appreciable amount of error, for respiration is always greatest at the start

of the experiment, at any rate when the insects are free to move, with the result that the calculated CO_2 output is in many cases slightly too high.

All results of oxygen uptake and CO_2 output are expressed as *mm.*^{3}*/mg. live weight/hour at normal temperature*, except where stated.

(2) *Respiration in oxygen.* The technique is similar to the above except that pure oxygen is passed from a cylinder through both flasks at a rate of 675 c.c./min. for 3 min. after adding the baryta.

(3) *Respiration in water.* The technique is similar to (1) except that CO_2 is not measured. Similar amounts of water are placed in the insect cups in the two flasks.

When oxygenated water is used, oxygen is bubbled through the water for at least 10 min., and the flasks are filled with oxygen as described in (2).

EXPERIMENTS

(*a*) *Blowfly larvae* (Calliphora erythrocephala)

As a suitable experimental animal the blowfly larva has been chosen for two particular reasons:

(1) It possesses only two pairs of spiracles situated at the extreme front and hind ends respectively. By ligaturing the blowfly larva immediately behind the front spiracles (Fig. 2, *1*) and in front of the hind spiracles (Fig. 2, *3*) the whole tracheal system can be shut off from its connexion with the outside air.

(2) In the blowfly larva the central nervous system is concentrated in a single mass situated in the front part of the body (Fig. 2). A ligature behind this place (Fig. 2, *2*) immobilizes the posterior part of the body owing to the separation from the central nervous system. Such hind parts live for at least 1 week, during which period the muscles retain their excitability and the heart beat persists. Since they do not exhibit any voluntary movements their metabolic activities can be regarded as the basal metabolism of the larva.

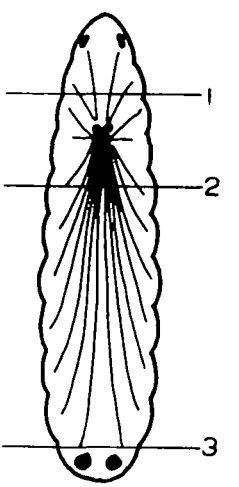

Fig. 2. Diagram of a blowfly larva, showing position of ganglion, spiracles, and also ligatures in front (1), and behind (2) the ganglion, and in front of the back spiracles (3).

In the main series of experiments shown in Fig. 3 the O_2 uptake and CO_2 output has been measured on the same batch of larvae (usually 10, weighing about 0·800 g.) under three different conditions:

(*a*) normal larvae,

(*b*) larvae ligatured behind the ganglion and front part removed,

(*c*) posterior spiracles also ligatured off.

After removal of the front part the O_2 uptake and CO_2 output are lowered by about one-half. This is probably entirely due to the immobilization of the larvae. The respiration remains normal, as can be concluded from the unchanged value of the R.Q.

After the hind spiracles also have been ligatured off O_2 consumption decreases to about one-quarter of the value in the once-ligatured larva. The CO_2 output, however, only decreases by less than one-half. As a consequence of this the R.Q. attains the high value of 1·34. This indicates that the O_2 uptake is not sufficient for supporting the metabolic processes and part of them is maintained by anaerobic

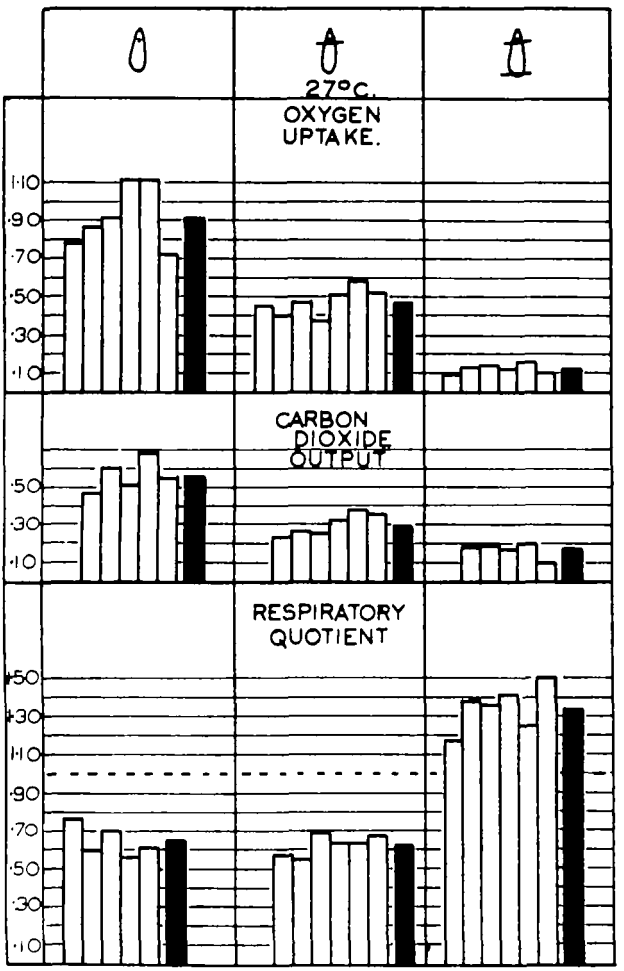

Fig. 3. Oxygen consumption, CO_2 production and R.Q. of normal larvae, larvae ligatured behind the ganglion and twice-ligatured larvae at 27° C. The black columns represent the average figures.

respiration. In the twice-ligatured larvae the O_2 uptake remains constant for at least 2 hr. The heart beat persists for the same period. The larvae die usually within 10–20 hr.

Fig. 4 represents the results of the identical set of experiments carried out at the lower temperature of 17° C. Apart from the general decrease of all values the results seem to be identical with those obtained at 27° C.

Another set of experiments (Fig. 5) has been carried out whereby the larvae were ligatured in front of the ganglion. In this case the ligature is placed at the very front end, just behind the front spiracles. Here the central nervous system remains included in the body and the larvae retain their mobility. In the larvae

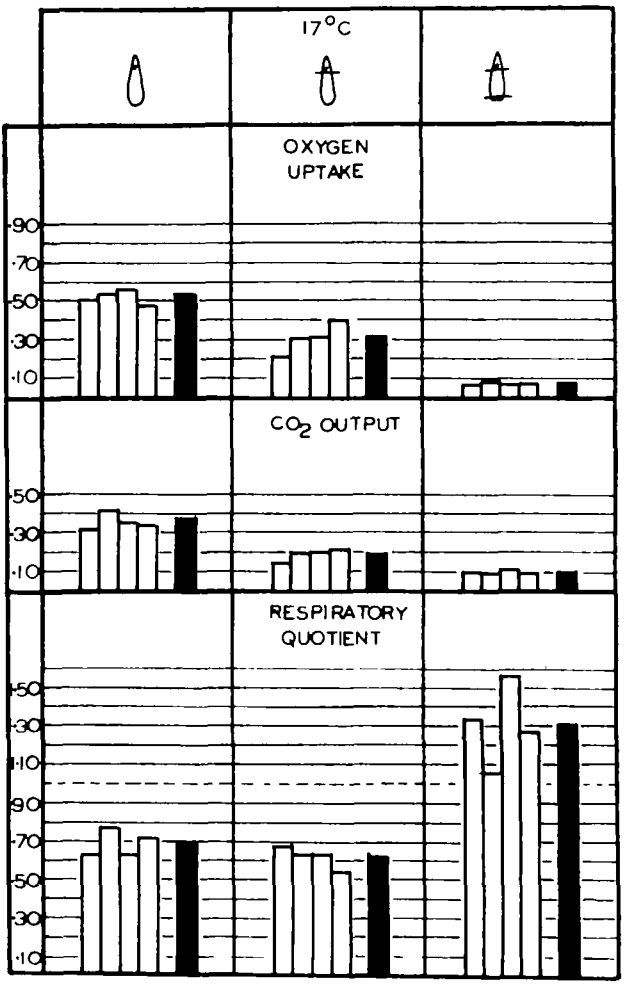

Fig. 4. Oxygen consumption, CO_2 production and R.Q. of normal larvae, larvae ligatured behind the ganglion and twice-ligatured larvae at 17° C.

so treated the proportion of the O_2 uptake in the once- and twice-ligatured larvae remains about the same as in the motionless larvae of Fig. 3, i.e. 0·67 : 0·15. But the absolute amount of oxygen consumption is distinctly higher (0·67 against 0·47), and the same holds for the amounts of CO_2 produced. The R.Q. of the twice-ligatured larvae of Fig. 5 seems to be significantly higher than that of the corresponding larvae of Fig. 3. This indicates that the mobility of the larvae leads to an additional

output of CO_2, which cannot be covered by the O_2 uptake in spite of its absolute increase.

The fact that more oxygen diffuses through the skin into the mobile double-ligatured larvae (ligatured in front of the ganglion) than into the immobile ones (ligatured behind) is easily explained. The diffusion of oxygen is controlled by the

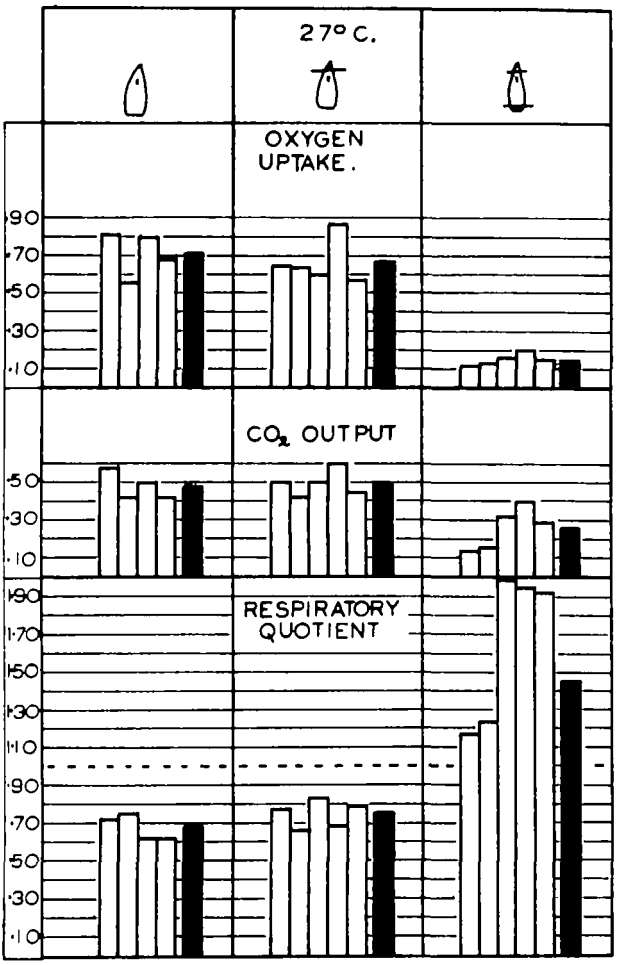

Fig. 5. Oxygen consumption, CO_2 production and R.Q. of normal larvae, larvae ligatured in front of the ganglion and twice-ligatured larvae at 27° C.

difference of oxygen tension inside and outside the body. We must expect that the muscular movements lead to an additional lowering of the oxygen tension in the tissues which necessarily increases the difference in oxygen tension.

In the twice-ligatured larvae the oxygen consumption is dependent on the oxygen pressure outside the body (Table I). Increase of the oxygen pressure to 100% increases the oxygen consumption to about four times the amount found in

air, whereas lowering the oxygen pressure to 7·5 and 5% decreases the O_2 consumption to less than one-half and one-third, respectively, of the amount found in air.

Table I. *Oxygen uptake of separate batches of twice-ligatured immobile larvae under different oxygen tensions*

Oxygen tension %	Oxygen uptake			
100	0·476	0·453	0·517	0·544
21	0·122 (mean, taken from Fig. 3)			
7·5	0·048	0·058	—	—
5	0·043	0·030	—	—

A very different result is obtained when the oxygen consumption of once-ligatured larvae is measured at various oxygen tensions (Table II). Here the oxygen consumption is almost independent of the oxygen pressure from 100% down to about 8%.

Table II. *Oxygen uptake of once-ligatured immobile larvae under different oxygen tensions. Each column represents results obtained from different samples of one batch of larvae during* 8 *hr. Gas mixtures made up in aspirator and controlled with Haldane apparatus in columns D, E, F and G, not controlled in columns A, B, C*

Oxygen tension %	A	B	C	D	E	F	G
100	0·378	0·396	—	0·530	0·532	—	—
21	0·440	0·476	0·445	0·504	0·548	0·422	—
11·5	—	—	—	—	—	0·403	0·439
10	0·437	—	0·437	—	—	—	—
8·8	—	—	—	0·522	0·477	—	—
7·5	—	—	—	—	—	0·364	0·350
5·7	—	—	—	0·367	0·385	0·355	—
5·0	0·379	0·381	0·411	—	—	—	—

In the experiments of Table II all the determinations of one column have been performed within 8 hr. with different samples of the same batch of larvae of equal age and reared together. We first attempted to determine the O_2 uptake in five different tensions of oxygen using the same lot of larvae for five determinations. This, however, did not give consistent results, as is seen in Table III. The oxygen uptake of the larvae tends to go down slowly during a set of experiments quite independently from changes in the oxygen tension.

Table III shows the falling off of the oxygen uptake when the same batch of larvae is used in a number of experiments. Thus in column A the value for 7·5% is less than for 5%, and although there is a slight increase in 10 and 21%, yet both these values are still below that for 5%. The same is shown in column B.

Table III. *Oxygen uptake of once-ligatured immobile larvae under different oxygen tensions. Each column represents results obtained from one sample of larvae during* 1 *day in the sequence indicated by arrows*

Oxygen uptake %	A	B
100	0·487	—
↓		
5	0·372	—
↓		
7·5	0·338	0·388
↓		
10	0·347	0·353
↓		
21	0·363	0·373

It is well known that moving animals "settle down" gradually in the vessel of a respiration apparatus which causes the oxygen uptake to fall off. In our experiments, however, the larvae were all ligatured behind the ganglion and therefore motionless and this fall in the oxygen uptake was quite unexpected.

Krogh (1916) has pointed out that one should expect the oxygen uptake to be independent of the oxygen tension as long as there is a positive oxygen tension in the tissues and "that the oxygen pressure becomes the limiting factor only when the oxygen supply fails and the oxygen tension in some of the tissues becomes zero". Gaarder (1918), continuing Krogh's arguments, suggests that since the O_2 uptake is governed by the difference between internal and external O_2 tension, this difference should be found to be constant over a range of concentrations above that at which the O_2 uptake begins to fall off. Supposing this point to be about 5%, when (according to Krogh) the internal O_2 tension is zero, then a similar difference of 5% should be expected at higher external oxygen tensions. This would indicate an internal O_2 tension of about 16% when the insect is in air. His measurements were in close agreement with these conclusions.

In the blowfly larvae the oxygen uptake begins to fall off at about 7·5% oxygen tension (Table II). One might therefore assume an internal oxygen tension to be about 14% when the larva is in air. In the double-ligatured larva we should expect the oxygen tension in part of the tissues to be zero already in air, especially since some anaerobic respiration is taking place.

In order to get direct evidence of the value of the O_2 tension in ligatured and unligatured larvae, measurements have been carried out with a method developed and described by Krogh (1911, 1913, 1915). This method consists of introducing a small air bubble into an animal and analysing it about 1–2 hr. later after which time it is expected to have come into equilibrium with the gas pressure in the tissues. The gas bubble is squeezed out and collected under water. Its diameter is first measured, and the oxygen is then absorbed in pyrogallic acid. The diameter is measured again and the decrease in volume is calculated. The details of the method are fully described by Krogh (1911, 1915). This method is not exact, but gives a fair indication of the composition of the gases measured.

The bubbles were measured in two ways, with a camera lucida and by projection on a screen. The results were further checked by analyses with an Utrecht gas pipette (described by Jordan-Hirsch (1926); see also Fraenkel (1935, p. 896)). In this case the bubbles were collected from about twelve larvae for each analysis, and since the collection of the bubbles takes some time, the results may be rather high, owing to absorption of oxygen from the water.

We obtained the following results:

Method	Unligatured larvae % O_2	Double ligatured larvae % O_2
Utrecht pipette	15·8	4·5
Krogh's method using		
(i) camera lucida	14·35	2·0
(ii) projection on screen	16·6	4·9

These figures agree fairly well with those expected in the case of the unligatured larvae in air. The O_2 tension inside the double-ligatured larvae is very low, as was expected. The condition of zero tension was not found, but it should only be expected in part of the tissues, presumably inside the most active ones.

In the tissues of the intact larvae—and we should expect the same for the once-ligatured ones—the partial pressure of oxygen amounts to about 15 %, in the double-ligatured larvae to 2–4 %. The difference of the oxygen pressure inside and outside the larvae in the former case is 6 %, in the latter case 17–19 %. We must therefore expect that a very much greater amount of oxygen diffuses through the skin into the double-ligatured larvae than into the intact ones. It is not possible to measure the amount of oxygen diffusing through the skin in the intact blowfly larva, but an attempt to calculate it will be found in the Discussion.

The arrangement of the spiracles in the blowfly larvae makes it easy to block them by ligaturing, but this method is only applicable in a few types of dipterous larvae. It was desirable to find another method which could be more widely applied amongst insects. With this end in view respiration experiments have been carried out with the blowfly larvae submerged in water. It was assumed that the spiracles would be hereby blocked and the measurable respiration would be due to diffusion through the skin.

In the first set of experiments the oxygen uptake has been measured with larvae submerged in aerated water. Fig. 6, *3* shows that the quantity of oxygen consumed was very low, only about one-tenth that of the normal larvae, and about one-half that of the twice-ligatured ones. This is surprising in view of the theory that the oxygen uptake is solely dependent on differences in partial pressure of oxygen, for the partial pressure of oxygen in water saturated with air is equal to the partial pressure of oxygen in air.

When using oxygenated water for the same experiments the amount of oxygen dissolved in water is increased about five times (5·5 c.c. of O_2 in aerated water, 26 c.c. of O_2 in oxygenated water, per 1000 c.c. at 27° C.). Fig. 6, *4* gives the

results of experiments performed with blowfly larvae immersed in oxygenated water with the apparatus filled with oxygen. The oxygen consumption is raised to about four times the amount of the larvae in aerated water (0·27 against 0·07). Here again the value is considerably lower than that obtained for double-ligatured mobile larvae in oxygen (Fig. 6, *2*) which is 0·38, although the partial pressure of oxygen is the same in both cases.

This question will be dealt with in the Discussion.

The oxygen consumption of larvae immobilized by ligaturing behind the ganglion (Fig. 6, *5*) in oxygenated water has been found to be slightly smaller than that of the intact (mobile) larvae in the same medium (0·19 against 0·27). There is a very striking difference in the behaviour of the intact larvae in oxygenated and aerated water. The former remain active throughout the period of the experiment (2–3 hr.), the latter become immobilized within half an hour.

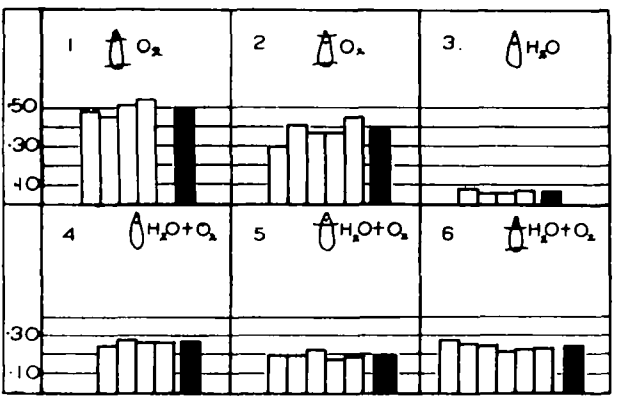

Fig. 6. Oxygen consumption of blowfly larvae under different conditions of ligaturing in air, oxygen, aerated and oxygenated water.

In order to find out whether the spiracles function at all under water by means of gas exchanges at the interphase of water and tracheal air, experiments with twice-ligatured larvae (ligatured behind the ganglion) in oxygenated water were performed (Fig. 6, *6*). The larvae consumed almost exactly the same amount of oxygen as the unligatured larvae in the same medium (Fig. 6, *4*). This shows that no measurable oxygen uptake is taking place through the spiracles under water.

(*b*) *Experiments on other insects*

An attempt has been made to extend the examination of the respiration through the skin to other insects. Only large lepidopterous larvae could be examined under conditions comparable to the ligaturing of blowfly larvae in air. In other insects the respiration of the normal insect in air has been compared with that of the insect submerged in oxygenated water. Although it can be safely assumed that the spiracles are not functioning under water and the oxygen uptake measured is taking place by diffusion through the skin, there is at present no means of proving whether the oxygen uptake in air after complete closing of the

spiracles would be the same, or lower as in the case of the blowfly larvae. No other reliable method of sealing the spiracles could be found. The practice of submerging insects in water is not generally applicable since in most cases the insect skin cannot be wetted entirely with water owing to air-retaining hairs, folds or covered spaces such as exist beneath elytra of beetles.

(1) Chaerocampa elpenor *larva*

Large caterpillars have been ligatured into pieces of two or three segments and the oxygen uptake of these pieces has been measured (*a*) with the spiracles open, (*b*) after the spiracles have been closed with grease. The result (Fig. 7) shows that after the sealing of the spiracles the oxygen uptake falls to about one-fifth of the value measured before. This result is in principle identical with the results obtained with blowfly larvae.

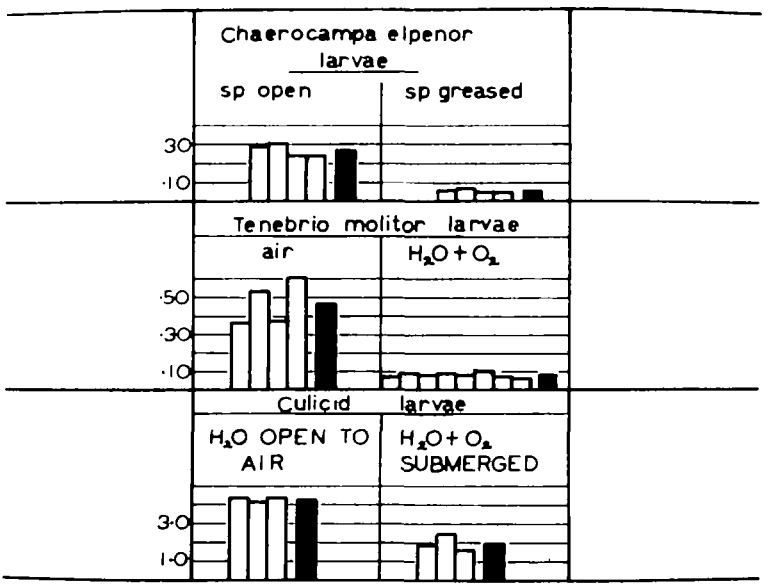

Fig. 7. Oxygen consumption of the larvae of *Chaerocampa elpenor*, *Tenebrio molitor* and *Culex* sp. with the spiracles open and closed either by grease or by immersion in oxygenated water.

(2) Tenebrio molitor *larvae*

The O_2 uptake of the mealworm has been measured first in air, then in oxygenated water (Fig. 7). In the latter case it is reduced to about one-fifth (0·09–0·47). This result is again very similar to that obtained with blowfly larvae.

(3) *Larvae of* Culex *sp.*

Finally the oxygen uptake of *Culex* larvae has been measured first with free access to the water surface, and then forcibly kept submerged in oxygenated water. Here about one-half of the amount of oxygen normally consumed penetrates through the skin (Fig. 7). Uptake expressed as $mm.^3$/larva/hr.

DISCUSSION

It is surprising that oxygen uptake through the skin in insects has hardly ever been taken into account in spite of the fact that in a large ecological group, namely in aquatic larvae, with a closed tracheal system, respiration normally takes place in precisely this way. From this one could have expected that some gaseous exchange should take place through the insect cuticle in terrestrial forms.

There are only three very incomplete records in literature which suggest that some respiration takes place through the skin in insects.

(1) v. Buddenbrock & v. Rohr (1922) measured the respiration of the stick insect, *Dixippus morosus*, in an arrangement by which the anterior and posterior ends were hermetically isolated and the respiratory exchange of both parts could be measured independently from each other. They were able to show that in the hind part after closing the spiracles with lanolin some oxygen uptake still occurred. Since the results are only expressed in mm. of the manometer and no weight of the insects is given it is impossible to estimate the amount of oxygen diffusing through the skin. (The method by which the results were obtained seems to us to be of rather doubtful value since it relies on the complete closing of at least 16 spiracles of the abdomen and also on the hermetical separation of the two chambers into which the anterior and posterior parts of the insects respire, two conditions very difficult to achieve and maintain.)

(2) Raffy (1931) brought larvae of *Dytiscus* into flasks entirely filled with water. After 2–4 hr. 0·012 and 0·019 c.c. oxygen/g./hr. were found to be consumed from the oxygen dissolved in the water. The spiracles were in open contact with the water throughout the experiment.

(3) Only very recently Maloeuf (1936) published some data from which he claims to have proved for the first time gas exchange taking place through the outer integument in insects. He placed the aquatic hemipterid *Belostoma* into a closed vessel completely filled with water. Under these circumstances, when prevented from reaching the air, gas exchanges take place between the aqueous medium and the subelytral air film (this had been previously demonstrated by Ege (1915) and others). After the subelytral air film had been removed a certain small amount of respiration still went on but was further reduced by closing the spiracles. This also shows that some gaseous exchanges occurred through the spiracles under water.

From these data and from the experiments reported in the present paper there cannot be any doubt that respiratory gaseous exchanges do take place in insects through the skin.

The O_2 uptake of the mobile double-ligatured larvae in air is about twice that of unligatured larvae in aerated water. The same holds approximately true for the difference of the O_2 uptake in the twice-ligatured larva in oxygen and oxygenated water. These findings do not agree with the conception of respiration as a diffusion process which is solely controlled by difference in the partial pressure of oxygen inside and outside the animal (as pointed out especially by Winterstein (1921),

Carter (1931), Krogh (1919) and others). This means that the rates of diffusion of oxygen through the skin should be equal from air or from aerated water, or again equal from gaseous oxygen and oxygenated water. Carter, in a comparison of the efficiency of aerial and aquatic types of respiration, comes to the conclusion that "the respiration in water should be more efficient than in air, if the structure of the respiratory epithelia are similar", and also provided that the water is kept in constant motion over the respiratory surface. This superiority of the gill over the lung is due according to him to the fact that the thickness of the stationary layer of water covering the respiratory epithelium is very much thicker in respiratory organs exposed to air than in those exposed to water. In our experiments with blowfly larvae we compare the diffusion of oxygen through an epithelium exposed to gas or to water saturated with the gas. There is no reason to assume that the stationary layer of water on the surface of the skin is different under the two conditions; for in air or pure oxygen the skin is practically dry and in water the fluid is kept moving continuously over the surface of the animals. According to Winterstein and Carter there is every reason to expect equal values for the oxygen uptake for the larvae in gas or in water saturated with it. Yet the oxygen uptake is almost double as much in the gas as in water saturated with it. This difference might suggest that in our experiments the mixing of the water is not sufficient and that in water the oxygen tension in the immediate neighbourhood of the larvae is lowered owing to the slow diffusion of oxygen in water. We assumed at first that the shaking of the apparatus would provide sufficient mixing, the more so since the larvae themselves could be seen to move passively in the water. Furthermore the fact that the consecutive readings of the manometer did not fall off over a period of 2 hr. seemed to rule out the possibility that the water was gradually being depleted of oxygen. However, Krogh (1919) has shown how difficult it is to get effective mixing when invasion of oxygen into water is concerned and moreover shows in the same paper, in an arrangement which provided very effective mixing of the fluids concerned, that the same amount of oxygen passes through a membrane into a fluid independent of whether the gas outside is in gaseous state or dissolved in the same fluid (reduced blood inside, oxygenated blood outside the membrane). We might therefore expect that under conditions of ideal mixing the oxygen uptake of the double-ligatured larvae in air would be equal to that of the unligatured larvae in aerated water.

The oxygen uptake of the twice-ligatured larvae has been found to be about one-quarter of that of the once-ligatured ones. But, as has been pointed out above, it would be wrong to assume that in the unligatured larvae one-quarter of the O_2 uptake passes through the skin and three-quarters through the spiracles. Since the oxygen tension in the tissues is about 15% in the normal larvae, and near to zero in the twice-ligatured larvae, the amount of oxygen diffusing through the skin in the normal larvae must be necessarily much less. There seems to be no direct way of measuring it in the blowfly larva, but we can get information about this value indirectly. The difference of the O_2 tension inside and outside the normal larvae is about $21-15=6\%$. Since the O_2 tension inside the double-ligatured larvae

approaches zero, we have only to measure the oxygen uptake of the twice-ligatured larvae in a gas mixture containing about 6 % of oxygen, in order to know how much oxygen diffuses through the skin when the difference of the oxygen tension outside and inside is about 6 %. The O_2 consumption of the twice-ligatured larvae amounts

at 5 % to 0·036 mm.^{3}/mg./hr.
at 7·5 % to 0·053 mm.^{3}/mg./hr. } mean taken from Table I.

Since the standard metabolism in air is about 0·470 mm.^{3}/mg./hr. the proportion of oxygen diffusing through the skin in the immobile larva breathing through the hind spiracles is about one-tenth of the whole O_2 consumption.

One has frequently stated that insects can pass considerable periods under water and still recover (e.g. Plateau, 1872). This has always been accepted as a proof of the occurrence of anaerobic respiration. From the experiments reported above it appears that this conclusion is not correct. An appreciable amount of oxygen passes from the water into the insect by way of the skin. Furthermore, unless the insects are submerged in water with great care after removing all the air adherent to the unwettable parts—this can only safely be done by previous bathing in strong alcohol—gaseous exchanges between the water and the attached air film or air bubbles may play a very considerable part in the respiration of the submerged insects.

SUMMARY

1. When blowfly larvae are paralysed by ligaturing behind the ganglion the resultant respiration of the hind parts represents the basal metabolism of the animal.

2. When the hind spiracles are also ligatured off, all respiration takes place by diffusion through the skin and is about one-quarter of the basal value. The R.Q. of the twice-ligatured larvae is 1·34. This indicates that part of the metabolic processes are maintained by anaerobic respiration.

3. The O_2 tension inside the larvae has been measured and is about 15 % inside the normal larvae and 2·4 % inside the double-ligatured larvae.

4. Therefore a much larger amount of oxygen diffuses through the skin in the double-ligatured than in the normal larvae, and it has been found by calculation for the normal larva to be one-tenth of the basal value.

5. When insects are submerged in water their spiracles are not able to function and all respiration takes place by diffusion through the skin.

6. In the normal blowfly respiration is independent of the O_2 tension from 100 % O_2 down to about 7·5 %, whereas in the double-ligatured larvae it is entirely dependent on the oxygen tension.

7. Experiments with other insects, *Chaerocampa elpenor* larvae (spiracles blocked with grease), *Tenebrio molitor* larvae and *Culex* sp. larvae (submerged in water), gave results similar to those obtained with the blowfly larvae.

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