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GAS EXCHANGE RHYTHMS OF *GALLERIA MELLONELLA* L. *(LEPIDOPTERA, PYRALIDAE)*

Clear cycles of discontinuous respiration in mobile prepupae, pharate pupae, pupae and imagos were ascertained by means of electronic respirometer (working also as actograph), differential calorimeter, infrared gas analyzer, and thermal conductivity detector (catharometer). One abrupt abdominal contraction before every CO_2 burst was characteristic for the mentioned preimaginale stages. Such expiratory stroke was externally unnoticeable, but on recording of respirometer it was fixed as a sharp peak. The most clear pattern in periodic CO_2 emission was expressed in pupae whose CO_2 cycles lasted 10—22 sec at 30 °C. In imago such ventilation movement is absent and a CO_2 burst lasted somewhat longer.

The gas exchange cycles were formed in the stage of mobile prepupa. If these cycles were absent in this stage, they were not detected in the following stages either.

Only 30—40% of the individuals from the laboratory population and 70—80% of the individuals from the wild population collected directly from beehives showed a clear pattern of cyclic gas exchange. The rest of the individuals had irregular respiration rhythms, but still the pupal development in this case proceeded normally.

The presented data affirmed that in this species the diffusive gas exchange is supported by the elements of active ventilation.

Introduction

Gaseous diffusion is the basic component in insect respiratory mechanism, and, by the theory of pure diffusive respiration, it has been suggested that pure gaseous diffusion alone can meet the needs of small insects or the inactive stages of larger species. Up to the present time several types of active and passive respiratory movements have been described by which gaseous diffusion is supported. Ventilating muscular movements take the form of dorsoventral or longitudinal pumping strokes while acting on the compressible regions of the tracheal system driving air in and out of open spiracles (Miller, 1974). In most larger insects pumping movements are performed by hemolymph (Miller, 1964).

In many insects the muscular ventilation is combined with discontinuous respiration. However, often also active ventilating movements alternate with discontinuous respiration, which is characterized by the cyclic CO_2 release. In this case the metabolic CO_2 is retained within the insect and released during brief periods of bursts. Discontinuous respiration is widespread in insects in general, but thorough experimental analysis of this type of breathing has been performed on large lepidopterous pupae, who are the most suitable objects for the study of the respiratory movements and the functioning of spiracles (cf. Schneiderman and Williams, 1955; Buck and Keister, 1955; Schneiderman, 1960). According to the mentioned investigations, insects showing discontinuous respiration neither breathe solely by diffusion nor perform active ventilation. Instead, they develop intratracheal vacuum which sucks air into their tracheal system.

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Diffusive cyclic gas exchange may be significantly supported by the mass transfer as well as by the muscular movements. Three types of pupal length changes have been observed during the respiratory cycle in *Hyalophora cecropia*: 1) passive changes accompanying each intratracheal pressure change, 2) active slow tone changes in abdominal muscles, starting with a burst of CO_2 and shortening the pupa, 3) volleys of active contraction-relaxation cycles (Brockway and Schneiderman, 1967).

Kestler (1984) and Slama (1988) established that in discontinuous respiration may accompany also active respiratory movements and even pumping ventilation.

It has been suggested that many groups of insects release their CO_2 continuously because of their high metabolic rate. In fact, there are only a few studies on the mode of gas exchange in small insects. The respiration in diapausing prepupal stages of *Cephala abietis* and in the pupae of *Dolerus nigratus* has been described as continuous, whereas in the pupae of *Bupalus piniarus* it has been found discontinuous (Slama, 1960). In a formicine ant *Camponotus vicinus* CO_2 emission has been established as discontinuous (Lighton, 1988). Cyclic CO_2 release is also known in the active imago of *Ips sextentatus* (average weight 18 mg) with the metabolic rate of about 2000 mm^3 O_2/h/g (Кузнк, 1976).

There is also a scarcity of studies about the formation of respiratory cycles during the individual development of an insect. Observing respiration rhythms in *Dermestes lardarius* in pupa and imago, and comparing experimental data on respiratory rhythms in a great number of species from six ordos brought us to the conclusion, that individual development of insects with open tracheal system should reveal characteristic respiration rhythms specific to the species, which correspond to changes in the physiological state and whose specificity depends on environmental conditions (Tartes, 1990).

In this study we present our experimental data regarding the rhythms of respiration in the last instar larvae, pupae and adults of *Galleria mellonella.*

Material and methods

The larvae, pupae and adults of *Galleria mellonella* were taken from standard cultures kept on a semiartificial diet at 30 °C in constant darkness (Sehnal, 1966). In addition, the caterpillars and pupae of a wild population were collected from infested beehives and were kept under the same conditions. The pupae were staged from larval-pupal ecdysis (day 0). The pupae averaged 110 mg.

Respiratory measurements were performed by means of a continuously recording differential electrolytic microrespirometer combined with a calorimeter (Fig. 1). The oxygen generating unit consisted of a 3 ml flask containing saturated aqueous copper sulfate solution as an electrolyte. Special electrodes for switching the oxygen generating unit on and off were not used in this respirometer. Oxygen generation was continuous, while the current level was changed according to changes in the insect oxygen uptake rate. The corrected electrochemical equivalent of O_2 has been reported as 209.5 µl O_2/mA/h (Moulder et al., 1970; cited by Taylor, 1977). An XY-recorder (Endim, VEB) was used to record the level of the O_2 uptake and respiratory rhythms. In addition to the mentioned recorder, an integrator of current (X 606) complete with an impulse counter and a numeric recorder for averaging the results of 1 hour were exploited. The current integrator was useful in case of a large amplitude of cyclic gas exchange.

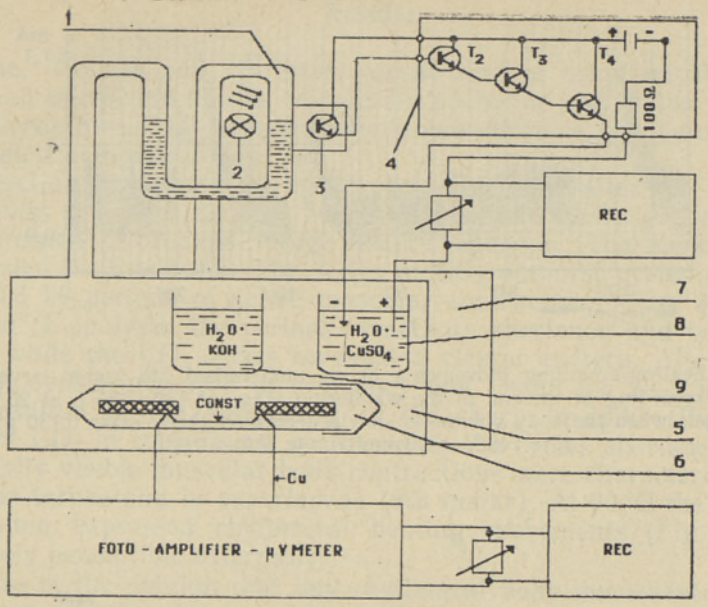

Fig. 1. Principal scheme of the respirometer combined with a differential thermocouple calorimeter.
1 — glass capillary half-filled with ethanol; *2* — source of the ray of light; *3* — photodiode; *4* — simple current amplifier; *5* — respiration chamber block; *6* — thermocouple calorimeter; *7* — compensation chamber; *8* — oxygen generating unit with electrodes; *9* — CO_2 absorbent flask.

The described respirometer registered the down-spike resulting from a CO_2 burst and also from the increase in the body volume. The up-spike was recorded by the sudden cyclic O_2 uptake or by the abrupt decrease in the body volume. The respirometer was sufficiently sensitive to register externally unnoticeable abrupt changes in the body volume. In this way the respirometer also acted as an actograph, and this did not disturb respirometric measurements. The recordings of mentioned body movements were regarded as respirometric actograms.

The level and rhythms of thermogenesis was recorded with a differential thermocouple calorimeter (Cu-Const) placed in the respiration chamber. In this way we succeeded in the synchronous recording of thermograms and respirograms. The apparatus was placed in a 1 l thermos inserted in the thermostat (Куузик et al., 1985).

The level and rhythms of the CO_2 output were determined with an infrared gas analyzer (Infralyt-4, VEB, Junkalor Dessau; further IRGA). The IRGA for the CO_2 monitoring system was based on the method of Turner et al. (1977).

RQ values were determined by means of a modified method of Mitchell (1973) and Tadmour et al. (1971), using the gas-chromatographic micromethod for respirometry. A gas-tight syringe (10 ml) was used as a respiratory chamber, connected to the dosage loop by a polyethylene tube (Ø 1 mm).

Respiratory cycles were also studied by the direct method, using the thermal conductivity detector of a gas chromatograph (Chrom 3, Czechosl.) or catharometer (Куузик, 1976). In principle, this method is the same as the diaferometric method described by Punt (1956).

All the figures presented here are direct photos of records.

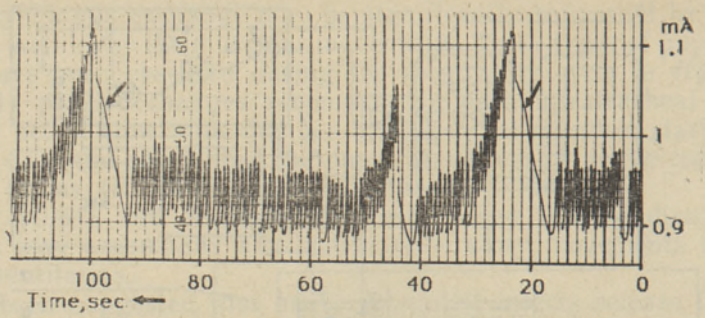

Fig. 2. The heating-breathing movements of an undisturbed 7th instar larva from the respirometer recording at the end of the wandering stage at 130—135 h at 20 °C. Arrows indicate periods when the body volume is slowly decreased (body mass 0.130 g; metabolic rate 1490—1500 mm^3O_2 h/g; R.Q.=0.95).

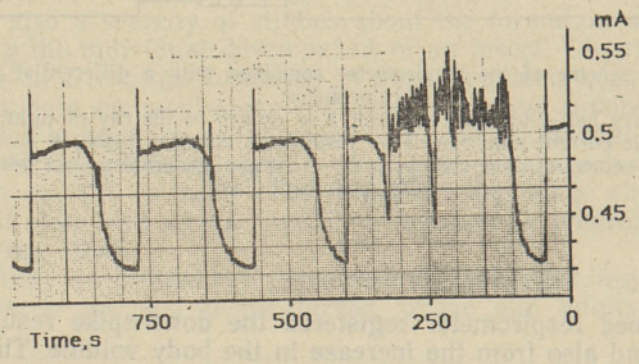

Fig. 3. Respirometric recording of cyclic CO_2 release with a muscular activity period of a mobile prepupa in cocoon at 27 °C (body mass 0.105 g; metabolic rate 970—980 mm^3O_2/h/g; R.Q.=0.91).

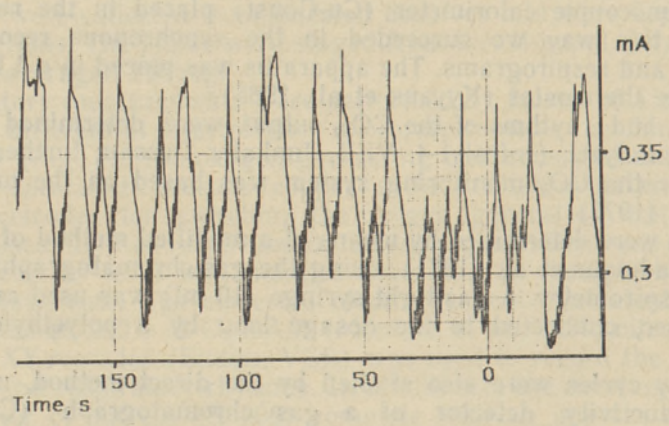

Fig. 4. Respirometric recordings at cyclic CO_2 release of a pharate pupa at 170—172 h after ecdysis at 27 °C (body mass 0.120 g; metabolic rate 635—640 mm^3O_2/h/g; R.Q.=0.84). Muscular microconstrictions are distinctly expressed on the falling line of the recording.

Results

Larvae. The 6th and 7th instar larvae showed arhythmical muscular macro- and microcontractions ceaselessly up to the end of the wandering stage. Microcontractions were externally unnoticeable, yet perceivable on respirometric actograms (Fig. 2).

The cyclic CO_2 release showed cyclic CO_2 bursts after the wandering stage within the tight cocoon, which means that cyclic gas exhange is already formed in prepupal stage before apolysis. The mentioned CO_2 cycles lasted 3—5 minutes. The series of CO_2 outburst cycles were often interrupted by periods of active muscular contractions (Fig. 3). Toward the period of apolysis, the periods of activity shortened and became less frequent while the CO_2 cycles revealed a clearer pattern. After the apolysis, CO_2 cycles increased in frequency and lasted for 2—3 min. These events resulted in the shortening of the sharp up-spike (Fig. 4). The amount of CO_2 in every burst decreased as the cycles shortened. Periods of externally visible muscular body contractions were characteristic in the last instar larvae and in superlarvae (8th instar). At 20 °C the 7th instar larvae often expressed rhythmical heating movements (Fig. 2), which were barely perceptible externally.

We are of the opinion that any rhythmical body movements in larvae also served as muscular ventilation. The heating movements were often synchronized by the group effect in dense located larvae at suboptimal temperatures.

Pupa. The cycles of CO_2 bursts were still shortened and lasted for 10—20 sec after the larval-pupal ecdysis (Fig. 5). As the longterm recording on calorimetric thermograms showed, the only periods of activity in an undisturbed pupa were limited by the times of wriggling or rotation movements (Fig. 6). Before the pupal-adult transformation the oxygen uptake raised markedly and the CO_2 release became more frequent (lasting 8—12 sec).

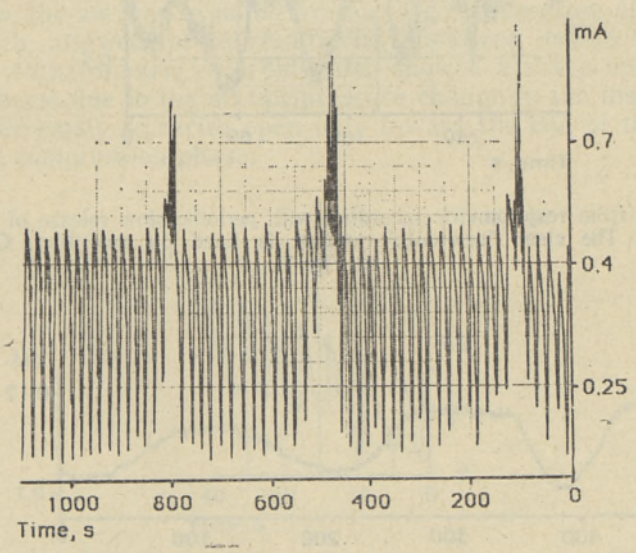

Fig. 5. Respirometric recording of CO_2 cycles of a male pupa at 72 h after ecdysis with 3 wriggling periods at 30 °C (body mass 0.102 g; metabolic rate 800—820 $mm^3O_2/h/g$; R.Q.=0.63).

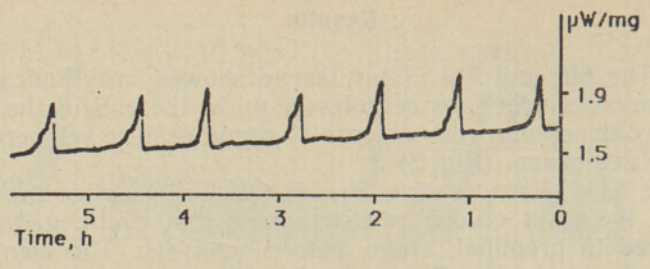

Fig. 6. Calorimetric thermogram with periodical rotation movements of a male pupa at 96 h after ecdysis at 27 °C (initial body mass 0.108 g).

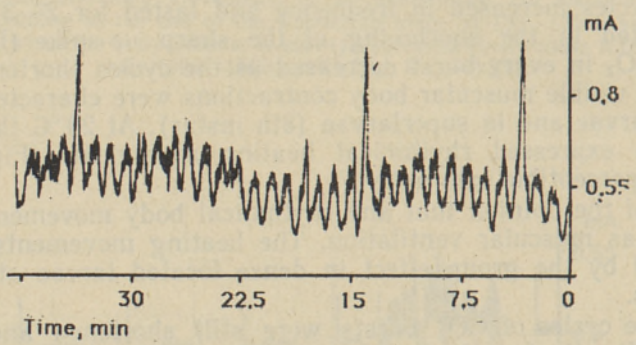

Fig. 7. Recording of respirometer from respiratory rhythms with cyclic but slow CO_2 release in female imago at 27 °C. Three higher peaks indicate the short periods of muscular activity (body mass 0.103 g; metabolic rate 1100—1120 $mm^3O_2/h/g$).

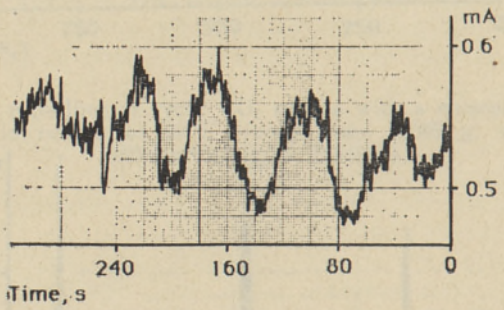

Fig. 8. A detail from respirometric recording with periodic slow release of CO_2 in female imago at 27 °C. The clear "sawtooth" pattern is fixed on recording. Other dates as in Fig. 7.

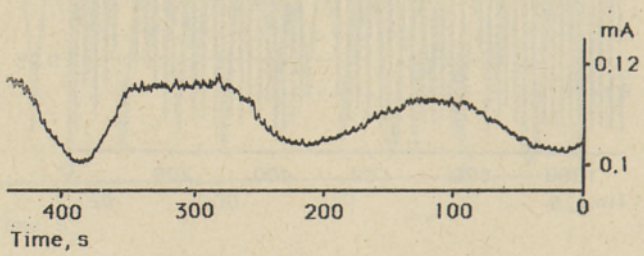

Fig. 9. The wavy shaped O_2 uptake level in male imago on the respirogram at 22 °C (body mass 97 mg; metabolic rate 230—240 $mm^3O_2/h/g$).

Imago. The undisturbed imago did not show typical CO_2 cycles as the pupa did. Still, distinct periodical changes in the O_2 uptakes and CO_2 outbursts were noticed. The respirograms presented well-fixed microcontractions or micropulses causing a serrate recording line (Fig. 7 and 8). We suppose that due to the frequent bursts of CO_2 the amount of CO_2 retained in the body was smaller and therefore the peaks of the CO_2 on respirometric actograms were considerably shorter than those in the pupa. The frequency of rise-fall periods depended on the metabolic rate. In the case of the low O_2 uptake level (300—400 $m^3O_2/h/g$) the period lasted 3—4 min (Fig. 7 and 8), but when the imago had a higher metabolic level (700—800 $m^3O_2/h/g$) the mentioned period lasted 0.6—1.2 min. The individuals without the cyclic CO_2 release were characterizied by a wavy line of O_2 uptake level (Fig. 9).

Various phases of the respiration cycle

According to the data presented above, gaseous exchange cycles in *Galleria mellonella* showed some kind of similarity to the cycles of big lepidopteran pupae. Though the respiratory cycle in *Galleria mellonella* is generally relatively brief, and each CO_2 burst contains less than 1 µl of this gas, we cannot regard these bursts as microcycles. The latter are characteristic of the flutter period which consists of series of microcycles without a clear pattern, varying in duration from 3 to 60 sec; these were thoroughly analyzed in the pupae of *Hyalophora cecropia* (Levy and Schneiderman, 1966; Brockway and Schneiderman, 1967; Kestler, 1984; Slama, 1988).

The respiratory cycle of *Galleria mellonella* showed four phases in respirograms.

1. The first phase began with one vigorous contraction of the intersegmental muscle of the abdomen. We presume that all the spiracles were tightly closed in this phase. This was obviously the typical pressure phase as it had been surveyed by Miller (1964, 1974). In the compression phase, as it was supposed, movements of hemolymph inflated arthrodial membranes and, also, the air was expelled from a larger proportion of the tracheal system, which allowed pressures to be equalized before the spiracles opened. The catharometric recording also showed a sharp up-spike before the CO_2 outburst due to the abrupt pressure change in the insect-container (Fig. 10). Obviously spiracles open only toward the end of the expiratory stroke in the compression phase.

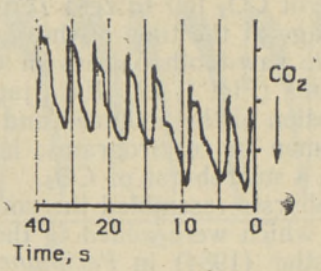

Fig. 10. Catharometric qualitative record of cycles of a mobile prepupa in cocoon at 150—154 h after last larval ecdysis at 27 °C (body mass 0.125 g; metabolic rate 850—900 $mm^3O_2/h/g$; R.Q.=0.85).

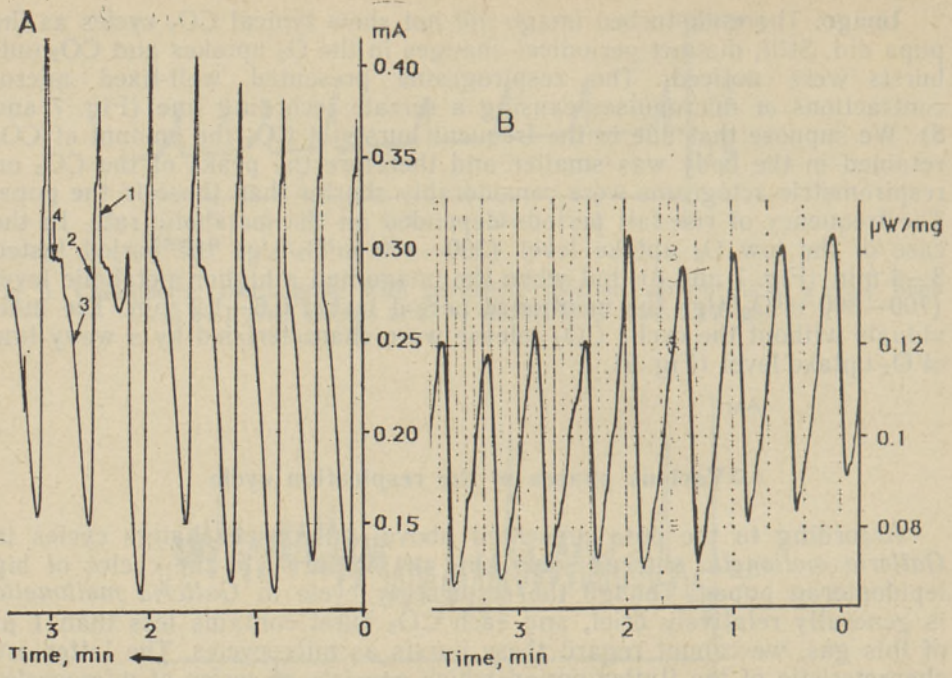

Fig. 11. Synchronous records from a respirometer (*A*) and calorimeter (*B*) of a male pupa at 70—74 h after ecdysis at 30 °C (body mass 0.112 g; metabolic rate 620 $mm^3O_2/h/g$; R.Q.=0.68).
Arrows indicate the phases of respiration cycle.

In the respirometric actograms of the pupa the compression phase was recorded as a sharp up-spike lasting from 0.3 to 0.8 s. The up-spike denoted an abrupt shortening of the abdomen and a decrease of the body volume (Fig. 11*A*). In the larval stage the up-spike caused by the compression was longer and more vigorous, lasting less than 0.2 s as it was established by using the high speed of the pen driver. Externally the compression phase occurred without any visible motion in the larva and pupa.

2. The second phase began with the opening of the spiracles and a CO_2 burst (Fig. 11*A*). As it was measured by IRGA, each of these bursts of the 7th instar larva contains 0.2—0.4 μl CO_2 at 30 °C. In the pupal stage, each CO_2 output contains a considerably smaller amount of this gas. Synchronous registration with the respirometer and calorimeter yielded a simultaneous peak. The peak in the calorimetric thermogram is due to the warming effect of the abrupt release of CO_2 or to the warm air with a high CO_2 concentration (Fig. 11*B*).

It appeared from IRGA records that after the CO_2 output spiracles were closed as the level of CO_2 fell to zero (Fig. 12).

During the larval stage at the time of the tight cocoon, but before the apolysis, a characteristic saw-tooth pattern of CO_2 bursts was recorded in IRGA and respirograms (Fig. 4; 12). Each jag of the saw-tooth pattern denotes a weak compression of the abdomen and the corresponding micro-shortening of the abdomen in respirograms; however in the records of IRGA each jag denotes a microburst of CO_2.

The mentioned microbursts resembled the small CO_2 bursts caused by single pumping volleys which were added to the main, continuous efflux of CO_2 observed by Kestler (1984) in *Periplaneta americana*. Cockroach ventilation periods connected with the movement pattern of spiracles and the CO_2 release is described as the CFV type of discontinuous respiration (each cycle consists of a ventilation, flutter and constriction period) (Kestler, 1984).

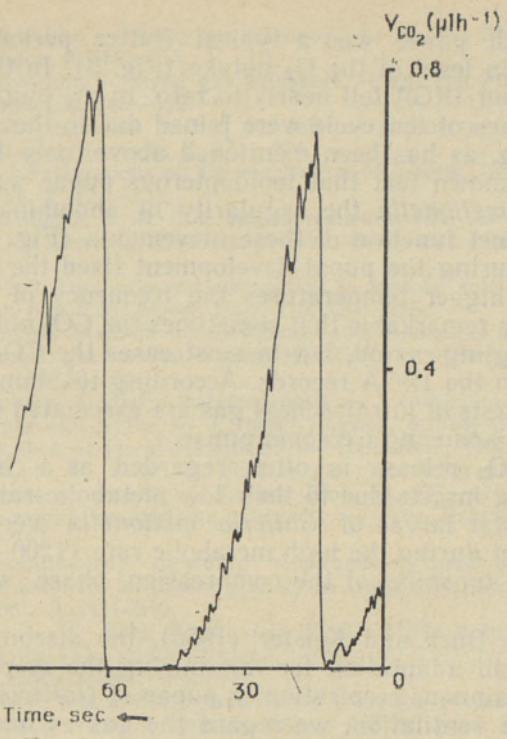

Fig. 12. IRGA recording from peakes of CO_2 microbursts on the falling line of a CO_2 cycle of a pharate pupa at 10—12 h before pupal-imaginal ecdysis at 22 °C (body mass 0.113 g; metabolic rate 530—550 $mm^3O_2/h/g$; R.Q.=0.80).

At the same time CO_2 microbursts in 7th instar larvae of *Galleria mellonella* obviously correspond to the extracardiac pulsation in the hemocoelic pressure discovered by Slama (1988) in the pupae of *Actias selene* and *Hyalophora cecropia*. According to Slama (1988), there is an increasing evidence that insect respiration is regulated by the same system that regulates the hemocoelic pressure.

3. The third phase denoted the absorption of CO_2 in the respiration chamber and also corresponded to the falling period of the CO_2 output. This phase in pupae was characterized by the comb-tooth pattern on the recordings of the respirometer resulting in abdominal microconstrictions and corresponding to microbursts of CO_2 (Fig. 13).

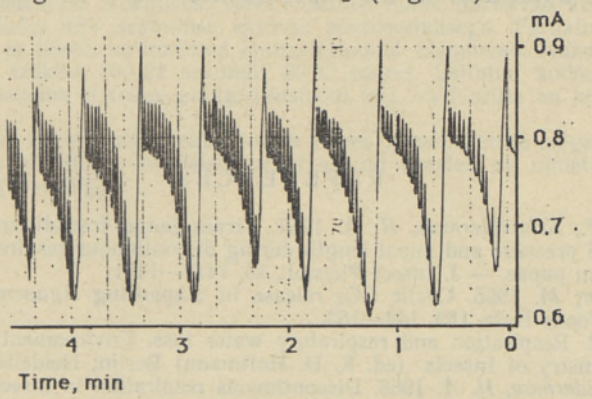

Fig. 13. "Comb-tooth" pattern from respirometric actograms of a pharate pupa at 7—8 h before ecdysis at 27 °C (body mass 0.114 g; metabolic rate 1400—1420 $mm^3O_2/h/g$; R.Q.=0.78).

4. The fourth phase was a typical flutter period, the respirogram showing a certain level of the O_2 uptake (Fig. 3). In this period the CO_2 output level by our IRGA fell nearly to zero. In the pupal stage mostly the 3th and 4th phases of the cycle were joined due to the short cycles of gas exchange lasting, as has been mentioned above, only 10—22 s.

It is a well-known fact that lepidopterous pupae wriggle periodically. In the *Galleria mellonella* the regularity of abdominal rotation periods indicates a distinct function of these movements (Fig. 6). The records of thermogenesis during the pupal development fixed the regularity of these movements. At higher temperatures the frequency of wriggling periods was greater. It is remarkable that sometimes the CO_2 output level increases during the wriggling period, but in most cases the CO_2 output level falls as it was seen in the IRGA records. According to Slama (1988), the brief expiratory outbursts of intratracheal gas are associated with the abdominal rotation in the diapausing *Cecropia* pupae.

The cyclic CO_2 release is often regarded as a characteristic phenomenon in resting insects due to their low metabolic rate. It is remarkable that the last instar larvae of *Galleria mellonella* were able to show the cyclic CO_2 output during the high metabolic rate (1200—1300 $mm^3O_2/h/g$): in this case the up-spike of the compression phase was extraordinarily high and rapid.

According to Buck and Keister (1955), the discontinuous respiration is regarded as an adaptation for minimizing the respiratory water loss. As far as discontinuous respiration in pupae of *Galleria mellonella* is supported by active ventilation, we regard the gas exchange in this species as diffusive-convective, with suction ventilation. Kestler (1984) regards the convective gas exchange as advantageous for water retention; it also supports CO_2 release in the shorter cycles.

It is remarkable that only 30—40% individuals of laboratory population showed a clear intermittant gas exchange in their pupal stage. On the other hand, in the wild population dominated (70—80%) individuals with clear periodic CO_2 emission. Irrespective of the gas-exchange type, the pupal development was terminated normally. We can therefore conclude that *Galleria mellonella* is a rather suitable object for examining the problem of cyclic CO_2 release and whether it is involved in diminishing the weight loss in pupae.

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VAHALEEDIKU (*GALLERIA MELLONELLA* L., *LEPIDOPTERA, PYRALIDAE*) GAASIVAHETUSE RÜTMID

Kasutades elektronrespiromeetrit, diferentsiaalkalorimeetrit, gaasikromatograafi, soojusjuhtivusdetektorit ja infrapunast gaasianalüsaatorit, tuvastati vahaleediku gaasivahetuses selgesti väljendunud tsüklilisus. Gaasivahetuse tüklid hakkavad kujunema eelnuku staadiumis, vaheldudes siin arütmilise aktiivse ventileerimisega. Faraatnuku staadiumis tsüklid sagenevad ja lihaste arütmilised kontraktsioonid taanduvad. Nukustaadiumis vältab gaasivahetuse tsükkel 10—22 sekundit 30 °C juures. Esitatud andmed näitavad, et vahaleediku gaasivahetus ei toimu puhta difusiooni teel, vaid selles on ka aktiivse ventilatsiooni elemente.

Laboratooriumis kasvatatud populatsioonis esines gaasivahetuse selgesti väljendunud tsüklilisus vaid *ca* 30—40%-l isendeist, tarust võetud isendeil oli nimetatud gaasivahetuse tüüp valdav (70—80%).

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РИТМЫ ГАЗООБМЕНА У ПЧЕЛИНОЙ ОГНЕВКИ *GALLERIA MELLONELLA* (*LEPIDOPTERA, PYRALIDAE*)

С помощью электронного респирометра, детектора теплопроводности (катарометр), дифференциального термопарного калориметра и инфракрасного газового анализатора выявлены четкие циклы газообмена в стадиях подвижной предкуколки, фаратной куколки, куколки и имаго у пчелиной огневки. Для названных преимагинальных стадий перед каждым прерывистым выделением CO_2 характерно одно резкое сокращение брюшных мышц (экспираторное движение), что, однако, внешне остается незамеченным, но на записи респирометра отмечается резким пиком. Экспираторное сокращение брюшка у имаго отсутствует и прерывистое выделение CO_2 происходит медленнее, чем у куколки.

Циклы газообмена формируются в стадии подвижной предкуколки: если в этой стадии названные циклы отсутствуют, тогда они не будут выражены и в последующих стадиях.

В лабораторной популяции четкие циклы газообмена обнаружены только у 30—40% особей, а в «дикой» популяции, взятой из ульев, прерывистое дыхание выявлено у 70—80% особей. Куколочное развитие протекало нормально независимо от типа газообмена.

Приведенные в работе данные показывают, что газообмен у пчелиной огневки происходит не только в результате одной чистой диффузии, но и с участием элементов активной вентиляции.