FUNCTIONAL DESIGN OF THE TRACHEAL SYSTEM OF FLYING INSECTS AS COMPARED WITH THE AVIAN LUNG

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A process as demanding in power as that of flapping flight influences most physiological systems very greatly and above all the respiratory system. In the thorax of adult winged insects, it has become so intricate and integrated by fusion and extension that it is difficult to describe in comparative or in functional terms. In fact, because of lack of knowledge about the functional morphology little is known about the supply of oxygen to the wing muscles and the exchange of respiratory gases between the thorax and the ambient air.

There are two major reasons for being interested in the respiratory system of flying insects. The oxygen uptake of active wing muscle is enormous, 1.4-7.3 ml. O₂ per gramme muscle per minute (N.T.P.). This represents an unparalleled record as to power expenditure of living tissue, up to 2.5 W./g. (for review see Weis-Fogh, 1961). Since the metabolism is aerobic and since most insects can change from the non-flying state to a state of sustained flight and back again almost instantaneously and without any significant after-effects (Chadwick & Gilmour, 1940; Krogh & Weis-Fogh, 1951), the supply of oxygen and fuel must be adequate and must have reached an intensity and perfection higher than found in wingless animals.

Another reason for interest is the fact that flapping flight of birds and insects requires an energy expenditure which is 10-100 times greater than is found in individuals which are not flying, so that many physiological systems are designed to function at two quite distinct rates of activity. Some processes and structures are concerned mainly with the one level and some with the other but, as examples will show, one cannot know beforehand how to interpret them.

In the non-flying state, the gaseous exchange of large and medium-sized insects depends on the combined effect of diffusion and ventilatory movements executed mainly by the abdomen, here called abdominal pumping. From circumstantial evidence, it has often been assumed that, during flight, the thorax is ventilated by an additional mechanism coupled to the wing movements (cf. Krogh, 1941) but no proof of such a thoracic pumping has been put forward as yet. On the contrary, the local ventilation of the thorax has been disputed because the abdominal pumping usually persists or is increased during flight (Fraenkel, 1932a). The latter view is also in accordance with the generally accepted model of the pterothorax. According to that, the wings are moved by slight alterations of the curvature of the nota (Snodgrass, 1935) which will allow for some mixing of the air entrapped in the thoracic system but not for an adequate exchange with the atmosphere.
The qualitative principles involved in these and related problems are studied in the present paper. In two other articles, the quantitative aspects of diffusion and ventilatory mechanisms are treated in some detail (Weis-Fogh, 1964a, b). The studies are based mainly upon locusts and dragonflies. A preliminary report has been published (Weis-Fogh, 1956a) and the main material put at the disposal of Dr P. L. Miller (1960a, b, c) for his elegant studies on the control of ventilation in locusts.

MATERIALS AND METHODS

Adult desert locusts (*Schistocerca gregaria* Forskål, *phasis gregaria*) were supplied by the Anti-Locust Research Centre, London. Dimensions and weights were calculated for animals of average size (Weis-Fogh, 1952a). Adult dragonflies (*Aeshna, Libellula, Sympetrum*) were caught in nature.

**Flight.** Locusts were suspended from the pronotum and dragonflies from the sternum and placed in front of an open-jet wind tunnel, observed in stroboscopic light and photographed by flash light (Weis-Fogh, 1956b).

**Total tracheal volume.** The soft abdomen and the hydrofuge spiracles make the method applicable to any large insect. The insect is made heavier than water by means of lead wire; it is weighed under water with detergent added to avoid bubbles, the jar with the submerged preparation is then evacuated and the pressure suddenly restored. This causes the tracheal system to collapse completely without any entrance of water. The difference in weight before and after evacuation represents the entrapped air volume.

**Agar injection of tracheal system.** Frozen sections and partial injection with wax or stained oil were used but in order to obtain a more complete picture it was necessary to fill the entire system uniformly with a semi-transparent stained material. The large thin-walled air sacs, the soft abdomen and the arthrodial membranes prevented the use of viscous, melted wax (Krogh, 1917) and, in connexion with the black deposits of sulphides, also of light petroleum (Wigglesworth, 1950). All external surfaces were therefore made rigid by covering them with a thick layer of adhesive wax (4.5 g. resin + 10 g. beeswax), except for the spiracles, which were held open by means of pieces of inserted metal wire. The injection fluid was 1.5-2% agar dissolved at 90°C in distilled water, and after addition of 10-20 ml. indian ink and 10 ml. crude detergent per 100 ml. agar solution, it was stored at 70°C and filtered through cotton wool immediately before use. The injection took place in a Y-tube submerged in water at 47°C and with the wax-clad insect in one branch and the agar solution in the other (Text-fig. 1a). The filter pump (d) is operated by hot water which is at 50°C to begin with. The temperature is slowly decreased to 44°C. At 47°C the injection liquid and the tissues begin to boil gently, driving out the atmospheric air in about 1 min. The liquid is then poured over the preparation and the pressure is very gently raised by letting in air from the trap between stopcocks (2) and (3), bringing it up from 68 mm. Hg (saturated water-vapour pressure at 44°C) to 150 mm. Hg in about 45 min. The injection is then complete and the system can be opened to the atmosphere. The slow uniform increase in pressure is essential for uniform filling. Otherwise some air sacs become over-filled and others collapse. After quick cooling and removal of the wax and other unessential parts, the preparation is fixed in 4% formaldehyde, dehydrated in 70,
80, 85, 90 and 96% ethanol (24 hr. in each) and transferred to pure aniline oil (R.I. 1.59, sp. wt. 1.02 g./ml.). The linear shrinkage of test blocks of agar was 3-5%, according to size, so that both the organization of the tracheal system among the now transparent and rather hard muscles and the volume of its major components could be studied (after suitable correction for the 10-17% volume shrinkage).

RESULTS

Each wing muscle of an insect can be considered as an entity. It receives one or a few large primary air tubes or air sacs from which a dense system of secondary tracheae branch off and distribute themselves transversely between the muscle fibres, eventually dividing up into a system of tertiary tracheae and then into tracheoles (cf. Text-fig. 6). In wing muscle of large and medium-sized insects, it can be shown that the primary system must be ventilated very effectively during flight, while diffusion can account for the exchange of respiratory gases in the remaining parts of the muscle (Weis-Fogh, 1964a). We shall therefore confine ourselves to the primary trunks (which may run inside the muscle mass or at its surface) and to the other gross structures in the wing-bearing segments.

(a) Tracheal system of the locust thorax

Gross morphology. The papers by Vinal (1919), Jannone (1940), Albrecht (1953) and Miller (1960c) offer much important information about the system in grasshoppers but do not describe the basic ventilatory mechanisms or how the wing muscles are supplied. The main results of the present investigation are summarized in Text-fig. 2, which should be consulted throughout this paragraph. It is derived from the detailed dissections in Text-figs. 3-5, Pl. 1, figs. 1, 2, from direct observations as in Pl. 1, figs. 4, 5, and from measurements on flying locusts as in Text-fig. 7.
It is not possible with certainty to homologize the various trunks and air sacs in the thorax with those in the abdomen but it is convenient to divide the system into groups (Table 1) and to indicate how it may be related morphologically to the abdominal system described by Vinal (1919) and Albrecht (1953). In the anatomical drawings, freely exposed tracheae are hatched transversely while the margins of air sacs are drawn with a brush border. When tracheae or air sacs pass beneath other structures, these signatures are absent and the margins are indicated by broken lines provided the structure is a muscle or another solid body; if the overlying structure is part of the

Text-fig. 2. Principles of the tracheal organization and of the supply to the wing muscles in the pterothorax of Schistocerca gregaria. A narrow transverse section of the skeletal box is shown. Arrows indicate the wing movements and the corresponding up and down movements of the nota which result in air moving in and out of the spiracles (Sp). Only the right-hand side is shown, exploded laterally for the sake of clarity.

Three muscles are drawn with sharp edges. They represent a simple depressor (mesial), an elevator (intermediate) and a controller-depressor (lateral). In this and the following drawings, the tergo-pleural tracheae (Ti) and the sternal tracheae (Ts) are hatched transversely. In addition, the pleuro-coxal tracheae (Tpl) are striped longitudinally.

Air sacs (1) and (2) represent the mesial group of the tergo-pleural system; their actual shapes and connexions are shown in Text-fig. 3 A. The intermediate group is situated on either side of the elevators (for details see Text-figs. 3 B and 4 A). Some of its air sacs ventilate muscles indirectly (3 and 4) via longitudinal tracheae; others supply the muscles directly (5) or fill up 'empty' crevices close to the moving nota (6, 7). In the present drawing the lateral subdermal air sacs in Text-fig. 4 B are represented by (9) and the ventral subdermal air sacs in Text-fig. 5 by (11). Air sac (10) is a typical representative of the coxal groups belonging to the pleuro-coxal system.

Note that there are no functional connexions with the sternal tracheae (liquid block indicated) but extensive interconnexion between the remaining parts of the same side.
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The tracheal system, full lines are retained. Intramuscular trunks, however, are also drawn in full line but with the fibre signature superimposed. The air sacs are numbered without reference to the segment to which they may belong. The muscles are numbered according to Snodgrass (1929) with a few modifications and consist of three groups, the dorsal-longitudinal simple depressors of the wing, the dorso-ventral simple elevators and the lateral, dorso-ventral controller-depressors (Wilson & Weis-Fogh, 1962).

When the locust is not flying, the anterior four pairs of spiracles open during abdominal inspiration and close during expiration (McArthur, 1929), giving rise to a unidirectional flow of air, in through the first four spiracles and out mainly through spiracles 5–10 (Fraenkel, 1932b). During flight, spiracles 1 and 4–10 remain synchronized with the abdominal movements but spiracles 2 and 3 are kept wide open (Miller, 1960c). In addition Miller (1960b) has shown that spiracle 1 has a dorsal orifice connected with the cephalic tracheae and a ventral orifice connected with the thoracic system with a small anastomosis in between. During powerful ventilation and in the presence of high carbon-dioxide tensions the ventral orifice may be partially occluded by the simultaneous contraction of the opener and closer muscles during expiration (when the valve usually tends to close). During flight, however, this occlusion probably does not take place although the valve maintains synchronized movements with the abdominal pumping. In any case, more of the cycle is spent near the open position than when the animal is not flying (Miller, 1960b, c).

Main groups. The divisions and subdivisions of the tracheal system in Table 1 require the following comments in addition to those offered in the legends for Text-figs. 3–5. The first major division, the tergo-pleural system, is the most important since it is connected directly with the first three pairs of spiracles and since its tracheae (Tt) and air sacs (At) supply the major volume of the musculature. Like the dorsal system in the abdomen it includes a pair of paracardial tracheae and air sacs (cf. 1 At and 2 At) and like the visceral abdominal system it has a number of dorsal air sacs, of which the large central air pool 3 At is the most important. The abdominal air sac 1 abA clearly belongs to this system but has no direct connexion with the pterothorax and, due to the occluded tracheae at the fourth spiracle (4 Sp; Miller, 1960c), only with the fifth spiracle (5 Sp).

The subdivisions of the tergo-pleural system are not clearly separated from one another but may, nevertheless, serve a descriptive purpose. The mesial group in Text-fig. 3A is situated between, and ventral to, the dorsal longitudinal muscles, which receive a dense supply of secondary tracheae emerging especially from the central pair of air sacs (3 At, Pl. 1, fig. 3). Wide direct tracheae connect the mesial group with the first three spiracles. It is obvious from Pl. 1, fig. 1, that the air volume in 3 At and 1 abA depends on the degree of filling of the crop and also that the location of these air sacs and the thin flexible walls separating them mean that they are influenced simultaneously and in the same way by thoracic volume and pressure changes. The anterior extension of 3 At joins the cephalic system and, via anastomoses in the head, it is therefore connected with the sternal system. There are, however, no direct anastomoses between the two sides of the pterothorax. The intermediate group in Text-figs. 3B and 4A is by far the most intricate. It is situated on either side of the elevator muscles, which are supplied mainly by longitudinal tracheae connected dorsally to the tergo-pleural air sacs and ventrally to the pleuro-coxal system. The
Text-fig. 3. Dissection of the tracheal system in the pterothorax of the right-hand side of *Schistocerca gregoria*.

(A) Longitudinal section in the plane of symmetry with no muscles removed. The mesial group of the tergo-pleural system is dotted. Note the inlets from spiracles 1 and 2 to the large central pool 3 At. It has no connexion with the adjacent abdominal air sac 1 Abd which connects with spiracle 5 (not shown; the tiny trachea from spiracle 4 is occluded).

(B) Same, after removal of the dorsal longitudinal muscles and of the mesial group. The intermediate group of the tergo-pleural system is dotted. Ventrally it is connected at many points with the pleuro-coxal tracheae (longitudinal striation). Note that the latter system has no direct connexion with spiracle 3, that its segmental anastomosis with the sternal tracheae is non-functional (Miller, 1960c; not drawn in the metathorax) and that it is connected to the upper cephalic tracheae by means of a narrow tube.
Text-fig. 4. Dissection of the tracheal system in the pterothorax of *Schistocerca gregaria*.

(A) The lateral part of the intermediate group of the tergo-pleural system, as in Text-fig. 3 B, after removal of the elevator muscles.

(B) The left-hand side of the thorax drawn with transparent cuticle in order to show the subdermal, heat-insulating air sacs belonging to the lateral group of the tergo-pleural system.
**lateral group** in Text-fig. 4B fill out the considerable space between the pleural walls and the controller depressor muscles (Pl. 1, fig. 2). Most of these muscles receive their supply of secondary tracheae directly from the flattened air sacs which, taken together with sternal and notal air sacs, constitute an insulating air cushion round the central core of pterothoracic muscles. The lateral air sacs are directly connected with the first three spiracles and intercommunicate extensively.

Table 1. **Divisions and subdivisions of the tracheal system in the pterothorax of Schistocerca gregaria, according to this study (A means air sac, T trachea), the functional connexions of the groups with the spiracles (Sp) by means of direct tracheal trunks, the approximate location relative to skeleton and wing muscles, and the probable homologues with the abdominal systems according to Albrecht (1953) and Vinal (1919; in brackets)**

<table>
<thead>
<tr>
<th>Classification applied</th>
<th>Functional connexion with spiracles</th>
<th>Location</th>
<th>Suggested homologues in abdomen</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Tergo-pleural system (suffix i)</strong>:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mesial group (1 to 3 At)</td>
<td>1, 2, 3 Sp</td>
<td>Mainly dorsal</td>
<td>Dorsal plus visceral systems (Dorsal)</td>
</tr>
<tr>
<td>Intermediate group (4 to 15 At)</td>
<td>1, 2, 3 Sp</td>
<td>Surrounded elevators, supplies wings</td>
<td></td>
</tr>
<tr>
<td>Lateral group (16 to 26 At)</td>
<td>1, 2, 3 Sp</td>
<td>Between pleura and controller-depressors</td>
<td></td>
</tr>
<tr>
<td><strong>Pleuro-coxal system (suffix pl)</strong>:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Coxal group (1 to 2 Apt)</td>
<td>1, 2 Sp</td>
<td>Mainly ventral</td>
<td>Pleural or spiracular system (Supraventral)</td>
</tr>
<tr>
<td>Ventral group (3 to 10 Apt)</td>
<td>(Supplied via coxal group)</td>
<td>Supplied via ventral cord, main connexion between head and abdomen</td>
<td></td>
</tr>
<tr>
<td><strong>Sternal system (suffix i)</strong>:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5 Sp and possibly 3 Sp (Miller, 1960c)</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

The second major division is the ventrally placed **pleuro-coxal system**. It probably corresponds to the pleural or spiracular system in the abdomen because it has segmentally arranged anastomoses with the sternal system placed at either side of the ganglionic chain. However, these anastomoses degenerate and become liquid-filled and non-functional after the first nymphal stage, making possible an effective unidirectional flow of air in the non-flying animal (Miller, 1960c) and blocking the exchange of air between the two sides. The pleuro-coxal tracheae (Tpl) are indicated by longitudinal hatching on top of the usual cross-striation. They communicate with 1 Sp and 2 Sp but not with 3 Sp and function as ventral collecting tubes for the intermediate group of the tergo-pleural system. In addition, each leg receives a trachea from the pleuro-coxal system. Its air sacs (Apl) fall into two groups: the *coxal group*, which is directly connected with the primary trunks to the dorso-ventral muscles, and the *ventral group*, which forms a subdermal cushion covering the sternal plastron.
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(Text-fig. 5). The ventral air sacs do not supply muscles directly but, like other air sacs, they function as hydraulic air-bellows, as can easily be seen through the sternal cuticle of a living locust.

Text-fig. 5. Dissection of the tracheal system in the pterothorax of Schistocerca gregaria. The subdermal air sacs belonging to the ventral group of the pleuro-coxal system together with the sternal system. On the left-hand side the air sacs (crosses) are seen through the cuticle, which has been removed on the opposite side, where the exposed air sacs are dotted.

The sternal or paraganglionic system (Ts and As, Text-figs. 3 A, 5) has connexion with spiracle 3 through a flattened, ribbon-like (non-functional?) trachea (not drawn; Miller, 1960c). Apart from this it is almost isolated from the pterothoracic system and forms the main throughway between head and abdomen.
Without exception, the primary and secondary tracheal supplies to the wing muscles comply with the schemes in Text-fig. 6 and its legend. It is characteristic and significant that all muscles have connexions with more than one of the first three ipsilateral spiracles but no connexion with the opposite side. Since one of the connexions is short and direct it has been drawn in full line.

Supply type:

1. Centro-radial
2. Latero-radial
3. Latero-linear

Text-fig. 6. Three types of tracheal supply to the wing muscles of locusts. The primary supply is drawn horizontally while the secondary supply is indicated on the vertical transections of the muscle. The scheme seems to be applicable to most insects.

Typical examples of each type are seen in Text-figs. 3 and 4, as follows: type (1), muscle 90, 113; type (2), muscle 89, 103, 112, 118, 129, 133; type (3), muscle 81, 97, 98, 99, 127, 128.

Most muscles have a shunted system (shunt drawn in broken line), as for instance muscle 118 with its two air sacs 5 At and 2 Api in Text-fig. 3B.

The general principle is that a muscle receives a large longitudinal trunk or a longitudinally arranged air sac emerging from one of the spiracular plexi, the primary supply (drawn horizontally). In case of a trachea, the distal end invariably widens into a thin-walled air sac of much greater capacity. The intramuscular trachea in muscle 90 (Text-fig. 3B) is no exception since the air sac (6 At) was removed by accident, the corresponding muscle 119 in the metathorax retaining its air sac (8 At). When the primary supply consists of an air sac, as for instance 18 At and 19 At for muscles 98 and 97 in Text-fig. 4B, there may be no distal air sac present, but in all cases the implication is that the primary system is bound to be strongly ventilated whenever the pressure or the volume of the thorax changes.

As to the secondary supply, it is characteristic that it originates as closely spaced tracheae running normal to the muscle fibres. The proximal parts are often oval in cross-section and are undoubtedly ventilated to some extent by intramuscular pumping (see later) but they soon become almost circular. Direct microscopic inspection of the contracting first basalar muscle of dragonflies distinctly showed that even the proximal parts of the secondary supply remain wide open so that air ventilation would only amount to some tidal mixing. This implies that the remaining exchange must depend
on diffusion according to the three supply types in Text-fig. 6, which are convenient for a mathematical treatment (Weis-Fogh, 1964a).

In the centro-radial type, the primary trunk is intramuscular and the secondary tracheae branch off in a radial pattern; i.e. the diffusion pathways are of a radial type. The latero-radial type only differs from the former in that the primary trunk is outside the muscle. The latero-linear type is characterized by a regular supply of parallel secondary tracheae emerging from an air sac covering one side of the muscle surface. The dorsal longitudinal depressors and the controller-depressors offer typical examples (cf. Pl. 1, figs. 1–3).

(c) **Notal movements in locusts**

Pressure changes brought about by abdominal movements can ventilate the thorax due partly to displacement of blood and partly to the flexible walls of the air sacs, such as \(3At\) and \(1abA\), and this is the usual mechanism when the locust does not fly. During flight, my own experiments with blocked abdominal ventilation (Weis-Fogh, 1956a, 1964b) and Miller's (1960c) tests with animals without abdomen indicate that a thoracic mechanism is operating, the principle of which becomes apparent from the flash photographs in Pl. 1, figs. 4, 5. In contrast to what is generally believed, the main movements of the nota do not consist in changes in their curvature but in a distinct bulk movement of the large plates which is of considerable amplitude. These movements are strictly coupled to those of the wings. When the wings move up the nota go down and vice versa. The total migration of the mesonotum is illustrated in Text-fig. 7 as a function of the stroke angle of the forewings. The normal stroke angle during horizontal flight is 68° (Weis-Fogh, 1956b) and, since the mesonotum moves down and up as a whole and since the anterior margin of the metanotum follows it while the posterior part remains fixed, the volume change due to notal movements can be estimated from the notal areas to be about 20 \(\mu l\) per wing stroke. More refined measurements including pleural movements confirm that this figure is approximately correct. It will also be shown that this amount of volume change is more than sufficient to account for the oxygen uptake during flight and that only one-third of the thoracic pumping actually results in a renewal of air within the thorax proper, i.e. about 7 \(\mu l\) per stroke (Weis-Fogh, 1964b).

(d) **Tracheal volume, ventilation and diffusion**

In accordance with Clarke (1957), the total air volume entrapped in a desert locust was found to decrease as the size of the fat body and the amount of eggs and food increased. In mature locusts of average size, the tracheal system holds about 500–950 \(\mu l\). The agar casts showed that 100–150 \(\mu l\) belong to the pterothoracic air sacs and 20–30 \(\mu l\) to the large abdominal air sac \(1abA\). In females the capacity of the two large thoracic sacs \(3At\) may be reduced to only 25 \(\mu l\) by the presence of eggs but it amounts to about 90 \(\mu l\) in a full migrant of average size. The filling of the remaining pterothoracic air sacs does not vary much with age or sex and amounts to 30–40 \(\mu l\), the largest pair \(10Ap\) holding only 5 \(\mu l\). We have seen that all parts of the thoracic system are extensively interconnected, that it is almost completely isolated from the remaining systems and that it communicates with the exterior through spiracles which remain open during flight. The actual thoracic ventilation of 7 \(\mu l\) per wing stroke is then only
5–7% of the summed volume of all the pterothoracic air sacs, 100–150 μl. In Text-fig. 2 one must imagine that the empty space is filled with haemolymph so that the notal movements result in hydraulic pressure changes ventilating all air sacs present. Air is thereby driven in and out of all of them and through all primary trunks in both directions. Since the relative tidal volume is small, the average composition of the air is almost independent of the contraction phase of any given muscle group. It is therefore justifiable to consider air diffusion in the secondary and tertiary tracheae as a steady-state process.

![Text-fig. 7. Dorso-ventral movements of the mesonotum during flight of a small male and a large female (the results being corrected to a locust of average size; ordinate), as a function of the stroke angle of the forewings (abscissa). The stroke angle is the difference between upper and lower position of the long axis of the wing measured in the stroke plane. During horizontal sustained flight it amounts to 68° (indicated).](image)

(e) Dragonflies

The small pterothoracic nota of dragonflies move in the same way in relation to the wings as has been found in the locusts (Pl. 1, figs. 6, 7 and 8). However, the movements of the pleural walls are much more conspicuous and important for the thoracic ventilation than is the case in locusts. In Pl. 1, figs. 6, 7 and 8, the pleura and the margins of the carinal cleft are maximally separated when the wings are held in the resting position (fig. 7) but come closer together when they are moved up (fig. 6) or down (fig. 8). Exactly the same is seen during actual flight and the volume changes have been recorded (Weis-Fogh, 1964b). The large wing muscles all receive one or a few axial primary trunks (Clark, 1940; Miller, 1962) from which the secondary tracheae branch
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off transversely in an exceedingly regular fashion, making possible detailed estimates of the diffusion pathways (Weis-Fogh, 1964a). The primary trunks enter near to the ventral end and emerge from the muscle at the dorsal cap tendon, where they invariably enlarge into conspicuous air sacs. As in locusts, the mesial air sacs are also present as well as the subdermal tergo-pleural system, which is enormously developed but does not supply the muscles (seen through the cuticle in Pl. 1, figs. 6, 7 and 8). The latter system serves as a thermal insulator (Church, 1960). In short, the tracheal system of the dragonfly pterothorax resembles the locust system but it is more uniform in that all large muscles are supplied according to type (1) in Text-fig. 6 and there are only few shunting tracheae present.

DISCUSSION

The available structural information and a few functional observations make it possible to outline the types of solution adopted by insects and birds.

(a) Comparison with other insects

The exchange of air between the wing muscles and the ambient atmosphere involves three different mechanisms: diffusion, thoracic pumping (i.e. volume changes coupled with the wing movements) and abdominal pumping. Whereas the exchange closest to the sites of respiration is always due to diffusion, diffusion alone is sufficient only in small insects like Drosophila and must be augmented by ventilation in large and medium-sized species (Weis-Fogh, 1964a). In dragonflies the abdominal pumping is small and is not increased during flight (Fraenkel, 1932a; Miller, 1962), while thoracic pumping is dominant and sufficient (Weis-Fogh, 1964b). In the locust this mechanism is assisted by abdominal pumping although the respiratory value of the latter is small, at least as far as the wing muscles are concerned. According to observations by Fraenkel (1932a), the same should be true in large moths (Chaerocampa, Sphinx) since the abdominal movements stop when flight starts and are resumed at a lower level after some seconds of activity. The same is true during ‘fanning’ before flight starts (Sotavalta, 1954). In accordance with this, I have observed that the notal movements of ‘shaved’ specimens result in considerable changes in thoracic volume. It is also probable that large flying beetles ventilate the thorax mainly by thoracic pumping since abdominal movements cease or become reduced during flight (Fraenkel, 1932a) and since the major movement of the metanotum of Oryctes seems to correspond to that of locusts and is of 0.5 mm. amplitude (Burton, 1962). However, the typical abdominal pumping and the correspondingly high metabolic rate of the wing muscles in Geotrupes and Oryctes preparing for flight (Krogh & Zeuthen, 1941; Krogh, 1948) strongly indicate that, in contrast to grasshoppers, moths, and dragonflies, the tracheal system in large Lepidoptera and Coleoptera must be in wide and open connexion with the thoracic system. This is also apparent from Straus-Durckheim’s etchings (1828).

The thoracic volume changes of flying Hymenoptera are very small and, since the thorax contains a highly developed and voluminous system of air sacs, the tidal volume changes may be insignificant and become of little importance. In the honey bee, Dreher (1936) found that, as to gross features, the air sacs are distributed and supplied
in a way similar to that found in the locust: a large tergo-pleural system is divided into a mesial group (Dreher's 'supraoesophageal' group), an intermediate group ('dorsal muscular') and a lateral group. All groups are interconnected and are supplied from the first three spiracles, of which the second is small and unimportant. However, this complex is also connected directly with the very large first pair of abdominal air sacs, which are strongly ventilated by abdominal pumping during flight (Fraenkel, 1932a). As in beetles preparing for flight, abdominal pumping must be responsible for the entire ventilation when, for instance, an excited non-flying wasp retains a high thoracic metabolism and temperature without visible wing movements (Sotavalta, 1954; Weis-Fogh, 1956a, 1964b). In accordance with the insignificant role of thoracic pumping in Hymenoptera, Bailey (1954) observed that nervous control of the spiracles in bees may result in a unidirectional air stream during flight, in through the first and out through the third spiracle. In flying locusts there is no such unidirectional flow in the thoracic system proper but only in the cephalic, sternal and abdominal systems.

The tracheal system of Diptera, taken as a group, resembles that of Hymenoptera both in small forms depending on diffusion (Drosophila; Weis-Fogh, 1964a) and in large flies like Eristalis (Gäbler, 1930) in which it is likely that abdominal pumping is present.

Thus in many small insects diffusion is sufficient, while in large insects ventilation is essential and is executed either by means of thoracic pumping or abdominal pumping. All possible combinations of these three means of transport are probably to be found.

(b) Comparison with birds

The avian lung holds a fairly constant volume of air and is ventilated mainly by means of the blind-ended posterior air sacs of the thorax in much the same way as are the individual wing muscles in insects. The comparison goes further in that both structures absorb oxygen and liberate carbon dioxide at very high rates; in both we find a direct connexion, a shunt, between wind pipe and air sac in parallel with the tubes from which diffusion and exchange take place. According to the descriptions and discussions by Zeuthen (1942), Hazelhoff (1943, 1951), Biggs & King (1957) and Salt & Zeuthen (1960), the main shunt in the bird consists of the relatively wide mesobronchus, and the respiratory organ as a whole may be compared with the centrodental-type wing muscle in Text-fig. 6. The axial trachea then corresponds to the system of parallel parabronchi the bore of each of which is controlled by epithelial muscles (Zeuthen, 1942). In both systems the function of the shunt remains a problem which we shall now discuss.

Both in birds and in insects the stroke volume is usually much smaller than the capacity of the air sacs. At steady state, the composition of the air in a non-absorbing air sac then corresponds to that of the mixture of air entering the sac during inspiration. At a given rate of absorption in lung or muscle tissue, and at a given stroke volume, the average composition of the gas in the air sacs is independent of the presence or absence of a shunt but the absorbing tissue will suffer lower O₂ and higher CO₂ tensions if a shunt is operative than if it is absent. Thus, a shunt neither improves the exchange of respiratory gases nor does it necessarily involve hyperventilation.

A unidirectional flow in the system such as that proposed by Hazelhoff (1943, 1951)
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is rather unlikely because the inhaled air will pass mainly through the shunt which, according to him, should correspond to the main tube in a venturimeter. The ventilation of the lung itself would therefore be confined mainly to the period of expiration and the system becomes so inefficient that we shall discuss this possibility no further.

We must, then, conclude that the possible advantage of the shunt is to be found in connexion with processes other than maximum ventilation of the absorbing tissue, as pointed out by Zeuthen (1942) in the case of birds. The problem is whether the function of the shunt is the same in birds and insects or whether the striking similarity in the design of the supply systems is correlated with different functional needs and therefore to be considered as incidental. Although next to nothing is known about the respiratory movements and the flow of air in birds which actually fly, the evidence as presented here is in favour of the similarity being incidental.

Zeuthen (1942) calculated that with open parabronchi the resistance in the parabronchial tubes of a pigeon is smaller than or of the same magnitude as the resistance in the shunting mesobronchus. He was inclined to consider the shunt as a device whereby hyperventilation during flight would ensure that the major part of the metabolic heat is removed by evaporation. This he considered essential in view of the thermal insulation of the body and the wings but, as stressed by Salt & Zeuthen (1960), such a mechanism implies that the bird must evaporate water at a rate from 5 to 20% of its body weight per hour. The bird should therefore carry about ten times more water than fuel in the form of fat and this would make it impossible to cross a large lake without drinking (Weis-Fogh, 1952b), a result hardly in accordance with observation. It should be stressed that the rough estimates of the metabolic rates offered by Zeuthen (1942) for a flying pigeon are in accordance with more complete calculations and estimates for other birds (cf. Weis-Fogh, 1961). Opinions, then, differ because Zeuthen considers the wings so well insulated that the major part of the heat must be dissipated by evaporation. However, the underside of the wing usually has but a thin feather cover and both the wings, the feet and the base of the beak are usually supplied with a dense system of arterio-venous anastomoses and the skin and the feather follicles are heavily vascularized. A rough calculation shows that, if only 10% of the blood flow is directed towards the wings, the beak and the legs (if not drawn up), the difference in temperature between outgoing and ingoing blood to these areas need be less than 3° C. and the temperature gradient across the feather only a few degrees in order to account for the thermal balance of a swiftly flying pigeon which does not make use of hyperventilation (details are not given here). According to this, the bird is air-cooled like all other flying machines. The estimate obviously needs experimental verification but, taken together with the observed performance of birds, it indicates that hyperventilation is neither of normal occurrence during flight nor is it essential. However, the function of the shunt may still be to facilitate hyperventilation and therefore to increase evaporation when the bird is thermally stressed but not flying. As discussed by Salt & Zeuthen (1960) this situation is accompanied by vigorous panting and under these conditions the air-cooling system is of little use. The rationale of the design seems to be the following: during flight the parabronchi are fully open and the shunt is of comparatively little consequence. During thermal stress at rest the parabronchial muscles in the epithelium increase the resistance compared with that of the mesobronchus so that panting results in a predominant ventilation of the non-absorbing,
wet surfaces without the risk of washing out carbon dioxide from the blood and thereby of counteracting panting and evaporative cooling.

Flying locusts do not hyperventilate (Weis-Fogh, 1964b) and do not possess any means of altering the relative resistance between the axial trachea and its shunt. Moreover, the main tracts of the tracheal system have dry and fairly water-proofed walls. When the thoracic temperature exceeds about 42° C. the animals pant violently but the evaporation is bound to occur in the muscles and not in the air sacs. The main function of the shunt therefore seems to be to facilitate exchange of gas by diffusion when the insect is not flying. Thus, Table 2 in the subsequent paper (Weis-Fogh, 1964c) indicates that many centro-radial flight muscles are so long (5–10 mm.) that they cannot be adequately supplied by diffusion during rest. In this case, a shunt means improved exchange since the muscle is being supplied from both ends.

Both in birds and in insects the shunted system can then be considered as an adaptation to the non-flying state in systems designed primarily for operation at much higher rates of exchange. In birds it makes possible an increased evaporation during panting without the danger of apnoea due to the washing out of carbon dioxide. In insects it increases exchange by diffusion.

CONCLUSIONS

The present investigation is confined to some qualitative principles which are further analysed quantitatively in two subsequent papers.

(1) The tracheae and the air sacs in the thorax of adult desert locusts, Schistocerca gregaria, were studied in detail by means of a new agar-injection technique.

(2) In each side of the thorax the system supplying the wing muscles is virtually isolated from that of the other side and from that of the abdomen.

(3) Each wing muscle receives a primary supply, consisting either of a longitudinal trachea which ends in an air sac or of an air sac applied to the muscle surface. In both cases the primary supply has direct and wide ipsilateral connexion with at least one spiracular plexus in the thorax itself.

(4) Measurements of tracheal volumes and of notal movements showed that, when the locust wings move up and down, the nota move down and up like plates. This results in a local renewal of the air in the thoracic system which is independent of the abdominal pumping. The thoracic pumping directly ventilates all primary supplies and all thoracic air sacs. The principles are summarized in Text-fig. 2 and apply also to dragonflies, in which, in addition, lateral movements of the pleura contribute significantly to the pumping.

(5) The secondary supply to the wing muscles consists of a system of transverse diffusion tracheae arranged quite regularly and often according to a plan suitable for mathematical treatment of diffusion, as summarized in Text-fig. 6.

(6) During flight thoracic pumping seems to be the predominant form of ventilation, not only in grasshoppers and dragonflies, in which the thoracic system is almost isolated from the abdomen, but also in large moths and beetles. Hymenoptera and Diptera rely upon diffusion and abdominal pumping only.

(7) The primary supply to a wing muscle is often provided with a shunt (shown by broken lines in Text-fig. 6) in the same way as the mesobronchus provides a shunt between the gas-absorbing lung tissue and the 'inert', large posterior air sacs in birds.
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(8) It is argued that the shunt need not result in any hyperventilation and that it does not play any role in thermal economy of the flying animals, neither in birds nor in insects. In non-flying insects it facilitates air diffusion. In non-flying birds under thermal stress the shunt and the epithelial muscles in the parabronchi together make possible panting and increase in ventilation without the risk of washing out CO$_2$ from the blood.

SUMMARY

1. The wing muscles of locusts are supplied with air by means of a system of air tubes which communicate only with the first three pairs of spiracles. Both in locusts and in dragonflies each muscle receives a direct supply ending in a large air sac, the primary supply. It is automatically ventilated by thoracic pumping due to the movements of nota and pleura which accompany the wing movements.

2. The secondary supply of transverse diffusion tracheae branches off from the primary supply, often according to geometrical patterns suited for quantitative studies.

3. During flight, thoracic pumping appears to be the only mechanism responsible for the ventilation of the thorax in grasshoppers, dragonflies, moths and beetles, while Hymenoptera and Diptera rely on the usual abdominal pumping.

4. In many wing muscles from large insects there is a wide shunt between the primary supply and the terminal air sac, resembling the shunting mesobronchus in the lung of birds. In both groups of animals the shunt is considered to be of little significance during flight.

5. In insects the shunt facilitates diffusion when the thorax is not ventilated during rest.

6. In resting birds under thermal stress, it is concluded that contraction of the epithelial sphincter muscles in the parabronchi makes possible hyperventilation of the moist air passages via the mesobronchus, removing excess heat by evaporation without causing apnoea due to the washing out of CO$_2$.

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REFERENCES


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EXPLANATION OF PLATE

Fig. 1. Right half of the thorax of *Schistocerca gregaria* to show the large central air sac *At*, its tracheal connexions, and the numerous secondary tracheae supplying the dorsal longitudinal muscles in the mesothorax. The large primary tracheae running from spiracle 3 to *At* supply the metathoracic muscle, as seen through the abdominal air sac *abA*. Note the filled crop and intestinal diverticula.

Fig. 2. The left-hand side of the thorax of *Schistocerca gregaria* is opened to show the deep and extended system of subdermal air sacs from which large parts of the controller-depressor muscles are supplied with secondary tracheae. Some of the primary trunks from spiracle 2 are also seen.

Fig. 3. Photomicrograph of the inner surface of *At*, from which secondary tracheae emerge and disappear between the fibres of the dorsal longitudinal muscle in the mesothorax.

Figs. 4, 5. The notal movements of *Schistocerca gregaria* during flight: flash exposure. The locust is suspended from the prothorax, which was firmly fixed to the pterothorax so that the cut, white pronotal reduplication could be used as a fixed line of reference. A white dot of paint at the left anterior part of the mesonotum (prescutum) indicates the vertical movements, down in fig. 4 and up in fig. 5. The postnotum behind the metanotum does not move while the anterior margin of the metanotum follows the mesonotum.

Figs. 6, 7, 8. The fresh pterothorax of a dragonfly (*Aeshna*) viewed from in front after removal of head and legs. Fig. 6, wings pushed up; fig. 7, wings in resting position; fig. 8, wings pushed down. Note the opening and closing of the anterior slit, the *carina*, indicating the lateral movements of the pleura. The up and down movements of the notum are also distinct.