

CAMBRIDGE MONOGRAPHS IN
EXPERIMENTAL
BIOLOGY

—9—

INSECT FLIGHT

BY
J.W.S. PRINGLE



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INSECT FLIGHT

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And under the firmament were their wings straight, the one toward the other: every one had two, which covered on this side, and every one had two, which covered on that side, their bodies.

And when they went, I heard the noise of their wings, like the noise of great waters, as the voice of the Almighty, the voice of speech, as the noise of an host: when they stood, they let down their wings.

EZEKIEL I. 23, 24.

PREFACE

THE flight of insects has interested zoologists from the earliest times. It is the most obvious of the characteristics which have made this class of animal successful in the colonization of a wide variety of terrestrial environments, and the insect's precision in aerial manoeuvres commands the admiration of the naturalist even in these days when man's conquest of the air is no longer a novelty. To the serious student, however, small size and the speed with which the wings are moved in the more efficient fliers combine to make accurate description of the mechanics of flight a more difficult task than for some of the other types of animal locomotion. It was only with the introduction of photographic and other instrumental aids towards the end of the nineteenth century that a beginning was made with the accumulation of quantitative data which could form the basis on the one hand for aerodynamic theories and on the other for physiological analysis of the properties of muscles and other structures comprising the flight system.

A landmark in the history of the subject was the publication in 1934 of Magnan's book, *Le Vol des Insectes*. The researches summarized in that book have provided the material for the chapters on insect flight in most text-books of entomology in the succeeding twenty years, and are still of great value. But it is impossible to read some of these accounts without being impressed by the apparent isolation of zoological thought of the time from the parallel progress being made in the sciences of aeronautics and comparative physiology. Reports about the speed of flight of certain flies were widely quoted which bore no relation to physical possibility, and theories were propounded in conflict with principles which were fundamental in other fields of study. One of the characteristics of modern biology is the breakdown of the boundaries which separate its subdivisions, and nowhere is this more fruitful than in behavioural studies where mechanics and physiology are integral to a more profound understanding. The new approach is well illustrated by L. E. Chadwick's chapters on insect flight in K. D. Roeder's

Insect Physiology, but progress has been sufficiently rapid since 1953 to justify a fresh review of our state of knowledge.

I wish particularly to acknowledge my indebtedness to Dr Torkel Weis-Fogh, who has been a constant source of help and inspiration in the preparation of this book, and who has himself made many of the discoveries which make possible a new synthesis. Many others have helped by discussion and in the search through the literature; especially I should like to thank Prof. E. G. Boettiger, Dr R. M. Baranowski, Dr Jean Hanson, and Dr J. Smart for allowing me to read and quote from their unpublished papers. Dr G. Salt kindly read the manuscript and made several useful comments.

J. W. S. P.

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CHAPTER I

General Anatomy of the Wings and of a Wing-bearing Segment

THIS monograph deals with the subject of insect flight from a functional and physiological point of view. In order to understand how an insect flies, however, it is necessary to have a clear picture of the anatomy, and in this introductory chapter a brief summary is given of the general plan of the skeletal and muscular structures comprising the machinery of aerial locomotion in the group. Detailed treatment of this aspect of insect flight is to be found in most text-books of entomology, in particular in Snodgrass (1935). Great differences of detail are found in the different orders, but a combination of anatomical and physiological studies has now made it possible to establish the essential features of the evolution of most of the main types of flight mechanism found in the Pterygota.

The wings of insects arose in the Devonian or Lower Carboniferous as lateral expansions of the thoracic nota, and it is generally agreed that their original function was to enable the insect to glide from trees to the ground; fossil types are known with pronotal as well as meso- and metanotal expansions of this region of the exoskeleton. This originally continuous fold between the tergal and pleural sclerotizations soon narrowed, and in all modern winged insects definite regions of wing articulation are formed by more elaborate folding and local thickening of the basal region. The pattern of tergal and pleural sclerotization in the meso- and metathorax is also constant in its main features (fig. 1). Both tergum and pleuron are divided into anterior and posterior portions by an internal fold. The scutum bears on its lateral edge the anterior notal process, which forms the main dorsal support for the wing; the posterior notal process is also formed by a fold of the scutum, but usually is rigid with the scutellum. The two main pleural sclerites, the episternum and epimeron, are separated by an internal ridge or suture, which serves to strengthen the lateral wall of the thorax and is often

continued in its middle region into an apodeme for the attachment of the pleurosternal muscle. At its upper end the pleural ridge reaches the pleural wing process; below, it helps to form the main articulation for the coxa of the leg. The thoracic box is completed below by the sternum.

In the dorsal region of a wing-bearing segment there are usually present large, intersegmental phragmata which serve for the attachment of the dorsal longitudinal muscles. The phragmata are internal folds not of the tergum proper but of intercalated sclerites; the posterior intercalated sclerite, or

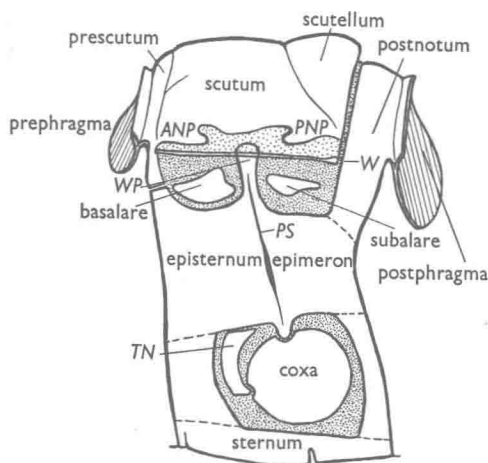


Fig. 1. Diagrammatic lateral view of a typical wing-bearing segment. *ANP*, anterior notal process; *PNP*, posterior notal process; *PS*, pleural suture; *TN*, trochantin; *W*, wing (cut through); *WP*, pleural wing process. (Redrawn from Snodgrass, 1935.)

postnotum, may be large and then forms a complete dorsal bridge between the two pleura behind the wing. A narrow anterior bridge may be formed between the prescutum and the episternum.

At the upper edge of the pleuron, below the wing fold, two regions, known as the basalare and subalare, may become detached as separate sclerites. These bear the dorsal insertion of important muscles which serve to twist the wing about the transverse body axis by ligamentous cuticular attachments to sclerites of the wing base.

The sclerotization of the wing itself is a subject which has been

much studied by systematic entomologists, since the pattern of wing venation is often the best preserved feature of insect fossils, and serves as a ready means of identification of many orders and families. In a discussion of the origin of wings and of venational types, Forbes (1943) distinguishes four or five main evolutionary lines; of these, there is general agreement only that the Odonata and Ephemeroptera stand distinct from other modern orders in the structure of the basal wing sclerites and in their inability to fold the wings back over the abdomen when at rest. In the other

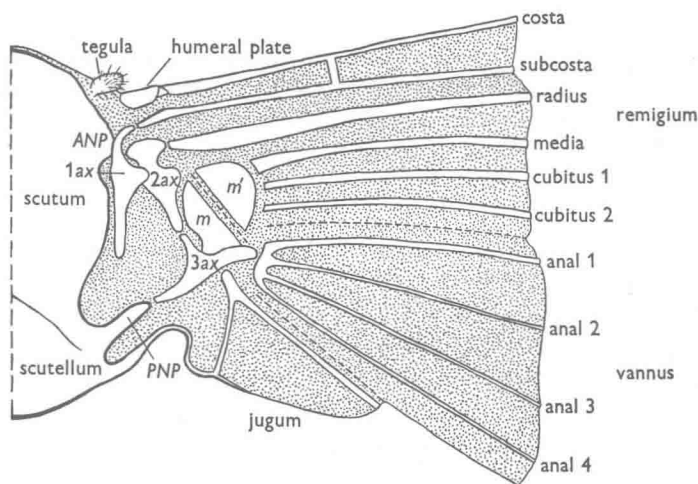


Fig. 2. Diagram showing a typical arrangement of the basal wing sclerites, and the naming of the principal wing areas and veins; the interrupted lines show the main regions of wing-folding. ANP, anterior notal process; *m*, *m'*, median plates; PNP, posterior notal process; 1ax, 2ax, 3ax, axillary sclerites. (Redrawn, with alterations, from Snodgrass, 1935.)

orders of the Pterygota (Snodgrass, 1909, 1927; Comstock and Needham, 1898, 1899; Comstock, 1918), the wing veins, the basal sclerites and the wing muscles have an arrangement which can be referred to a basic plan, with a knowledge of which the various modifications are more readily visualized.

The three or four axillary sclerites bear a constant relationship to the wing processes of the notum and pleuron and to the main wing veins (fig. 2). The 1st axillary articulates with the anterior notal process, and in some orders (e.g. Hymenoptera) its posterior arm, which may be directed diagonally downwards, is also in close association with the posterior notal process.

Laterally the 1st axillary abuts on the end of the sub-costal vein and forms a complicated articulation with the 2nd axillary. The 2nd axillary usually supports the radius, and its lower surface rests on the pleural wing process; it may also have a strong connexion to the median plate. The 3rd axillary is the pivotal sclerite for the wing-flexing mechanism. It has three articulations: basally with the posterior notal process and the posterior arm of the 2nd axillary, and distally with the anal wing veins. A 4th axillary is present as a distinct sclerite only in Orthoptera and Hymenoptera and lies between the 3rd axillary and posterior notal process.

The power for the up- and downstrokes may have been derived primitively from the direct muscles; these are dominant in the Blattoidea and remain important in all Orthoptera, Coleoptera and Odonata. Elsewhere there is a tendency for the main power for the stroke to be provided by indirect muscles, which in some of the highest orders become very large and occupy most of the volume of one or both of the pterothoracic segments; the direct muscles here are reduced in size but always remain of importance for the control of the wing beat.

The indirect muscles are arranged in two functional groups. The dorsal longitudinal muscles, running from prephragma to postphragma (fig. 3A), are usually described as producing in the main an arching of the tergum, raising the notal processes relative to the pleural process and so depressing the wing (Chabrier, 1822). In fact, in many insects there is an equally important approximation of the anterior and posterior notal processes (Janet, 1899) due to the development on each side of the notum of a line of weakness between scutum and scutellum. The oblique dorsal muscle may act synergically with the dorsal longitudinal muscle, but has a functionally antagonistic action in many orders. The dorsoventral muscles, running from tergum to sternum, act in opposition to the dorsal longitudinal muscles and supply power for the upstroke by lowering the anterior notal process relative to the pleural process. The oblique intersegmental muscle has a variety of roles but may have become an indirect wing depressor in the metathorax of Odonata (Clark, 1940).

The direct muscles can be divided into the basalar and subalar muscles, which act on the wing by virtue of the ligamentous attachment of these sclerites to the wing base, and those

muscles which are inserted directly on to the axillary sclerites. The mode of operation of the direct muscles varies greatly in different insects and has been worked out in only a few examples. The flexor muscle (fig. 3), however, has the same action in all wing-flexing insects, and this is conveniently described now. It runs from the pleuron to the middle of the 3rd axillary, often reaching this sclerite by a slender apodeme, and may be composed of several branches arising on the episternum, the pleural ridge and the epimeron. Its contraction rotates the 3rd axillary dorsally and inwards about the axis

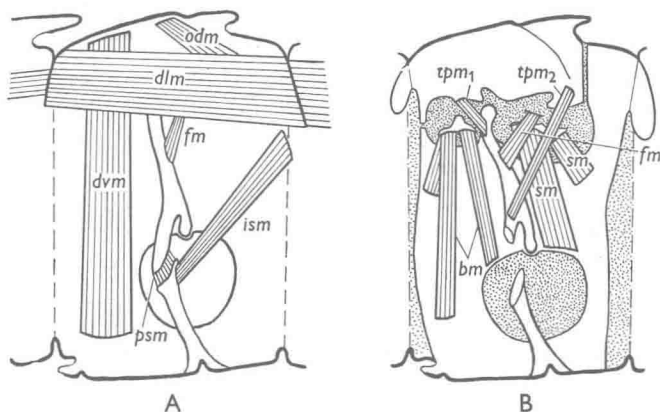


Fig. 3. Diagrammatic view of the muscles on the right side of a wing-bearing segment, seen from within. A, indirect and some lateral muscles; B, lateral muscles. *bm*, basal muscles; *dlm*, dorsal longitudinal muscle; *fm*, flexor muscle; *ism*, oblique intersegmental muscle; *odm*, oblique dorsal muscle; *psm*, pleurosternal muscle; *sm*, subalar muscles; *tpm*, tergopleural muscles; *dvm*, dorsoventral muscle. (Redrawn from Snodgrass, 1935.)

formed by its articulations with the 2nd axillary and the posterior notal process (or the 4th axillary when present), thus carrying the vannal area of the wing dorsally and posteriorly by rotation about the 2nd axillary sclerite (fig. 2); folding of the wing along definite lines and some movement of the other axillary sclerites relative to each other and to the notal processes accompanies this complicated action.

In addition to these direct and indirect muscles whose general mode of action in the flight machine has been known for a long time, there are certain muscles, which may be called accessory indirect muscles, whose important role has only recently been

demonstrated. The pleurosternal group is most commonly represented by a short but powerful muscle linking the pleural and sternal apophyses (fig. 3A). These structures form a system of internal bracing for the walls of the pterothorax, and in some insects the two apophyses are rigidly fused; where the muscle exists across the gap, its contraction influences the elasticity of the thoracic box, with corresponding changes in the insect's flight (see Chapter 2). Also in this category come a variety of tergopleural muscles, one of which, running from the posterior part of the scutum or scutellum to the pleural ridge, may be of considerable size in some orders. All these muscles influence flight by altering the relative position of moving parts or by changing the elastic properties of the pterothoracic box, rather than by direct action on the wings themselves.

Finally, it must be mentioned that leg muscles may become incorporated into the flight machinery. The coxa and even the trochanter of the leg are moved partly by muscles which have their origin on the tergum. When, as in the *Diptera* and some *Coleoptera*, parts of the coxae become rigidly attached to the wall of the thorax, such muscles may function as accessory dorsoventral muscles in the upstroke of the wing. Even when the coxa remains movable, the upper insertion of some of its muscles may be transferred to the wing or epipleural sclerites (basalare or subalare) and the muscles then have a double role; in the metathorax of a cicada the same muscle raises the hind legs into a position close to the body and also brings the hind wing forward into the flight position. Examples of other functions of muscles which are secondarily drawn into the flight machinery will be mentioned in later chapters.

CHAPTER 2

The Form and Mechanism of the Wing Beat

LIFT and propulsion are produced in the majority of insects by active movement of the wings and not solely by the air flow resulting from the insect's forward motion. Forward motion of the body as a whole may be necessary for flight, but in the most advanced fliers, which can hover or fly backwards and sideways, the analogy of a helicopter is closer than that of a conventional aeroplane. Unlike a helicopter the movement is oscillatory rather than rotary and the axis of rotation is horizontal rather than vertical, but in both types of flying machine changes in the angle of attack of the wing in different parts of the stroke are necessary to produce lift, propulsion and control.

KINEMATICS. The movement of the wings during flapping flight is an extremely complicated action involving, as well as elevation and depression, promotion and remotion (fore and aft movement), pronation and supination (twisting) and changes of shape by folding and buckling. The kinematics have been fully described in only one example, the locust *Schistocerca gregaria* (Jensen, 1956). Earlier studies using high-speed photography (Magnan, 1934) or reflecting markers glued to the wing (Marey, 1868*a, b*; Hollick, 1940) have provided only incomplete information which is inadequate for an aerodynamic analysis or for a full understanding of the mechanism of the articulation and the role of the various muscles. There is also the difficulty that the form of the wing beat is greatly affected by the 'relative wind' which includes a component due to the translational velocity of the insect as a whole; studies with fixed insects are therefore likely to be of limited value unless a wind tunnel is available and care is taken to ensure that the air flow is correctly adjusted to the conditions found in free flight.

The movement of the fore wing of *Schistocerca* during steady forward flight is shown in fig. 4. Relative to the insect the wing tip moves in an irregular loop; relative to the air it is an

irregular saw-tooth curve. The hind-wing movement is similar but not identical. At the mid-point of the wing the oscillatory component of the movement is smaller relative to the translational component, while at the base only the translation is significant. Fig. 4 also shows the twist and changes of wing section during the stroke in a particular set of experiments. At the base the inclination of the wing was constant and equal to the body

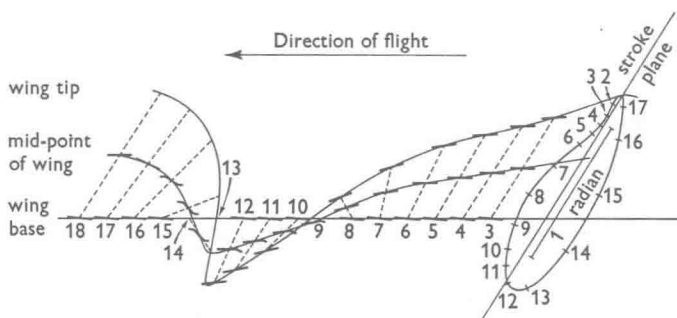


Fig. 4. The movement of the fore wing of *Schistocerca gregaria* (redrawn from figs. III, 5, III, 6 and III, 8 of Jensen, 1956). The closed curve shows the path of the wing tip relative to the insect. The open curves show the path relative to the air, on a projection designed to show the movement of the axis of the wing. Angles of attack are shown by the short lines, which also illustrate the changes in wing section at the mid-point of the wing.

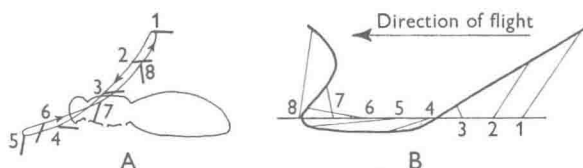


Fig. 5. A. Diagrammatic lateral view of the wing trajectory of *Volucella*, showing the changes in wing twisting during the stroke. B. The path of the wing tip through the air during forward flight. (Redrawn from Magnan, 1934.)

angle; from points 9 to 12 the middle of the wing was bent along the vannal fold to produce a flap; on the upstroke it was doubly bent into a Z-section. Comparable but less exact data for the wing-tip movements of *Volucella* (Diptera) in free flight are given by Magnan (1934) from analysis of high-speed photographs (fig. 5).

Studies using gold leaf and other reflecting materials on the wing tips have given information about the amplitude and form of the stroke in a wider range of insect types. In this way