Hodgkins Fund

THE FLYING APPARATUS OF THE BLOW-FLY

A CONTRIBUTION TO THE MORPHOLOGY AND PHYSIOLOGY OF THE ORGANS OF FLIGHT IN INSECTS

WITH TWENTY PLATES

BY

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The present investigation on the flying apparatus of the blow-fly was carried on at the Zoological Laboratory of the German University at Prague, with the assistance of a grant from the Hodgkins Fund of the Smithsonian Institution. It was under the supervision of Prof. R. von Lendenfeld of that laboratory.

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I. INTRODUCTION

When I began, some two years ago, to investigate intimately the flying apparatus of the Diptera, I intended to make it a comparative study; but, on obtaining an insight into the literature on the flying organs of insects, I abandoned this idea because I found the necessary foundation for a comparative work wanting: there does not exist a single exact, perspicuous and well-illustrated description of a Dipterous insect. I determined, therefore, to confine my studies to a careful examination of the organs of flight in a single species.

An examination of the literature of the subject showed me how inexact the illustrations are and how difficult it is to use them to any advantage in determining the parts of the actual object. From the rough and almost useless drawings of Lowne (1890-1895) to the beautifully executed but quite schematic plates of Künckel (1875-1881), there is nothing that really approaches nature.

In order to avoid the mistakes of my predecessors I made use of photography for the graphic representations. This had not hitherto been done, and indeed it seemed unlikely that it would be possible to obtain good photographs of the thorax and wing-skeleton on account of the yellow color of the chitin forming the hard parts, and the apparent impossibility of obtaining sharp definition upon the plate of all parts of such plastic bodies as are found in the skeleton of the flying apparatus.

After many unsuccessful attempts I finally succeeded, by means of plates ("color") sensitive to yellow color and a Zeiss binocular, in producing stereoscopic views true to nature in every particular except that of color (see the section on material and methods of research). Some schematic drawings, especially of muscles, were necessary for further elucidation.

The movement of the wings was studied by means of kymographic curves and serial photographic representations of Calliphora vomitoria in the act of flight, made by Prof. von Lendenfeld.

I abandoned my original intention to introduce a nomenclature applicable alike to all higher insects, because I recognized that that could properly be done only by means of very extensive studies in comparative anatomy and embryology. I had, therefore, to content myself with selecting from the names already in use those which appeared to me most suitable; such old appellations as were directly contrary to the truth being replaced by new terms. At the same time I allowed myself, especially in the designation of parts not hitherto named, to be guided, as was F. Voss (1905), by the prin-
ciple that topographic relationship should be considered as of the first importance. In cases where this was not quite practicable, as, for example, in the case of the middle pieces of the wing-joint, I gave to the entire group a collective designation of a topographic character, and distinguished the separate parts by means of letters or figures. For new terms I mostly used Greek stems with Latin terminations.

And now I wish to thank most heartily my honored instructor, Professor von Lendenfeld, for his valuable advice and suggestions. Also I would thank his assistant, Dr. Emanuel Trojan, for his ever ready assistance and his interest in my work.

II. HISTORICAL SURVEY

I found in the literature but very few papers on the flying apparatus of the Diptera. The principal contributions to this subject are the work of Künckel d’Herculais on the Syrphidæ (1875-1881), in which, however, the flying apparatus is treated quite incidentally, Hammond’s work on the thorax of Calliphora vomitoria (1879), and the monograph on the blow-fly by Lowne (1890-1895), in both of which the flying apparatus is also described very superficially.

The historical development of our knowledge of the means of flight of insects in general is summarized below.

The first notable works on this subject were published in the first half of the nineteenth century. At that time it was chiefly the French who concerned themselves with this subject, especially Latreille (1819), Chabrier (1822), Audouin (1824), and Sträuss-Dürkheim (1828). At about the same time there appeared the works of Kirby and Spence (1823-1833) and Burmeister (1832). All these works treat of the entire insect world or at least of a large portion of it. Only in the second half of the nineteenth century and later have special works on the organs of flight of insects been published. The most important of these are von Lendenfeld’s work on the flight of the dragon-flies (1881), Luks’ articles on the musculature of insects (1883), Amans’ anatomical and mechanical studies on the organs of flight in insects (1883), Adolph’s description of the venation of the wings of Diptera (1885), Redtenbacher’s comparative studies (1886), Marey’s (1860-1872), Pettigrew’s (1872-1873), and von Lendenfeld’s mechanico-physiological works, and the exact description of the thorax of Gryllus domesticus by Voss (1905).
III. DESCRIPTION

A. ANATOMICAL SECTION

I. MATERIAL AND METHODS OF RESEARCH

As an object of investigation the blow-fly, Calliphora vomitoria, was chiefly used, the Syrphidae being also studied incidentally. The blow-fly was selected because it is easily procured in large numbers and is of considerable size. Besides, this species appeared as a favorable object because of the very strong development of its skeleton.

The first investigations were made with an ordinary microscope, but the inadequacy of this apparatus soon became apparent, and later only the binocular was used. The skeleton was studied in preparations in which the soft parts had been removed with liquor potasse. The best results are obtained when the thoracic segments required are left at ordinary temperature about a week in a 50 per cent solution of the alkali. Boiling in the same liquid removes the muscles at once, but this method has the great disadvantage of causing the chitinous parts, chiefly the membranes and ligaments, to shrink. If the preparation appears to be too dark it can be bleached by long immersion in 50 per cent liquor potasse. Rapid bleaching may be attained by means of a mixture of chlorate of potash and a little hydrochloric acid.

Ordinary Canada balsam preparations of the smaller and thinner parts can be made without any difficulty. The preparations of larger parts, such as median sections of the thorax, were made in the following manner. Small glass dishes with base ground flat were filled with Canada balsam dissolved in chloroform, and this was boiled until bubbles ceased to rise. The specimen was cleared up with oil of cloves and then immersed in the balsam while the latter was still warm and soft. It was then properly oriented and protected with a cover-glass.

Wings, before being placed in the balsam, were boiled in chloroform according to Walter's method (1907), and thus the tracheae (veins) were freed from air.

Series of cellloidin-sections were prepared both of parts previously treated with liquor potasse and of parts simply hardened in alcohol. From the latter, however, no good sections of the skeleton and the smaller steering muscles could be obtained, because the very brittle chitin, especially in the complicated articular structures, broke before the knife. When the chitin was bleached and softened by
liquor potassæ it could, of course, be cut easily enough, but then it showed deformations. The results of serial sections were satisfactory only in studying the larger muscles (pl. 4A, fig. 10).

Cross-sections of the wings imbedded in celloidin were easily prepared and gave excellent results (pl. 4B, figs. 12, 13, 14).

The stereoscopic pictures which illustrate this paper were photographed with a Zeiss binocular on color plates (Westendorp and Wehner). The contour drawings, with their lettering were produced as follows: The original stereoscopic photographs were enlarged by means of an episcopie, projected upon transfer paper and copied thereon. These copies were then mounted on cardboard, provided with the lettering, and then again photographed and reduced to the size of the original stereoscopic photographs.

2. GENERAL REMARKS UPON THE THORACIC SKELETON OF THE DIPTERA

Apart from the much debated microthorax, the thorax of insects consists of three segments: the pro-, meso-, and metathorax. These three segments are developed very unequally. In insects capable of vigorous flight the segment or segments bearing the wings are better developed than the others. In the Diptera the mesothorax, which bears the single pair of wings, is developed much better than the other two. The prothorax is greatly reduced. In each segment there is to be distinguished: the notum or dorsal portion, usually composed of the three parts, præscutum, scutum, and scutellum; the pleuræ or lateral portions, usually composed of the two parts, episternum and epimerum; and the sternum or ventral portion.

Kolbe (1893) named the endoskeletal processes which extend inward from the notum, the pleura and the sternum: phragmae, apodemæ and apophyses, respectively. By prefixing the syllables pro-, meso-, or meta- he designated the segment to which each belongs.

In Calliphora vomitoria the mesothorax forms by far the greatest part of the whole thorax. The entire back of the thorax is covered by the uncommonly well-developed mesonotum.

I should like here to make some remarks concerning the determination of the limits between the thoracic segments. Könekel d'Herculais (1875) expressed the view that the mesonotum consists of præscutum, scutum, scutellum and postscutellum. The deep notches between the parts he considers as præscutum and scutum, and the parts he considers as scutum and scutellum render it not
improbable, however, that these three pieces are primary segments of the insect's thorax and not, as Künckel and Lowne think, parts of the mesothorax. I will not here pursue this question further, and provisionally accept the ideas of Künckel and Lowne in spite of my doubts as to their correctness.

3. THE SKELETON OF THE THORAX, SO FAR AS IT RELATES TO FLIGHT

The part of the thorax most important for flight is the mesothorax. In its skeleton we may distinguish exoskeletal and endoskeletal parts.

EXOSKELETAL PARTS

These are the mesonotum, the mesopleura and the mesosternum.

The Mesonotum

The mesonotum consists of four parts, the præscutum, scutum, scutellum and postscutellum.

*The præscutum* (pl. 1, fig. 1; pl. 2, figs. 3, 4; pl. 8, fig. 23; p), together with the scutum, scutellum, parapleurum and mesosternum, forms a group of the largest and strongest chitinous plates of the thorax. Beginning in the region of the cervical opening, the præscutum rises vertically upward, assumes near the limit between the first and second third of its length a horizontal position, and at the same time broadens out. From the angle between these two surfaces backward it is covered with hair. The hairs are directed backward and increase in length toward the scutellum. They are of two kinds: small, fine hairs and coarse bristles. The latter are arranged in irregular, longitudinal, and transverse rows. On the præscutum six longitudinal and three transverse rows of bristles can usually be distinguished. They fall out when the thorax is treated with liquor potassae, and their places of attachment then appear as circular holes. The hairy covering of the back appears to be especially liable to injury. The small hairs also are often missing in many places, their points of attachment appearing as small dots. Two shallow, longitudinal furrows divide the præscutum into three zones. These are continued on the scutum but are absent on the scutellum. Ventrally, the præscutum is separated from the paraopleurum by the pleural cleft. Laterally, toward the scutum, triangular areas, feebly chitinized and clear in appearance (pl. 2, fig. 3), border on the præscutum.
The scutum (pl. 1, fig. 1; pl. 2, figs. 3, 4; pl. 8, fig. 23; s) is the largest plate of the thorax. It is about twice as broad as long, slightly convex dorsally, and extends downward laterally in an obtuse angle to the root of the wing. Like the præscutum, it is provided with bristles which form six longitudinal and three transverse rows. Besides these rows there are usually present on its lateral parts, where the scutum bends downward, four bristles, one of which is situated on the tip of the spina scutalis (pl. 1, fig. 1; pl. 2, figs. 3, 4; pl. 8, fig. 23, sp). It is to be noted that the lateral parts of the scutum that slope downward toward the roots of the wings are not so strongly chitinized as the central part. Distally, these parts of the scutum are split into several parts, directly connected with the roots of the wings (see below). The scutum possesses two lateral, sharp, marginal projections, the spinae scutales (pl. 1, fig. 1; pl. 2, figs. 3, 4; pl. 8, fig. 23, sp), which extend obliquely forward and downward into the crista spinales, which separate the two (right and left) fossae præalares (pl. 8, fig. 23, f₁) from the fossae postalares (pl. 8, fig. 23, f). These two pairs of depressions have a special relation to flight. When the wing beats upward and backward, the rigid portions, the marginal veins and the remigium, come to lie in the fossae præalares, the flexible, posterior portions in the fossae postalares. When the wing makes its greatest excursion backward and upward the crista spinalis adapts itself exactly to the notch between the rigid and flexible portions of the wing. This view is opposed to that held by Lowne. That observer correctly describes (1890-1892) the spina scutalis as separating the fossae præalares from the fossa postalaris, but in an illustration (loc. cit., pl. 7, fig. 1) he shows the fossa postalaris in front of the spine, nearly in the position of the fossa præalaris. He correctly depicts an anterior fossa (pl. 2, fig. 3; pl. 8, fig. 23, f₁₁) at the boundary between the præscutum and the scutum, but he omits the special fossa præalaris. If the unnamed projection which appears in his drawing farther in front, near the scutum, is intended to represent the spina scutalis, it is incorrect, as this projection is in reality much nearer the scutellum.

The two processes which extend from the scutum to the root of the wing, and which articulate with the latter, are the processus præalaris (processus pteralis thoracis I; pl. 2, figs. 3, 4, ptI), corresponding to the fossa præalaris, and the processus postalaris (processus pteralis thoracis II; the great alar apophysis of Lowne; pl. 2, figs. 3, 4, ptII), corresponding to the fossa postalaris. The first
consists of two lobular parts, of which only the ventral one (the anterior præscutum of Lowne) extends right down to the root of the wing. The boundary between the two processes is formed by the cleft that runs along the crista spinalis. The ventral portion of the processus præalaris passes below into a narrow ligamentous band that thins out distally, and is attached to the inner side of the processus pteralis alæ 2 (the coracoid of Lowne, pl. 8, fig. 23, pt. 2). The processus præalaris and postalaris are connected with each other by a narrow, chitinous bridge which is very tender and easily destroyed in preparing the specimens (pl. 8, fig. 23; in all the other illustrations it is lost). The processus postalaris is a chitinous strip which decreases in size opposite the root of the wing, and has at its end a somewhat deep depression, the sella processus postalaris. In this lies, at an angle of 90 degrees, the proximal notch of the pterale A (pl. 8, fig. 24; pl. 9, fig. 25, pt. A). Lowne calls the processus præalaris the parascutum. I have found no evidence that it should be considered as a separate piece. At the point of separation of the ventral and dorsal portions of the processus præalaris a small finger-shaped process, the processus dactyloformis (pl. 2, figs. 3, 4, pd), is situated. This extends dorsally into the interior of the thorax.

The scutellum (pl. 1, fig. 1; pl. 2, figs. 3, 4, se) has, when looked at from above, the shape of an equilateral triangle. The sides of this triangle are convex, and one of its corners is anal. The anal portion overhangs. The scutellum is beset with bristles along its edge and also bears two bristles on its back. The scutum is connected with the scutellum by the two scutellar bridges (Lowne). Along the processus postalaris extends a cleft which widens toward the root of the wing to form the foramellar postalaris (the supratympanic fissure of Lowne; pl. 2, fig. 3, a1).

The postscutellum (pl. 2, fig. 3, ps) is cushion-shaped; upon it the scutellum rests. Toward either side it narrows considerably. I doubt whether the postscutellum belongs to the mesothorax, but, since there is not sufficient evidence in favor of any other view, I, for the present, accept this conception.

The Mesopleura

Each mesopleurum is made up of the parapleurum, episternum, parepisternum, epimerum and parepimerum.

The parapleurum (lateral plate of Lowne; pl. 2, figs. 3, 4, pp) is nearly quadrilateral. It is separated from the præscutum by the
pleural cleft; extends to the stigma anterius and ventrally reaches the mesosternum, with which, and with the paratrem of Lowne, it is connected by a bridge. Towards the anus a cleft, the fissura episternalis, separates the parapleurum from the episternum. A row of bristles runs along this fissure. The entire parapleurum is clothed with hair.

_The episternum_ (pl. 2, figs. 3, 4, _e_) is narrow and dorsally reduced to the processus pterales episterni (see C5). Ventrally it reaches the mesosternum, analwards the epimerum.

_The epimerum_ (pl. 2, figs. 3, 4, _ep_) has an elongated, oval shape, and is closely set with long hairs.

_The parepimerum_ (pl. 2, figs. 3, 4, _pm_) which Lowne calls the costa, lies dorsally between the episternum and the epimerum, leans upon the latter, and like the epimerum is covered with hair.

_The parepisternum_ (pl. 2, figs. 3, 4, _pe_ ) lies dorsally upon the epimerum. I give it this name because it is closely connected with the episternum. It is triangular and considerably thickened on one side in the form of a pediculated bud. Here, as in the case of the stroma of the processus pteralis thoracis, we may make an exception to the rule that names implying form should not be used, and from its uncommonly impressive and striking bud-like shape, call it the _calyx_.

_The Mesosternum_

The mesosternum (pl. 1, fig. 2; pl. 2, figs. 3, 4, _es_) consists of two symmetrical halves, from each of which a process extends to the anterior pair of stigmata. These halves are nearly quadrilateral in shape and strongly curved. With the two metasternums they form the principal part of the central portion of the thorax. They unite in the median plane, bend inwards (upwards), and form, when united, the mesosternal process (furca of the mesosternum, Lowne; pl. 1, fig. 2, _ap_; see also below under Endoskeleton). The “lateral plate of the postscutellum” of Lowne should be mentioned in passing as it is connected with the wing through the squama. It is approximately triangular, strongly convex, and separated from the processus postalaris by the foramen postalare (supratympanic fissure of Lowne).

ENDOSKELETAL PARTS

The endoskeletal parts that are here to be considered are the _præscutal crest_, the mesapodema, which is continued into the episternal border, the mesapophysis and the so-called parapterum.
The præscutal crest. A narrow endoskeletal crest arises from the dorsal side and projects inward. This cannot be considered as a phragma. I name this the præscutal crest (pl. 2, fig. 4, l). It arises from the boundary between the præscutum and the paratremata, bridges the former, follows the ventral edge of the præscutum, and ends at the boundary between the præscutum and the scutum. Here it is connected by ligamentous attachments with the parapleurum (pl. 2, fig. 4, pn).

The mesopodema (great entopleuron, Lowne; pl. 1, fig. 2; pl. 2, fig. 4, a) arises at the ano-dorsal curvature of the mesosternum. It does not wholly correspond to the apodema of Kolbe, but as it belongs almost entirely to the pleural portion of the thorax I will retain the above designation. Further on the mesopodema follows the curvature of the mesosternum as far as the parapleurum to the anal and ventral corner of which it is attached. From here it extends, in the shape of a crest, above the boundary between epimerum and episternum (pl. 2, fig. 4; pl. 10, fig. 28, l₁) to the root of the wing. I call this crest the episternal crest because it is attached to a process of the episternum, the processus pteralis thoracis IV. The episternal crest gradually passes into a tendinous ligament. The mesopodema bends first towards the anus and so forms, with the episternum, the episternal pouch, then it turns toward the head and projects toward the interior as a strong, jagged protuberance, the processus serratus (pl. 1, fig. 2, u).

The mesopophysis (pl. 1, fig. 2, ap) consists properly of two pieces, belonging to the two mesosternums. As already mentioned, the two mesosternums are joined to a single plate which projects vertically upwards into the interior (pl. 1, fig. 2, ap). This plate narrows distally, and finally again divides into two stalk-like pieces. These stalks diverge from each other and bear at their ends twisted cup-like enlargements, the processus alveolati (pl. 1, fig. 2, ap).

In conclusion, there should be mentioned a peculiar skeletal structure, the so-called

Parapleurum (Audouin, Lowne; pl. 2, fig. 4, pn). This lies near the parapleurum, and is not firmly attached to any portion of the skeleton. It consists of a stalk-like part, the stem, which terminates in an enlargement, the head. The anal portion of the head reaches as far as the root of the wing, while the rostral portion, as already mentioned, is united by a ligament to the end of the præscutal border. The parapleurum serves, as do the above-mentioned endoskeletal
structures proper, as surfaces of attachment for the muscles. (See Chapter VI.)

Near the root of the wing there are found two large openings in the lateral wall of the thorax, through which direct muscles of flight pass to the wing joints: the foramen præalare (pl. 2, fig. 3, o) and the foramen postalare (pl. 2, fig. 3, o').

4. THE WING

A. GENERAL OBSERVATIONS

The wing of Calliphora vomitoria (pl. 3, figs. 5, 6; pl. 5, figs. 15-17) is, when fully expanded, irregularly oval. It is, according to the size of the fly, usually 8.5 to 11 mm. long and 3.4 to 4.6 mm. in maximum width. Its horizontal projection (outline) has an extent of from 20 to 40 square millimeters. Its anterior margin appears as a continuous convex line. The curvature is slight at the base and in the middle, but increases distally and is most marked at the tip of the wing. The posterior margin is, on the whole, convex like the anterior, but notched in three places. The most distally situated notch is insignificant and situated a short distance distally from the middle of the wing. The two other notches are deep incisions and situated, proximally, near the root of the wing. They separate two small lobes from the main portion of the wing. The proximal lobe (nearest the body) is the squamula (text figure 2; pl. 5, figs. 15, 17, Sq), the distal lobe which lies between the two deep incisions is the lobulus (text figure 2; pl. 5, figs. 15, 17, lb').

B. THE VEINS AND FOLDS

The wing is, as Marcy recognized in 1860, somewhat warped and slightly convex above. Large and small folds, the former up to 100 μ in height, traverse the wing longitudinally. In the proximal part of the wing 8, and in its distal part 10 folds are to be distinguished. These folds decrease in height distally as they approach the margin of the wing. The anterior large folds are nearly parallel to the anterior margin of the wing, and extend to its end; the posterior smaller folds radiate somewhat in a fan-shaped manner and extend obliquely outward and backward. These folds disappear before reaching the margin of the wing. The posterior portion of the wing is creased by very small folds. These folds are numerous, closely crowded and directed backward and outward (pl. 5, figs. 15-17).
The wing is a thin, colorless, transparent and hairy membrane. It is supported by chitinous tubes, the so-called veins. The "venous" system formed by them consists of eight longitudinal tubes radiating in a fan-shaped manner from the wing-root, and of a number of transverse tubes, here and there connecting the longitudinal ones with each other. All these tubes (veins) diminish distally in width. The first longitudinal vein lies in the anterior margin of the wing. The longitudinal veins extend in the crests of the folds, but not all fold-crests are supported by veins.

The principal contributions to our knowledge of the anatomy of the wings of Diptera are by Redtenbacher (1886) and Adolph (1885). These distinguished investigators described the systems formed by the so-called "veins" and introduced a uniform nomenclature of the same, but they disregarded the other features of the wings. Adolph (loc. cit.), especially, has worked out a uniform scheme for the venation. He says that the wings of all Diptera agree in respect to the venation, and that they differ only by the veins being often replaced by folds, and vice versa. To investigate how far he may be right was foreign to the task before me. I shall use for the veins the designations proposed by Adolph (loc. cit.), and append in brackets those of Lowne (1890-1895).

Adolph (1885) divides the wing into three regions: an anterior one, the antica; a middle one, the media; and a posterior one, the postica. The antica is indicated by a, the media by m, and the postica by p. The veins are distinguished by the letters b or a, according to whether they lie in the crest of folds that rise above (convex folds) or sink below (concave folds) the general wing surface. If more than one vein (or fold) arises in a region the veins (folds) are distinguished by Roman numerals. The most anterior or marginal vein is not included in this system, but has its own designation (gi). In this article Adolph's designations will be employed.

Fig. 1. Diagrammatic profile view of the wing seen from before, showing the warping; gi, marginal vein.
I shall now describe the eight longitudinal veins.

*Gi, the marginal vein* (text fig. 2; pl. 5, figs. 15, 17; pl. 8, figs. 23, 24, gi), begins with a club-shaped swelling at the processus pteralis alae 1. It is notched in the flexible zone (vide infra), and extends, gradually diminishing in thickness, as far as the medio-marginal transverse vein of Lowne (text fig. 2; pl. 5, figs. 15, 17, q1).

The four following veins are joined basally to a single vein, the remigium (text fig. 2; pl. 5, figs. 15, 17; pl. 8, figs. 23, 24, re), which appears as a short and very strong tube. The remigium is the strongest vein of the entire wing.

*Iaa, the auxiliary vein (mediastinal)* (text fig. 2; pl. 5, figs. 15, 17; pl. 8, figs. 23, 24, Iaa) arises at the point where the anterior transverse vein (at) touches the remigium. Basally, in the flexible zone, it exhibits a transverse striation (vide infra).

*Iba (subcostal)* (text fig. 2; pl. 5; figs. 15, 17; pl. 8, figs. 23, 24, Iba) arises from the remigium and is about its middle strengthened by a swelling.

*Ilaa (radial)* (text fig. 2; pl. 5, figs. 15, 17; pl. 8, fig. 23, IIIaa) and

*IIIba (ulnar)* (text fig. 2; pl. 5, figs. 15, 17; pl. 8, fig. 23, IIIba) arise together from the remigium. They are connected with the latter by a piece which exhibits particularly clearly the transverse striation of the veins in the flexible zone (pl. 7, figs. 20, 21, 22). The place of common origin of these two veins is thickened and set with bristles. Between these two veins there are two high folds, one projecting upward (convex), Iiba, the other projecting downward (concave), IIIaa.

*Iam. Discoidal vein (median)* (text fig. 2; pl. 5, figs. 15, 17; pl. 8, figs. 23, 24, Iam). This is the first vein of the median area; it forms, with the IIbm and the transverse vein of the knee, the knee of the wing (jk). It is connected with Iiba, proximally, by the transverse vein of the knee (patagio-hypocostal), farther on by the median transverse vein (q), and at the tip by the medio-marginal transverse vein q2, with the end of the marginal vein. Between Iam and IIIba are found the folds IVaa and the Spuria, IVba.

*IIbm (submedian)* (same figs.) extends in the crest of a strongly protruding, convex fold right to the posterior margin of the wing. It arises from the knee of the wing and is connected with Iam by two transverse veins; the postical transverse (po) and the discoidal-
Longitudinal folds (longitudinal veins):

i. First depressed (concave) fold of the anterior region, auxiliary vein.
i. First raised (convex) fold of the anterior region, subcostal vein.
i. Second depressed (concave) fold of the anterior region, radial vein.
i. Second raised (convex) fold of the anterior region.
i. Third depressed (concave) fold of the anterior region.
i. Third raised (convex) fold of the anterior region, ulnar vein.
i. Fourth depressed (concave) fold of the anterior region.
i. Fourth raised (convex) fold of the anterior region, spuria.
i. First depressed (concave) fold of the middle region, discoidal vein.
i. First raised (convex) fold of the middle region.
i. Second depressed (concave) fold of the middle region, division vein.
i. Second raised (convex) fold of the middle region, submedian vein.
i. Third depressed (concave) fold of the middle region.
i. Third raised (convex) fold of the middle region.
i. First depressed (concave) fold of the posterior region, anonyma.
i. First raised (convex) fold of the posterior region.
i. Second depressed (concave) fold of the posterior region, anal vein.
i. Second raised (convex) fold of the posterior region, axillary vein.
i. Third depressed (concave) fold of the posterior region.

Other parts:
s. Transverse anal vein.
a. Anterior transverse vein.
s. Discoidal transverse vein.
s. Knee of the wing.
s. Lobulus.
s. Posterior transverse vein.
s. Median transverse vein.
s. Medio-marginal transverse vein.
s. Remigium.
s. Notch of the marginal vein in the flexible zone.
s.s. Squamula.
transverse (dit). Between Ibm and Iam are found the folds IIam (division vein), Ibm and IIIam.

Iap, the anal vein (same figs.), does not arise from the knee of the wing, as is shown by Lowne in his illustration (1890-1895, v. I, pl. 10, fig. 1), but reaches as far as the tau of Lowne, that is, the inner marginal vein of the lobulus (l.c., pl. 9, fig. 25; pl. 11, fig. 29, ie). It articulates with a branch of this vein by a protuberance at its base. This arrangement acts as a stop that prevents the anal portion of the wing from flapping too far downward. The anal vein is connected with the knee only by means of a band of chitin which, however, is not visible from above because it is covered by the knee of the wing. The anal vein is connected with the IIbm by the transverse anal vein (aq). Between the two last-named longitudinal veins lie the folds: IIIbm, Iap, the anonyma, the boundary between the area media and the area postica, and Ibp.

Ibp, the axillary vein (same figs.), is very feeble; it can just be made out as a vein. It arises at the tip of the inner marginal vein of the lobulus, with which it forms an acute angle. The last fold is IIIap.

The longitudinal and transverse veins divide the wing into the following fields (Lowne, 1890-1895):

The regio mediastinalis between gi and Iaa.
The regio subcostalis between Iaa and Iba.
The regio marginalis between Iba and IIaa.
The regio cubitalis between IIaa and IIIba.
The regio praepatagialis between IIIba and Iam, proximal.
The regio subapicalis between IIIba and Iam, distal.
The regio apicalis between gi and terminal border, distal.
The regio anterior basalis between Iam and IIbm, proximal.
The regio discoidalis between Iam and IIbm, distal.
The regio posterior basalis between IIbm and Iap, proximal.
The regio patagialis between IIbm and Iap, distal.

At the posterior border of the wing, in the regiones subapicalis, apicalis, discoidalis and patagialis there are found numerous small transverse folds, which extend toward the posterior border.

All the veins taken together appear as a net or framework composed of tubes, the meshes of which are occupied by the double hairy lamella that forms the wing plate. The lamella of the wing has a certain firmness. This prevents the posterior part, which is not supported by any veins, from collapsing.

¹I use the term regio instead of area (Lowne) in order to avoid a confusion with the terms area antica, media, etc.
THE PIOSITY

The anterior marginal vein bears large and small hairs which are directed obliquely forward, upward and outward. On its distal part the large hairs form two rows; proximally, the large hairs increase in number and size, and inside the notch (pl. 6, figs. 18, 19, s/) this vein is closely set with large bristles. The small hairs are not nearly so numerous as the large. The wing plate (lamella) is also thickly covered with hairs (pl. 4b, figs. 12-14). These are curved. The direction of their curvature is determined by the direction of the nearest longitudinal vein or fold. The hairs are inclined toward the wing margin, in the same direction as that taken by the nearest veins. Upon the anal portion, which comprises about two-thirds of the entire wing, the hairs are inclined outward and backward toward the posterior wing margin. To each hair of the upper side there is a corresponding hair on the lower side, the places of insertion of the dorsal and ventral hairs lying nearly opposite. It should be noted that the photographs of the sections do not give a reliable representation of the direction of the hairs, as the pressure of the cover-glass in thin sections generally changes their position more or less.

THE FLEXIBLE ZONE

(Pl. 6, figs. 18, 19, s/; pl. 7, figs. 20, 21, 22.)

The anterior marginal vein is incised anteriorly by a conspicuous notch (pl. 6, figs. 18, 19, s/). This is situated just above the anterior transverse vein. Closer examination with higher powers shows that this notch is in truth a transparent, only slightly chitinized and hairless part of the vein. In order to ascertain its significance I grasped the base of a fresh wing with the forceps and then bent the tip backward with a needle. Even with the unaided eye I could see that the wing was then always abruptly bent at the same place, and that this flexible point lies about one-sixth of the length of the wing distant from its base. On repeating this experiment under the binocular I found that the bending always occurred in a slightly curved zone beginning at the notch in the anterior marginal vein. I call this bending zone the flexible zone (pl. 6, fig. 18). It extends from the before-mentioned notch backward over the IIba, which there shows a bowl-like depression, parallel to the line formed by the anterior transverse vein and the knee of the wing. Just within (proximally from) this zone the strong re-
migium divides into three separate veins. The parts of these veins, especially of IIaa and IIIba, which are here still united, passing through the flexible zone, are lighter colored than their other parts. This lighter coloring is caused by the strong, dark chitin being here restricted to narrow, transverse belts, separated by belts of similar width, composed of weak and pale chitin (pl. 7, figs. 20, 21, 22). This portion of the vein is similar in structure to the ordinary tracheae within the body, except that the strong and dark chitin does not here form a continuous spiral band, but transverse belts or bars.

5. The Articulation of the Wing

(Pl. 8, figs. 23, 24; pl. 9, figs. 25, 26.)

The skeletal parts forming the articulation of the wing can be divided into three groups:

a. The thoracic parts (processus pterales thoracis).

b. The intermediate parts (pteralia), and

c. The alar parts (processus pterales alae).

In naming these parts I have avoided all terms relating to form or function and have designated them by letters and figures. I selected for the processus pterales Roman figures, for the pteralia capital letters, and for the processus pterales alae Arabic figures (for example Proc. pter. al. 1, etc.). This method is more practical than the application of the terms used for analogous, but in no way homologous, parts of the vertebrate skeleton to the insect skeleton. In certain cases where I have either been able to ascertain the function of a part, or where its form is so striking that it easily impresses itself upon the memory, I propose to substitute, for better orientation, instead of the above-mentioned designations, short terms such as calyx, stroma, etc. For the processus pterales thoracis I and II the well-founded, older names processus praecaliris and postalaris will be retained. Besides the parts belonging to the above-mentioned groups there are others found in the articulation of the wing which may be designated as stays.

A. The Thoracic Portion (Processus Pterales Thoracis)

This portion consists of six pieces:

1. Processus pteralis thoracis I (Processus praecaliris) (pl. 2, figs. 3, 4; pl. 8, fig. 24; pl. 9, fig. 25, pl). Described above with the scutum.
2. *Processus pteralis thoracis II* (Processus postalaris) (pl. 2, figs. 3, 4; pl. 8, figs. 23, 24; pl. 9, fig. 25, ptII). Described above with the scutum.

3. *Processus pteralis thoracis III* (pl. 2, figs. 3, 4; pl. 9, fig. 26; pl. 10, figs. 27, 28, ptIII). This process is the præ-epaulet of Strausse-Dürkheim (1828). It arises at the episternum, narrows to a thin band that suddenly broadens distally to a semi-circular piece, and is then drawn out into a delicate band which passes into the membrane (see pl. 9, fig. 26) inserted upon the processus pteralis alæ 3 below the pterale B (pl. 9, fig. 26, pt3).

4. *Processus pteralis thoracis IV* (pl. 2, figs. 3, 4; pl. 9, fig. 26; pl. 10, figs. 27, 28, ptIV). This process is the “great ampulla” of Lowne. According to its function and form it may be designated as *stroma* (cushion). It is a protruding cushion-shaped piece, united with the episternum by means of a broad band, and situated in the axillary cavity of the thorax. Between the distal end of this piece and the head of the processus pteralis thoracis III there is a triangular stay (pl. 9, fig. 26; pl. 10, figs. 27, 28, v).

5. *Processus pteralis thoracis V* (pl. 4A, fig. 11; pl. 9, fig. 26; pl. 10, figs. 27, 28, ptV). Four pieces combine to make up this process: the episternum, the parepisternum, the stroma and the episternal border. Three strongly chitinized bands arise from the episternum. These finally unite with the episternal border to form a strong chitinous bar which bears at the end the process. The process itself appears as an inflation. It bears, proximally from the stroma, three small spines and distally one larger one. The entire process somewhat resembles a comb with a handle.

6. *Processus pteralis thoracis VI* (pl. 8, fig. 24; pl. 9, fig. 26; pl. 11, fig. 29; ptVI). This process arises from the crest that runs along the “lateral plate of the postscutellum” (Lowne) and is joined to the squama. It is a short, distally thickened, chitinous piece, which shows a saddle-like depression that corresponds with a similar saddle surface in the processus pteralis alæ 4 (pl. 11, fig. 29, pt4).

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**B. THE INTERMEDIATE PARTS (PTERALIA)**

This group consists of three pieces:

1. *Pterale A* (pl. 3, fig. 8; pl. 4A, fig. 9; pl. 8, figs. 23, 24; pl. 9, fig. 25; ptA). This pterale is the “dens” of Lowne. It bears four large protuberances, two shorter proximally, and two longer distally directed ones. One of the proximal ones extends into the interior
of the thorax. This protuberance is the processus duplicatus (pl. 3, fig. 8; pl. 4, fig. 9, *du*). It is divided into two secondary protuberances by a shallow saddle. The proximal protuberances ride, as it were, on the sella processus postalaris. Of the distal protuberances, one, the processus analis (pl. 3, fig. 8; pl. 4, fig. 9, *an*), is directed anally, the other rostrally. The former corresponds to the notch in the processus pteralis alæ 4; the latter, the processus rostralis (same figs., *ro*), clasps the pterale B (pl. 8, fig. 24; pl. 9, fig. 25, *ptB*) and extends as far as the processus pteralis alæ 2.

2. *Pterale B* (pl. 3, fig. 7; pl. 8, fig. 24; pl. 9, figs. 25, 26; *ptB*). This pterale is the unguiculus of Lowne. It is situated vertically and connects the upper and under sides of the joint. From the upper side a strong protuberance, the processus proximalis (pl. 3, fig. 7, *s*) arises. This protrudes beyond the processus rostralis of pterale A. From the lower side two important protuberances, the processus dentales (pl. 3, fig. 7, *de*), arise. In the space between these two protuberances lies the anal convexity of the processus pteralis thoracis V. Besides those mentioned above there are three smaller protuberances which appear to be of minor importance.

3. *Pterale C* (pl. 9, fig. 26, *ptC*; pl. 10, figs. 27, 28, *ptC*). This pterale is the hypopterigium of Lowne. It consists of a skeletal piece surrounded by a hyaline elastic mass. The skeletal portion has somewhat the form of a pistil with a strongly expanded head and a conical stem. Pterale C is in contact with the stay *V*. The head of the pterale lies in the deep, strongly chitinized, articular fossa of the processus pteralis alæ 3 (see pl. 9, fig. 26).

C. THE ALAR PORTION (PROCESSUS PTERALES ALÆ)

The marginal vein and the remigium form the principal part of the alar portion of the joint. The remaining proximal parts of the wing take hardly any part in its formation.

Four processus pterales alæ are to be distinguished:

1. *Processus pteralis alæ 1* (pl. 8, figs. 23, 24; pl. 9, figs. 25, 26; *ptr*). This process appears as a continuation of the club-shaped basal protuberance of the marginal vein. It resembles a hand held hollow, articulates with the processus pterales alæ 2 and 3, and is separated from the marginal vein by a sharp incision and a clear, feebly chitinized zone. Rostrally, it is covered by a scale-like, hairy piece, the *tegula* (pl. 8, figs. 23, 24; pl. 9, figs. 25, 26, *t*), which extends over the whole joint. The names pre-epaulet, epaulet and sub-epaulet, with which Strauss-Dürckheim designated different portions
of this piece, and which Lowne afterward adopted, I do not consider suitable.

2. Processus pteralis alæ 2 (pl. 8, figs. 23, 24; pl. 9, fig. 25; pt 2). This process arises dorsally from the remigium. It has the shape of a rectangle with rounded corners, to which an oval piece is attached proximally. This oval piece extends distally to a notch of the remigium, into which it fits. As already stated the rectangular piece is embraced by the processus pteralis alæ 1. The processus pteralis alæ 2 is connected with the processus praearalis by a ligament.

![Diagram of the proximal part of the remigium from below. Diagrammatic. (Magnification 80x)](image)

pt 2, Processus pteralis alæ 2.
pt 3, Processus pteralis alæ 3.

3. Processus pteralis alæ 3 (pl. 9, fig. 26; text fig. 3; pt 3). This process is attached ventrally to the remigium. Its form reminds one of a compressed cornet or cone with oval base. It might be considered as having arisen from the ventral border of the remigium, which is, in this region, trough-shaped, being bent outward. The anal part of the curved surface is strongly chitinized, the part turned toward the marginal vein only slightly so, and compressed.

The head of pterale C fits into this strongly chitinized cavity, and thus the asymmetrical form of this pterale finds its explanation in the asymmetry of the processus pteralis alæ 3.
4. Processus pteralis alæ 4 (pl. 8, fig. 24; pl. 9, figs. 25, 26; pl. 11, fig. 29; pl. 10, figs. 15, 17; pl. 11, fig. 29, lo) from the wing proper extends as far as the origin of the axillary vein. The proximal part of this vein is a strongly chitinized thickening of the wing-lamella, and connected with the anal vein. This thickening forms at the same time the point of origin of an elevated (convex) fold which extends to the taen of Lowne (1890-1895, vol. 1, pl. 10, i) and passes into it. The crest of the fold, together with the tau, form the margin of the lobulus, and are together to be considered as its inner marginal vein (pl. 11, fig. 29, ic'). The proximal end of this vein loosely articulates by means of a sort of ball and socket joint with the posterior (anal) marginal thickening of the squamula (see pl. 11, fig. 29). This marginal thickening bends downward and inward, and passes into the processus pteralis alæ 4, which is, in truth, the proximal, terminal portion of the inner marginal vein of the squamula. As the proximal end of this is strongly chitinized and differentiated as an articulating part, I reckon it among the processus pterales. The processus pterale alæ 4 has a depression into which fits the anal process of pterale A. The surface of the terminal portion of the processus pterale alæ 4 is in one place saddle-shaped. This saddle fits, as already stated (see thoracic portion), onto the saddle of the processus pterale thoracis II. Between the remigium and the processus pterale alæ 4 lies a stay (pl. 9, fig. 25, 26), which occupies the entire space between these structures and pterale B. It is especially well developed near the processus pterale alæ 4, where it is thickened to a disk. This stay is connected with the remigium by a strip of chitin (pl. 9, fig. 25). The parts of the joint are united by a chitinous membrane, and they can be considered as strong, local thickenings of this membrane. These articulating parts may well be considered as originating, so far as they are independent of the veins, from stimulations acting on the covering membrane so as to induce them to increase in thickness locally. The uniting membrane is flexible, but of considerable tensile strength.

The foramina praælaris and postalaris are bridged over by loose ligaments: the ligamenta praælare and postalare.
6. The Muscles of Flight

The best way to study the muscles of flight is to make a median section of the thorax to work down laterally from this, and to observe with a binocular microscope. The illustrations to this paper relate throughout to preparations made and examined in this way. They show the successive muscular layers thus rendered visible.

Two kinds of muscles of flight are to be distinguished: indirect and direct. The former act indirectly upon the wings by compressing the breast longitudinally and vertically; the latter are attached to the roots of the wings and move them directly. The number of direct muscles is larger than is generally supposed; in Calliphora vomitoria there are no less than ten pairs. In the Libellulidae, where only direct muscles of flight occur (von Lendenfeld, 1881, p. 344), these muscles are correspondingly strong. In the Diptera, where the chief work of flight is performed by the indirect muscles, these
are very well developed, while the direct muscles which serve chiefly for steering are small and weak.

Künckel (1875, p. 175) divides the entire musculature of the Diptera into three groups, the depressors (abaisseurs), the elevators (elevateurs) and the steering muscles (directeurs). The depressors and elevators are indirect, the steering direct muscles.

A. INDIRECT MUSCLES

A pair of powerful muscles, the musculi dorsales (Künckel, 1875, p. 175) (text fig. 4, \textit{mm}; pl. 4, fig. 7, \textit{mm}; pl. 12, fig. 31, \textit{mm}) traverse the entire length of the thorax. Each of these consist of six separate parts of unequal length. The first, dorsal portion, extends from the boundary between the scutellum and postscutellum of the mesothorax to about the middle of the scutum, where it is inserted. Between this muscle, the scutellum and the anal portion of the scutum there is an empty (air-filled) space (pl. 12, fig. 31, \textit{lu}) which is to be regarded as an air-sac.

\begin{figure}
\centering
\includegraphics[width=\textwidth]{diagram.png}
\caption{Diagrammatic view of the more laterally lying indirect muscles. (Median section of the thorax.)}
\end{figure}

\begin{itemize}
\item \textit{ap}, Mesapophysis.
\item \textit{dvl}, Musculus dorsalis-ventralis primus.
\item \textit{dvII}, Musculus dorsalis-ventralis secundus.
\item \textit{dvIII}, Musculus dorsalis-ventralis tertius.
\item \textit{m}, Musculus latus.
\item \textit{st}, Stigma anterius.
\item \textit{tr}, Trochanter muscle.
\end{itemize}
Laterally from the two dorsal muscles, there are three powerful dorso-ventral muscles (text figs. 4, 5; pl. 4, fig. 32, \textit{dv}), each of which appears to be composed of four parts. The first three I designate with the numbers from I to III. The fourth is apparently not a muscle of flight.

The musculus dorso-ventralis I (text fig. 5; pl. 12, fig. 32; \textit{dvI}) is the strongest. It extends from the dorsal portion of the prescutum to the mesosternum.

The musculus dorso-ventralis II (text fig. 5; pl. 12, fig. 32; \textit{dvII}) extends from the rostral portion of the scutum to the metasternum.

The musculus dorso-ventralis III (text fig. 5; pl. 12, fig. 32; \textit{dvIII}) is attached to the scutum behind the musculus dorso-ventralis II, and extends to the "tympanic plate" of Lowne (s. l. 1890–1892, t. 7, figs. 2, 24), to the thickened margin of which it is fixed.

The fourth dorso-ventral muscle (text fig. 5; pl. 12, fig. 32, pl. 13, fig. 33; \textit{tr}), which is much the weakest of the four, must, from its position, be considered as a leg muscle. It arises from the scutum, at the edge of the prescutum, lies under the turbinate process of the mesapophysis, and is inserted on the trochanter of the second pair of legs.

As an indirect muscle of flight the broad, ribbon-like musculus latus is also to be mentioned. It lies between the mesapophysis and the mesopodema.

B. DIRECT MUSCLES

As mentioned above, ten direct muscles are to be distinguished on either side.

1. The \textit{adductor alae} (text fig. 6; pl. 13, fig. 33; \textit{md}). This muscle arises in the shape of a broad band from the mesopodema. Gradually attenuated, it extends to the foramen postalaris. It then becomes tendinous and passes through this foramen and is continued beyond in the ligamentum postalaris, stretched out between the processus pteralis thoracis VI, the processus pteralis alae 4, the processus postalaris and the pterale A.

2. The \textit{abductor alae primus} (text fig. 6; pl. 13, fig. 33; \textit{mbl}). This muscle arises from the point where the parapleuralum, the stigma anterus and the prescutum come in contact, close under the prescutellar edge. The muscle follows this edge, becomes broader distally, and attaches itself to the parapterum.

3. The \textit{levator alae primus} (text fig. 7, pl. 11, fig. 30, pl. 13, fig. 34; \textit{mel}). This muscle is delta-shaped. It arises at the ventral,
somewhat thickened edge of the parapleuratium and passes into a long, delicate tendon which is attached to the processus duplicatus of pterale A.

4. The levator alae secundus (text fig. 6, pl. 11, fig. 30, pl. 13, fig. 34; melII). This muscle is rhombic in shape. It arises close to the mesapodema, at the boundary between the parapleuratium and the mesosternum, and passes into a strong tendon which follows the episternal border alongside the supinator; apparently united with the tendon of that muscle, it passes to the foramen praelare.

![Diagram of the thorax muscles](image)

Fig. 6. Diagrammatic view of the direct muscles that lie nearer the median plane. (Median section of the thorax.)

- o, Foramen praelare.
- o, Foramen postalaris.
- pd, Processus dactyloformis.
- pe, Pareposternum.
- pII, Processus pteralis thoracis I.
- pII, Processus pteralis thoracis II.
- pIV, Processus pteralis thoracis IV.
- pA, Pterale A.
- st, Stigma anterius.
- st, Stigma posterius.

There its tendon is joined to the processus duplicatus of pterale A, while the tendon of the supinator alae passes into the ligamentum analale.
5. *The supinator ale primus* (text fig. 7, pl. 11, fig. 30, pl. 13, fig. 34; *msI*). This muscle is delta-shaped. It arises from the episternal pouch and passes into a tendon which, as mentioned above, is united with the tendon of the levator secundus. It passes beyond the pterale A, where the levator secundus is inserted, and into the anal ligament.

6. *The supinator ale secundus* (text fig. 7, pl. 11, fig. 30; *msII*). This muscle is likewise delta-shaped. It arises at the apodema, behind the supinator primus, and is continued in a long tendon which traverses the foramen postalare, and is joined to the ligma-

![Diagram of the thorax muscles](image)

Fig. 7. Diagrammatic view of the direct muscles that lie more laterally. (Median section of the thorax.)

*a*, Mesapodema.
*d*, Processus duplicatus (Pterale A).
*ma*, Musculus anonymus.
*mbII*, Musculus abductor ale secundus.
*mel*, Musculus levator ale primus.
*mp*, Musculus pronator ale.
*msI*, Musculus supinator ale primus.
*msII*, Musculus supinator ale secundus.
*o*, Foramen præalare.
*oI*, Foramen postalare.
*pd*, Processus dactyloformis.
*pe*, Parepisternum.
*pn*, Parapterum.
*pII*, Processus pteralis thoracis II.
*pIIV*, Processus pteralis thoracis IV.
*stI*, Stigma posterius.

mentum anale near the processus pteralis thoracis VI and the processus ale 4.

7. *The abductor ale secundus* (text figs. 6, 7, pl. 11, fig. 30; *mbII*). This is the strongest of the direct muscles. It lies under
the abductor primus, is delta-shaped, arises from the rostral and ventral border of the parapleurum, and is continued in a tendon which extends under the parapeterum, traverses the foramen postalarum and is inserted on the anterior border of the wing-joint, probably close to the depression of the processus pteralis alae 3. Lowne's view, that this muscle is attached to the parapeterum, is erroneous.

8. The pronator alae (text figs. 6, 7, pl. 11, fig. 30; mP). This muscle is similar in shape to the abductor secundus, but much more slender. It arises from the ventral border of the parapleurum, passes, together with the abductor secundus, below the parapeterum, and is continued into a tendon which passes through the foramen praetalare. Its insertion is similar to that of the abductor secundus. The exact spot of attachment could not be determined.

9. The musculus gracilis (text fig. 6, pl. 11, fig. 34; mg). This muscle is small and oval. It arises from the parapeterum and is continued in a delicate tendon which is attached to the processus dactyloformis of the scutum.

10. The musculus anonymus (text figs. 6, 7, ma). As the name implies, I was unable to determine with certainty the points of insertion and the function of this muscle. It covers the episternum, is very delicate and appears to be somewhat rudimentary.

B. PHYSIOLOGICAL PART

METHODS OF INVESTIGATION

The experimental study of the movements of the wings is rendered difficult by the small size of the latter and by the complicated nature and rapidity of the former.

Three methods have been employed for investigating the nature of the wing-movement. The oldest of these is the optical method, which has been employed particularly by Pettigrew and by Marey (1886, p. 93). This method is based on making the tip of the wing especially visible by attaching to it a bit of gold leaf and then examining the bright line produced by this glittering point when the insect is held in a beam of strong light and induced to move its wings. The bright line then seen has the shape of the figure 8. Another method is the kymographic, which was likewise employed by Marey. When using this method the insect is held near a revolving blackened cylinder in such a manner that the moving tips of its wings describe points or curves on it. Since the tips of the wings move in spherical surfaces, they either—when the insect is
held far—touch the cylinder only at two points during each beat, or—when it is held closer—produce a curve so blurred that not much can be learned from it. On account of this, Marey's kymographic tracings do not show very much.

The third method is V. Lendenfeld's (1903) photographic method, by means of which series of instantaneous views of flying insects can be obtained (pl. 19, fig. 53).

The above statements show that the problem of applying the kymographic method to the study of insect flight had not been satisfactorily solved. I tried, therefore, to adapt that method better to this end by devising a new kind of flight-kymograph (pl. 14, figs. 35, 36). This consists of a wooden frame 120 cm. long and 20 cm. high. In grooves in the upper and lower parts of the frame there slides a thin board, 50 cm. long. This board can be rapidly shot from one end of the frame to the other by means of a steel spring. To this movable board is attached a horizontal groove, semi-circular in cross-section; the radius of the semi-circle being equal to the average length of a blow-fly's wing. In this groove a strip of glazed, blackened paper is fitted.

A fly in the normal horizontal position is held fast before the groove with the blackened paper so that the root of the wing lies at a point of the axis of the semi-cylindrical surface formed by it. When the fly attempts flight the tip of the wing touches the blackened paper. The stop holding the spring is then withdrawn, the board with its groove and blackened paper slides past the fly and the tip of the insect's wing describes a curve on the latter. Curves procured in this way are shown on plates 16, 17 and 18.

**Flight**

If the fly remains at the same place in the air (hovers), as is frequently observed among the Syrphidae, each tip of the wing describes a figure 8. Although this fact was already known to Pettigrew, the general relations and the special peculiarities of this figure 8 have never been studied in detail. The tracings made with my flight kymograph (see above) show several things that had escaped the attention of Marey. In regard to the inclination of the 8 to the horizon, it was found that the long axis of the 8 is directed from above and behind, downward and forward, and that

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1 The expressions upward, downward, forward, and backward are always used in relation to the body of the fly.
the angle this axis makes with the horizon varies between about 30 and 60 degrees. Also the direction (inclination) of the down-stroke varies. The upper observed limit was 90 degrees. The lower loop of the 8 is, as already stated by Lowne (1890-1895, p. 204), considerably larger than the upper loop. I must remark, however, that I have never observed such an inclination of the 8 as Lowne describes, that indeed it would be contradictory to the observations I have made on the mechanism of the wing-beat described below. The direction of the wing-stroke is also incorrectly represented in Lowne's figure; von Lendenfeld's (1881, p. 368) accords better with my observations. As is incontestably shown in my kymographic curves (pl. 16, figs. 42, 43, 44), the movement of the wing whilst describing the lower curve of the 8 is, relative to the insect, a movement forward, and not, as Lowne says, a movement backward. The upper part of the 8, on the other hand, is described by the wing moving backward.

At rest the wings lie back upon the abdomen, projecting about a third of their length beyond it. When the insect wishes to fly it moves the wings (wing tips) somewhat forward, and at the same time raises them. Then it makes a little jump and commences to describe the figure 8 with the wing tips. Both wings are expanded nearly horizontally and moved simultaneously almost vertically downward so that they press downward upon the air with their entire surface. The unsupported anal portion of the wing remains somewhat behind, because it cannot overcome the resistance of the air so easily as the strongly supported anterior portion. That the wings are held nearly horizontally during the downstroke (it being understood that the insect is flying horizontally) is clearly shown by the kymographic figures (pl. 15, fig. 41; pl. 16, figs. 42, 43, 44), particularly in the curves made by a wing, the tip of which had been nipped off. These curves are not described by a point (the tip of the wing), but by a line (the transverse section of the wing along which the tip had been cut off). During the downstroke this line described a broad band, or, since only the veins leave a distinct mark, two parallel lines corresponding to the only two veins, IIaa and IIIb, which extend so far toward the tip. Arrived below, the wing glides horizontally forward and then turns, the marginal vein being in front, upward and backward. In this phase the torsion of the wing is at its minimum. The anal border follows the path of

1 See the chapter on the function of the muscles.
the marginal vein, so that in the kymographic figures (pl. 15, fig. 41; pl. 16, figs. 42, 43, 44) only a single tracing is visible. Arrived above the wing glides somewhat forward, not nearly so much, however as in the lower position, and with the marginal vein in front begins anew a downward stroke.

The modus operandi of this movement may be interpreted as follows: The downward movement is executed with great force while the surface of the wing lies nearly horizontal, only the anal marginal portion being bent slightly upward. The direction of this movement is nearly vertically downward, or downward and somewhat forward. There can be no doubt that the relief of the wing surface, the longitudinal folds and the hair increase the working pressure during the downstroke. The fly thus obtains during the downstroke a strong impulse upward, which overcomes its weight.

The great breadth of the lower loop of the 8 (pl. 15, fig. 41; pl. 16, figs. 42, 43, 44, 45; pl. 18, figs. 50, 51) shows that the wing moves upward much slower than downward. During this rather slow upstroke the wings become—if, as is usual, the insect flies forward—gliding surfaces, the fly glides forward, the slightest impulse to forward movement being sufficient to make the force of gravity effective for translation. At the same time the fly, of course, also slightly descends.

During the backward movement above mentioned the wing opposes only very little resistance to the air, but still enough to produce the necessary forward impulse. During this phase, also, there is descent. The upper horizontal movement backward is short in comparison with the lower forward one, and is in the main to be considered as the turning and adjustment necessary to make the wing ready for the next downstroke.

The rapidity of the forward progression chiefly depends on the angle of the long axis of the 8 with the horizon, and the insect flies fastest when the downstroke approaches a vertical direction. It can also be said that the progression is the slower the narrower the lower loop of the 8 becomes; and if it once becomes as narrow as the upper loop the beat of the wing will merely overcome the force of gravity and the insect will hover at the same spot, as the Syrphidae so often do.

The Function of the Muscles and the Joints

The downward movement of the wing is caused by the contraction of the two powerful indirect dorsal muscles. Jurine (1820, p. 95)
describes an experiment proving this, which I have repeated in the
following manner: From a recently killed fly whose wings are
raised, the abdomen and head are removed and the thorax grasped
in a broad forceps so that one of the points of the forceps is at its
anterior, the other at its posterior end. On compressing the forceps
the thorax is shortened just as it is when the dorsal muscle contracts.
Thus the forceps' pressure imitates the action of the muscle, and a
very slight pressure suffices to cause the wings to descend. The
high development of the dorsal muscles readily explains the great
force of the downward stroke of the wing.

That a contraction of the dorsal muscles must lead to a down-
ward movement of the wings follows from a consideration of the
anatomy of the skeleton. As the convexity of the back is increased
by the contraction of these muscles, the processus praecalaris (pl. 2,
figs. 3, 4, ptI), as well as the processus postalaris (same figs., ptII),
will be raised. By means of the processus postalaris the processus
duplicatus of pterale A (pl. 3, fig. 8; pl. 4, fig. 9; du) is also raised,
and the distal processes (processus rostralis and analis), acting as
levers, correspondingly depressed. These processes then press the
wings downward.

The dorso-ventral muscles act as antagonists to the dorsal. They
compress the thorax in a vertical direction and accordingly act as
raisers of the wings.

The function of the direct muscles was determined as far as pos-
sible under the binocular by pulling them with a fine forceps in the
direction of their length. In this way the function of most of them
could be made out quite clearly.

The adductor alae (pl. 13, fig. 33, ud) draws the wing backward
toward the body. It serves to bring the wing back from the position
of flight to that of rest.

The two abductors (pl. 11, fig. 30, mbII; pl. 13, fig. 33, mbI)
draw the wing horizontally forward. One of these two muscles
draws the wing when depressed and causes its forward movement
during and after the downstroke.

The two levators (pl. 11, fig. 30; pl. 13, fig. 34, mel, melI) raise
the wing, and at the same time draw it somewhat backward. Their
action has a similar effect to that of the dorso-ventral muscles. They
are inserted on the processus duplicatus of pterale A, and by their
contraction depress that process and thus cause the wing to rise.

The two supinators depress the anal portion of the wing, and
the pronator depresses its anterior border. By the action of these
muscles the torsion of the wing surface is produced and its degree changed as required. Apparently, in consequence of the action of the pronator, the torsion is increased during the downstroke.

The functions of the musculus anonymus and the musculus gracilis could not be ascertained.

Like von Lendenfeld (1884, opposed to Marey, 1886), I am of the opinion that the action of the direct musculature of the insect and not the resistance of the air chiefly causes the complicated changes in the shape and degree of torsion of the wings during their movement. The direct musculature serves also for steering. In several cases two muscles appear to perform nearly the same function. In these cases we may suppose that one of the two similar muscles is used in flight straight ahead, the second for steering. If the fly wishes to turn to the right or to the left it can, by means of the adductor, throw one wing back and by means of the abductor direct the other forward, and so turn the side of the contracted adductor.

A few additional remarks should be made about the wing-joint.

Doubtless an important condition for good flight is absence of jerks and an elastic, unhindered, smooth movement of the wing. Independent of the elasticity of the materials, peculiar devices especially adapted for this purpose, make sure of the movement being of this kind. The processus pteralis thoracis IV, designated stroma (pl. 9, fig. 26, *ptIV*), which is a process of the episternum, occupies the axillary cavity of the wing, and is so situated that it comes to lie under the terminal portion of the remigium, the processus pteralis alae 3 (pl. 9, fig. 26, *pt3*), during the downstroke. This piece, acting like an elastic cushion, probably mitigates the shock which might otherwise occur at the end of every downstroke.

The pterale C (pl. 9, fig. 26, *ptC*), that resembles an articular ball, and that fits into the socket of the processus pteralis alae 3, may serve a similar purpose. It is to be mentioned concerning this that the pterale C is actually in the socket of processus pterale alae 3 only when the wing is depressed. When the wing is raised, that ball and this socket are far apart. Pterale C may, therefore, also be considered as a sort of elastic buffer, serving to mitigate the shocks that might otherwise ensue at the ends of the wing-strokes.

The flexible zone also is a device serving this purpose. The broad wing of *Calliphora vomitoria* may, in view of the rapidity of the wing-beat, not be sufficiently elastic to permit an equable, unhindered movement. The hovering flies, whose wings are long and narrow,
and whose wing-veins are very delicate, have no devices of this kind to prevent jerks during flight. At every rapid change in the direction or velocity of the wing-movement considerable stresses must be produced, particularly in its basal part. The ill effects which these might otherwise have are avoided by the flexibility and elasticity of the wing which bends more or less at every stroke. If, as in the Syrphideæ, the wings are narrow and long, and the elasticity of the veins is sufficient to permit such bending, there is no special flexible zone. If, on the other hand, as in the blow-fly, the wing is short and broad and the veins are hard and inelastic, a special flexible zone is developed (pl. 6, figs. 18, 19, 31). This view is supported by the serial instantaneous photographs made by von Lendenfeld (pl. 19, fig. 53), which show that just after the down-stroke the distal portion of the wing is markedly bent.

It was not possible to ascertain the function of the curiously shaped processus pteralis thoracis V. Apparently this process can be interposed like a stop between pterale C and the socket of processus pterale alæ 3, and so hinder the buffer action of pterale C.

The processus pterale thoracis III as well as the processus pteralis thoracis I are articular connections. Parts of them are poor in chitin and therefore flexible, and they are firmly attached to the parts of the skeleton to which they belong.

I consider pterale B as a piece that serves to strengthen the joint. Like a clasp it aids in holding the upper and lower portion of the joint together.

The numerous small folds in the anal portion of the wing, already mentioned in the anatomical part of this paper, may serve to strengthen this region, which is but little supported by veins. This part of the wing is comparable to a Japanese paper fan, in which firmness is attained by radial folding.

IV. SYNOPSIS OF RESULTS

1. The constituents of the wing-joint can be divided into three morphological groups, quite distinct from each other:
   1. The processus pterales thoracis.
   2. The pteralia.
   3. The processus pterales alæ.

2. The wing-joint is an exoskeletal structure, and therefore fundamentally different from the articular structures of vertebrate animals.

3. This difference is chiefly due to the fact that in insects the flexibility of the material permits some relative movement of differ-
ent parts of the same piece of chitin. The strong chitinous portions of the insect's joint continuously pass into thinner chitinous parts, which unite them with each other, while in vertebrates the different skeletal pieces are isolated and held together by muscles and tendinous structures only. The joints of insects have no capsules like those of vertebrates.

4. Similarities between the articulations of insects and vertebrates can, therefore, never be true homologies.

5. The complicated parts of the joint serve definite ends.

6. The pterale A raises and lowers the wing, working like a single-armed lever.

7. The pterale B strengthens the joint in a vertical direction.

8. The pterale C prevents or softens, like a buffer, the shocks at the end of each downstroke.

9. The processus pterale thoracis IV, the so-called stroma, has a similar function. It also contributes to softening the shocks or jerks of the wing-movement, particularly at the end of the up- and downstrokes.

10. There is in the wing a device, the flexible zone, which prevents the insufficient elasticity of the organ from being injurious.

11. The flexible zone renders possible a free, pendular vibration of the middle and distal parts of the wing at each reversal of the movement.

12. While the indirect muscles produce the elevation and depression of the wings, the direct muscles change the shape and position of the wings themselves, and the course they travel during each beat.

13. The direct muscles are probably also the steerers.

14. The downstroke of the wing is forward relative to the insect, and directed, in ordinary forward flight, downward and forward also relative to the surrounding air. It produces an elevation of the insect's body, which overcomes gravity but retards the forward movement.

15. During the horizontal movement of the wings, when depressed forward and also during the upstroke, the wings act as gliders, counteract gravity and retard horizontal advance, or vice versa. The fly descending glides forward, or ascending loses its horizontal velocity.

16. The torsion of the wing attains its maximum at the end of the downstroke, because its anal portion lags behind the anterior
part during the downstroke in consequence of its flexibility and the resistance of the air.

17. Toward the end of the upstroke the torsion is at its minimum.
18. The folds of the surface and the hairiness of the wing affect and probably heighten its mechanical effect on the air.
19. The numerous small folds of the anal portion of the wing, which is poor in veins, serve to strengthen it.
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PLATE I

Fig. 1. Stereoscopic view of the dorsal portion of the thorax from without. (Magnified 10 diameters. Photographed with Zeiss binocular; Objective 55, Ocular 3.)

an, Processus analis of pterale A.  ptB, Pterale B.
fi, Fossa praesalaries.  s, Scutum.
fi, Fossa postalaris.  se, Scutellum.
p, Praescutum.  sp, Spina scutalis.
ptr, Processus pteralis alae 1.  t, Tegula.
pt2, Processus pteralis alae 2.  v1, Stay.
pt4, Processus pteralis alae 4.

Fig. 2. Stereoscopic view of the ventral side of the thorax from within. (Magnified 10 diameters. Photographed with Zeiss binocular; Objective 55, Ocular 3.)

a, Mesapodema.  pp, Parapleurum.
ap, Mesapophysis.  st, Stigma anterius.
es, Mesosternum.
THORAX OF THE BLOW-FLY
PLATE 2

Fig. 3. Stereoscopic view of the lateral wall of the thorax from without. (Magnified 10 diameters. Photographed with Zeiss binocular; Objective 55, Ocular 3.)

\[\begin{align*}
\text{e, Episternum.} & \quad \text{ps, Postscutellum.} \\
\text{ep, Epimerum.} & \quad \text{ptI, Processus pteralis thoracis I.} \\
\text{es, Mesosternum.} & \quad \text{ptII, Processus pteralis thoracis II.} \\
\text{fa, Fossa anterior.} & \quad \text{ptIII, Processus pteralis thoracis III.} \\
\text{l, Præscutal border.} & \quad \text{ptIV, Processus pteralis thoracis IV.} \\
\text{o, Foramen præalare.} & \quad \text{p, Scutum.} \\
\text{o, Foramen postalare.} & \quad \text{se, Scutellum.} \\
\text{p, Præscutum.} & \quad \text{sp, Spina scutalis.} \\
\text{pe, Parepisternum.} & \quad \text{st, Stigma anterius.} \\
\text{pm, Parepimerum.} & \quad \text{st, Stigma posterius.} \\
\text{pp, Parapleurum.} & \quad \text{es, ep}
\end{align*}\]
PLATE 2 (Continued)

Fig. 4. Stereoscopic view of the lateral wall of the thorax from within. (Magnified 10 diameters. Photographed with Zeiss binocular; Objective 55. Ocular, 3.)

\( \sigma \), Mesapodema.
\( \varepsilon \), Episternum.
\( \varepsilon \rho \), Epimerum.
\( \varepsilon s \), Mesosternum.
\( l \), Præscutal border.
\( k \), Episternal border.
\( o \), Foramen precalare.
\( o \nu \), Foramen postcalare.
\( p \), Præscutum.
\( p d \), Processus dactyloformis.
\( p e \), Parepisternum.
\( p w \), Parepimerum.
\( p n \), Parapterum.
\( p p \), Parapleuron.
\( p t I \), Processus pteralis thoracis I.
\( p t III \), Processus pteralis thoracis II.
\( p t III \), Processus pteralis thoracis III.
\( p t IV \), Processus pteralis thoracis IV.
\( p t IV \), Processus pteralis thoracis V.
\( s \), Scutum.
\( s c \), Scutellum.
\( s p \), Spina scutalis.
\( s t \), Stigma anterius.
\( s t \nu \), Stigma posterius.
PLATE 3

Fig. 5. Right wing viewed from above. Mounted in Canada balsam. (Magnified 10 diameters. Photographed with Zeiss planar 50 mm.)

Fig. 6. Right wing viewed from below. Mounted in Canada balsam. (Magnified 10 diameters. Photographed with Zeiss planar 50 mm.)

Fig. 7. Pterale B. (Magnified 45 diameters. Photographed with Zeiss achromat A, Ocular 2.)

\[ de, \text{ Processus dentales.} \]
\[ x, \text{ Processus proximalis.} \]

Fig. 8. Pterale A. (Magnified 45 diameters. Photographed with Zeiss achromat A, Ocular 2.)

\[ an, \text{ Processus analis.} \]
\[ ro, \text{ Processus rostralis.} \]
\[ du, \text{ Processus duplicatus.} \]
RIGHT WING AND PTERALE OF BLOW-FLY
PLATE 4A

Fig. 9. Pterale A. (Magnified 80 diameters. Photographed with Zeiss achromat A, Ocular 4.)

\(an\), Processus analis. \(ro\), Processus rostralis.
\(du\), Processus duplicatus.

Fig. 10. Cross-section of the Mesothorax. (Magnified 10 diameters. Photographed with Zeiss achromat A, Ocular 2.)

\(d\text{vII}\), Musculus dorso-ventralis secundus.
\(mm\), Musculus dorsalis.

Fig. 11. Processus pteralis thoracis V. (Magnified 45 diameters. Photographed with Zeiss achromat A, Ocular 2.)
PLATE 4B

Fig. 12. Cross-section of the wing. (Magnified 30 diameters. Photographed with Zeiss achromat A.)

\( gi \), Marginal vein.
\( I b a \), Crest of first raised (convex) fold of the anterior region.
\( II a a \), Second depressed (concave) fold of the anterior region.
\( III b a \), Crest of third raised (convex) fold of the anterior region.
\( I m a \), First depressed (concave) fold of the middle region, discoidal vein.
\( II b m \), Crest of second raised (convex) fold of the middle region.
\( II a p \), Second depressed (concave) fold of the posterior region, anal vein.

Fig. 13. Part of a cross-section of the wing. (Magnified 100 diameters. Photographed with Zeiss achromat A, Ocular 6.)

Fig. 14. Cross-section of the wing. (Magnified 30 diameters. Photographed with Zeiss achromat A.)

\( gi \), Marginal vein.
\( II a a \), Second depressed (concave) fold of the anterior region.
\( III b a \), Crest of third raised (convex) fold of the anterior region.
\( I m a \), First depressed (concave) fold of the middle region, discoidal vein.
\( II a p \), Second depressed (concave) fold of the posterior region, anal vein.
PLATE 5

Fig. 15. Stereoscopic view of the right wing from above. (Dry preparation. Magnified 4 diameters. Photographed with Zeiss binocular; Objective 55. Ocular 1.)

Longitudinal folds (longitudinal veins):

- **gi**, Anterior margin, marginal vein.
- **Iaa**, First depressed (concave) fold of the anterior region, auxiliary vein.
- **Iba**, First raised (convex) fold of the anterior region, subcostal vein.
- **IIaa**, Second depressed (concave) fold of the anterior region, radial vein.
- **IIba**, Second raised (convex) fold of the anterior region.
- **IIIaa**, Third depressed (concave) fold of the anterior region.
- **IIIba**, Third raised (convex) fold of the anterior region, ulnar vein.
- **IVaa**, Fourth depressed (concave) fold of the anterior region.
- **IVba**, Fourth raised (convex) fold of the anterior region, spuria.
- **Iam**, First depressed (concave) fold of the middle region, discoidal vein.
- **Ibm**, First raised (convex) fold of the middle region.
- **IIam**, Second depressed (concave) fold of the middle region, division vein.
- **IIbm**, Second raised (convex) fold of the middle region, submedian vein.
- **IIIam**, Third depressed (concave) fold of the middle region.
- **IIIbm**, Third raised (convex) fold of the middle region.
- **Iap**, First depressed (concave) fold of the posterior region, anotyma.
- **Ibp**, First raised (convex) fold of the posterior region.
- **IIap**, Second depressed (concave) fold of the posterior region, anal vein.
- **IIbp**, Second raised (convex) fold of the posterior region, axillary vein.
- **IIIap**, Third depressed (concave) fold of the posterior region.

Other parts:

- **aq**, Transverse anal vein.
- **at**, Anterior transverse vein.
- **di**, Discoidal transverse vein.
- **fk**, Knee of the wing.
- **lo**, Lobulus.
- **po**, Posterior transverse vein.

- **q**, Median transverse vein.
- **qi**, Medio-marginal transverse vein.
- **re**, Remigium.
- **si**, Notch of the marginal vein in the flexible zone.
- **sq**, Squamula.
PLATE 5 (Continued)

Fig. 16. Right wing from above. (Magnified 10 diameters. Photographed with Zeiss planar 50 mm.)

Fig. 17. Stereoscopic view of the right wing from below. (Dry preparation.) The enlargement and the designations are the same as in Fig. 15.
PLATE 6

Fig. 18. Flexible zone. (Magnified 35 diameters. Photographed with Zeiss apochromat 16.)

$gi$, Marginal vein.
$s1$, Notch.
$I\!a\!a$, First depressed (concave) fold of the anterior region; auxiliary vein.
$I\!b\!a$, Crest of first raised (convex) fold of the anterior region.
$II\!a\!a$, Second depressed (concave) fold of the anterior region.
$II\!b\!a$, Crest of third raised (convex) fold of the anterior region.
$I\!m\!m$, First depressed (concave) fold of the middle region; discoidal vein.
$II\!b\!m$, Crest of second raised (convex) fold of the middle region.
$II\!a\!p$, Second depressed (concave) fold of the posterior region; anal vein.

Fig. 19. Anterior portion of the flexible zone. (Magnified 120 diameters. Photographed with Zeiss apochromat 16, Ocular 6.)

$I\!a\!a$, Auxiliary vein.  $gi$, Marginal vein.  $s1$, Notch.
FLEXIBLE ZONE IN WING OF BLOW-FLY
PLATE 7

Fig. 20. The union of IIaa and IIIba in the flexible zone. (Magnified 350 diameters. Photographed with Zeiss achromat E, Ocular 2.)

Fig. 21. The union of IIaa and IIIba in the flexible zone. (Magnified 200 diameters. Photographed with Zeiss achromat E, Ocular 2.)

Fig. 22. The union of IIaa and IIIba in the flexible zone. (Magnified 100 diameters. Photographed with Zeiss apochromat 16, Ocular 6.)
PLATE 8

Fig. 23. Stereoscopic view of the side of the Thorax together with the wing-joint. (Magnified 10 diameters. Photographed with Zeiss binocular; Objective 55, Ocular 3.)

aq, Transverse anal vein.
f, Fossa postalaris.
f1, Fossa praecalaris.
f2, Fossa anterior.
fi, Marginal vein.
lo, Lobulus.
p, Preascutum.
po, Posterior transverse vein.
pp, Parapleurum.
pt1, Processus pteralis alae 1.
pt2, Processus pteralis alae 2.
ptII, Processus pteralis thoracis II.
ptA, Pterale A.
ptB, Pterale B.
re, Remigium.
s, Scutum.
se, Scutellum.
sp, Spina scutalis.
sq, Squamula.
Sq, Squama.
st, Stigma anterius.
Iaa, First depressed (concave) fold of the anterior region; auxiliary vein.
Iba, Crest of first raised (convex) fold of the anterior region.
IIaa, Second depressed (concave) fold of the anterior region.
IIIba, Crest of third raised (convex) fold of the anterior region.
Iam, First depressed (concave) fold of the middle region; discoidal vein.
IIbm, Crest of second raised (convex) fold of the middle region.
IIap, Second depressed (concave) fold of the posterior region; anal vein.
IIbp, Crest of second raised (convex) fold of the posterior region.
Fig. 24. Stereoscopic view of the right wing-joint from above. (Magnified 20 diameters. Photographed with Zeiss binocular; Objective a, Ocular 3.)

- **gi**, Marginal vein.
- **ie**, Vein of the inner margin of the lobulus.
- **lo**, Lobulus.
- **ptI**, Processus pteralis alae I.
- **pt2**, Processus pteralis alae 2.
- **pt4**, Processus pteralis alae 4.
- **ptIi**, Processus pteralis thoracis I.
- **ptII**, Processus pteralis thoracis II.
- **ptVI**, Processus pteralis thoracis VI.
- **ptA**, Pterale A.
- **ptB**, Pterale B.
- **re**, Remigium.
- **sq**, Squamula.
- **Sq**, Squama.
- **t**, Tegula.
- **v**, Stay.

**IaA**, First depressed (concave) fold of the anterior region, auxiliary vein.  
**Iba**, Crest of first raised (convex) fold of the anterior region.  
**lam**, First depressed (concave) fold of the middle region, discoidal vein.  
**lbbm**, Crest of second raised (convex) fold of the middle region.  
**lhap**, Second depressed (concave) fold of the posterior region, anal vein.
Fig. 25. Stereoscopic view of the right wing-joint from above. (Magnified 40 diameters. Photographed with Zeiss binocular; Objective 2, Ocular 3.)

gi, Marginal vein.
ie, Vein of the inner margin of the lobulus.
io, Lobulus.
plt, Processus pteralis aæ 1.
pltz, Processus pteralis aæ 2.
plt4, Processus pteralis aæ 4.
pltl, Processus pteralis thoracis I.
pltII, Processus pteralis thoracis II.
pltVI, Processus pteralis thoracis VI.
pltA, Pterale A.
pltB, Pterale B.
re, Remigium.
t, Tegula.
v, Stay.
WING-JOINTS OF BLOW-FLY
Fig. 26. Stereoscopic view of the left wing-joint from below. (Magnified 40 diameters. Photographed with Zeiss binocular; Objective a, Ocular 3.)

at, Anterior transverse vein.
e, Episternum.
gi, Marginal vein.
pce, Parepisternum.
pI, Processus pteralis alæ I.
pII, Processus pteralis alæ 3.
pIII, Processus pteralis thoracis III.
pIV, Processus pteralis thoracis IV.
pV, Processus pteralis thoracis V.
pVI, Processus pteralis thoracis VI.
pB, Pterale B.
pC, Pterale C.
re, Remigium.
sq, Squamula.
t, Tegula.
v, Stay.
laa, First depressed (concave) fold of the anterior region.
lba, Crest of first raised (convex) fold of the anterior region.
lam, First depressed (concave) fold of the middle region.
lbm, Crest of second raised (convex) fold of the middle region.
lap, Second depressed (concave) fold of the posterior region.
Fig. 27. Stereoscopic view of the episternal process from without. (Magnified 45 diameters. Photographed with Zeiss binocular; Objective a₂, Ocular 3.)

c, Episternum.
ep, Epimerum.
pe, Parepisternum.
pm, Parepimerum.
ptIII, Processus pteralis thoracis III.

PtIV, Processus pteralis thoracis IV.
ptV, Processus pteralis thoracis V.
PtC, Pterale C.
v, Stay.

Fig. 28. Stereoscopic view of the episternal process from within. (Magnified 45 diameters. Photographed with Zeiss binocular; Objective a₂, Ocular 3.)

a, Mesapodema (processus serratus).
c, Episternum.
l, Episternal border.
pe, Parepisternum.
pm, Parepimerum.

ptIII, Processus pteralis thoracis III.
ptIV, Processus pteralis thoracis IV.
ptV, Processus pteralis thoracis V.
PtC, Pterale C.
v, Stay.
EPISTERNAL PROCESS OF BLOW-FLY
PLATE II

Fig. 29. Stereoscopic view of the anal part of the wing-joint, from above. (Magnified 14 diameters. Photographed with Zeiss binocular; Objective 55, Ocular 3.)

aq, Transverse anal vein.
ie, Vein of the inner margin of the lobulus.
ilo, Lobulus.
pt4, Processus pteralis alae 4.
ptVI, Processus pteralis thoracis VI.
sq, Squamula.
Sq, Squama.
Iam, First depressed (concave) fold of the middle region, discoidal vein.
IIbm, Crest of second raised (convex) fold of the middle region.
Ilbp, Crest of first raised (convex) fold of the posterior region.
IIap, Second depressed (concave) fold of the posterior region, anal vein.
IIibp, Crest of second raised (convex) fold of the posterior region, axillary vein.
PLATE 11 (Continued)

Fig. 30. Stereoscopic view of the most external (lateral) direct muscles of flight. (Magnified 20 diameters. Photographed with Zeiss binocular; Objective a, Ocular 3.)

I, Præscutal border.
mbl, Musculus abductor alæ secundus.
mel, Musculus levator alæ primus.
ml, Musculus levator alæ secundus.
mp, Musculus pronator alæ.
msl, Musculus supinator alæ primus.
msll, Musculus supinator alæ secundus.
st, Stigma anterius.
st, Stigma posterius.
**Fig. 31.** Stereoscopic view of the more medially situated indirect muscles of flight. (Magnified to diameters. Photographed with Zeiss binocular; Objective 55, Ocular 3.)

- *dvI*, Musculus dorso-ventralis primus.
- *dvII*, Musculus dorso-ventralis secundus.
- *lu*, Air-sac.
- *m*, Musculus latus.
- *mm*, Musculus dorsalis.

**Fig. 32.** Stereoscopic view of the more laterally situated indirect muscles of flight. (Magnified to diameters. Photographed with Zeiss binocular; Objective 55, Ocular 3.)

- *ap*, Mesapophysis.
- *dvI*, Musculus dorso-ventralis primus.
- *dvII*, Musculus dorso-ventralis secundus.
- *m*, Musculus latus.
- *tr*, Trochanter muscle.
FIG. 33. Stereoscopic view of the most internal direct muscles of flight. (Magnified 10 diameters. Photographed with Zeiss binocular; Objective 55, Ocular 3.)

a, Mesapodema.  
ap, Mesapophysis.  
m, Musculus latus.  
mbI, Musculus abductor alæ primus.  
md, Musculus adductor alæ.

mp, Musculus pronator alæ.  
ptI, Processus pteralis thoracis I.  
ptII, Processus pteralis thoracis II.  
st, Stigma anterius.  
tr, Trochanter muscle.

FIG. 34. Stereoscopic view of the intermediate direct muscles of flight. (Magnified 10 diameters. Photographed with Zeiss binocular; Objective 55, Ocular 3.)

a, Mesapodema.  
ma, Musculus anonymus.  
mbI, Musculus abductor alæ primus.  
mel, Musculus levator primus.  
melII, Musculus levator secundus.  
mg, Musculus gracilis.

mp, Musculus pronator alæ.  
msI, Musculus supinator alæ primus.  
pd, Processus dactyloformis.  
ptII, Processus pteralis thoracis II.  
st, Stigma anterius.
DIRECT MUSCLES OF FLIGHT OF BLOW-FLY
PLATE 14

Fig. 35. Flight-kymograph ready for an experiment.

Fig. 36. Flight-kymograph after an experiment.

Fig. 37. The middle part of the apparatus represented in fig. 35, less reduced.
PLATE 15

Fig. 38. Incomplete Flight-curve obtained by Marey's method on a blackened cylinder. (Natural size.)

Figs. 39, 40. Incomplete Flight-curves obtained by Marey's method on a blackened cylinder. The cylinder was turned more slowly than in fig. 38, so that the parts of the curve overlap. The fly was held horizontally with the anterior end opposite to the direction of the movement of the cylinder. (Natural size.)

Fig. 41. Flight-curve obtained by means of the flight-kymograph. The fly was held horizontally with the anterior end opposite to the direction of the movement of the board. (Magnified 4 diameters.)
PLATE 16

Figs. 42-45. Flight-curve obtained by the flight-kymograph. The fly was held horizontally with the anterior end opposite to the direction of the movement of the board. (Natural size.) Figs. 42-44 are consecutive parts of a continuous curve.
FLIGHT-CURVES OF BLOW-FLY
PLATE 17

Figs. 46-49. Flight-curves obtained by the flight-kymograph. The fly was held horizontally with the anterior end in the same direction as the direction of the movement of the board. (Natural size.) Figs. 46-48 are consecutive parts of a continuous curve.
PLATE 18

Figs. 50-52. Flight-curves obtained by the flight-kymograph. The fly was held horizontally with the anterior end opposite to the direction of the movement of the board. (Natural size.)
PLATE 19

Fig. 53. Series of instantaneous photographs of a flying Calliphora vomitoria. Direct sunlight. Time of exposure for each individual image 1/42,000 of a second. Interval between successive images 1/2,150 of a second. The arrows show the succession of time: the upper row running from right to left, the lower row from left to right.

Upper row (the fly seen from behind).

a, Lowest position of wings.

ab, Raising of the wings (the wing cross-sections are steep).

b, Highest position of wings.

bc, Depression of wings (the wing cross-sections are at first horizontal and then inclined).

c, Lowest position of wings.

Lower row (the fly seen from above).

d, Highest position of wings.

dc, Depression of wings (the wing cross-sections are at first horizontal and then inclined).

e, Lowest position of wings.

ef, Raising of the wings (the wing cross-sections are steeply inclined, steepest in the middle of this phase of the movement).

f, Highest position of wings.