# ORGANIZATION OF THE FLIGHT SYSTEM OF THE MAYFLY <u>EPHEMERA</u> <u>VULGATA</u> L. (EPHEMEROPTERA)*

A. K. BRODSKIY (1970)

E. G. Bekker has drawn attention in a number of papers (1952, 1954, 1956) to the problem of the origin of the insect wing, a problem which is far from final solution. His theory is superior to the two earlier theories (the Oken-Gegenbaur hypothesis; Müller's "paranotal hypothesis") in that it traces the sequence of development of the "wing-like organ" of myriopods into an anatomically distinct wing. In Bekker's opinion, one stage in the development of the insect wing is realized in the wing apparatus of mayflies. Bekker concludes from his research that the pleural (subalar) muscles of mayflies, which he regards as homologous to the pleural muscles of the Symphyla, "are wholly concerned with flight". Unfortunately, the illustrations of Bekker's articles leave some doubt as to the actual function of the mesothoracic muscles of mayflies. Thus, for example, Figs. 64 and 68 in Bekker's 1954 paper give an incorrect representation of the position and operation of the subalar muscles.

Through clarification of the structural features of the mesothorax in mayflies it would appear to be possible to solve the question of the position of the order Ephemeroptera among the other insect orders. Martynov and Shvanvich differ in their evaluation of this order. The former, basing his view on the position of the wings at rest, assigns the order Ephemeroptera to the Palaeoptera, whereas Shvanvich takes the presence or absence of crossed wing muscles as fundamental and combines the Ephemeroptera with the other Neoptera. Bekker gives a third solution, dividing all the Pterygota into three divisions: Palaeoptera, Mesoptera and Neoptera. The division Palaeoptera is represented by the order Odonata, the division Mesoptera by the order Ephemeroptera, and the division Neoptera comprises all the remaining Pterygota. Therefore, we have three different theories concerning the position of the order Ephemeroptera in the system of the Pterygota.

In addition, study of the flight apparatus of mayflies is of considerable interest for clarification of the characteristic features of the primitive type of flight. The aerodynamic conditions of insect flight are uniform, but despite the rigidity of these conditions the problem of flight is differently solved by different groups of insects. Each flight system is an adaptation to a specific type of flight and is undoubtedly a result of the differentiation of a single initial scheme. It is natural to seek the primitive type of flight in groups whose flight function has not altered or has altered very little in the course of (geological) time. A knowledge of the features of a primitive type of flight should considerably facilitate solution of the problem of the development of the wing.

The species <u>Ephemera</u> <u>vulgata</u> L. has been found to be a suitable subject for investigation of the morphology and function of the wing muscles: the species is comparatively readily available, large in size (16 mm) and has a well-differentiated subalar sclerite. For purposes of comparison (since Bekker had studied the genus Siphlonurus) the general principles were traced throughout the entire order.

The terminology adopted by Knox (cited by Needham, 1935) has been used to denote the skeletal and muscular elements.

The author is deeply indebted to the late A. S. Danilevskiy whose valuable comments contributed significantly to the present study.

## DESCRIPTIVE SECTION

<u>Skeleton</u>. The scutum is suspended by the narrow prescutum from in front to the phragma of the prothorax. The prescutum is linked to the scutum by vertical oscillation of the scutum. The medial surface of the scutum is weakly sclerotized; longitudinal endoskeletal folds correspond to the lines of application of the main forces: the first parapsidal fold ($Par_1$) and the second parapsidal fold ($Par_2$) focus the tension of the cuticle produced by the tergosternal muscles on the point A (Fig. 1, A)**; the fold separating

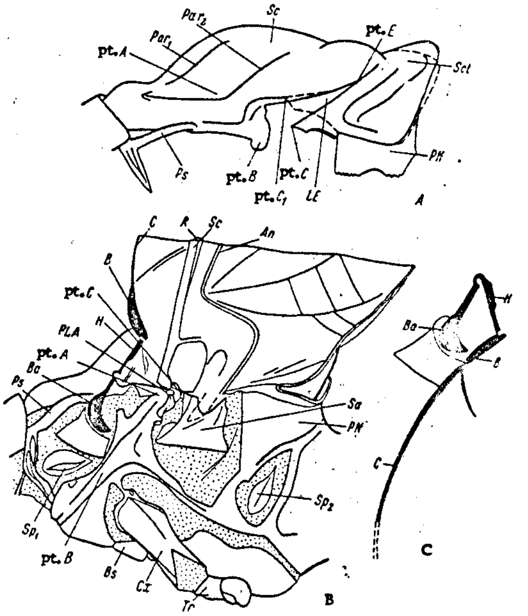

Fig. 1. Mesothoracic sclerite of <u>Ephemera</u> <u>vulgata</u> L., left side.

A) tergite, the dashed line shows the position of the arm of the scutellum when the wing is lowered; B) pleural region, wing raised, the dashed line shows the limits of the sclerite 3 Ax; C) position of costal vein with the wing lowered.

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*This paper is dedicated to the memory of A. S. Danilevskiy.

**Key to Figs. 1-5: An, basal anal vein; Ax, axillary sclerite; AWP, anterior wing process; B, bracket; Ba, basalar humeral plate; Bs, Basisternum; C, costal vein; Cx, coxa; Fu, furca; H, humeral plate; LE, scutellar suture; Par, parapsidal folds ($Par_1$ and $Par_2$, first and second folds); Ph, phragma; PLA, pleural wing process; PN, postnotum; Ps, prescutum; PWP, posterior wing process; R, radial vein; Sa, subalar sclerite; SC, subcostal vein; Sc, scutum; Sct, scutellum; Sp, spiracle; Tr, trochanter; other notations explained in text.

the parascutellar projection from the scutum focusses the action of the tergocoxal muscles. The scutellum is mobile relative to the scutum and is articulated to it by the scutellar suture, the extreme representation of which may be a slit. Three types of movement of the tergite are therefore effected in the mesothorax of E. vulgata: upward and downward oscillation of the scutum as a single nonpliable system, rotation of the scutellum relative to the scutum and forward and backward movement of the scutum. The posterior wing process is on the arm of the scutellum (pt. C in Fig. 1, A), the anterior process is on the parascutellar process (Pt. B in Fig. 1, A). The phragma of the mesothorax, which merges laterally with the postnotum, is closely connected with the scutellum.

The mesothoracic skeleton of E. vulgata comprises a light framework with large areas of thin cuticle between the skeletal folds (Fig. 1, B). The pleural wing process, which extends from below obliquely upward and caudad, corresponds to the line of greatest stress of the wall. Its lower end extends to the supporting sclerite of the tergosternal muscles which are the most powerful muscles raising the wing. This determines the distinctive position of the pleural process, since there is a real threat of outcurving of the body wall along this line. The arms of the pleural process lose their supporting function. Points A and B (Fig. 1, B) are the most heavily sclerotized. A ridge linking the pleural process to the postnotal bridge extends caudad from point B at a right angle; a weak projection articulating the pleural process to the coxa extends at an angle of 45°. The pleural wing process completes a sclerite of intricate form, which is capable of limited rotation around the vertical axis. The episternite and the epimerite are reduced to small areas of cuticle adjacent to the pleural process.

The sternite consists of five sclerites (Fig. 1, B): a narrow basisternum, two sclerites supporting the tergosternal muscles and two sclerites supporting the subalar muscles.

Axillary apparatus. It is difficult to elucidate the arrangement of the axillary apparatus partly because not all the elements lie on the same plane and partly because of the formation of combinations of fused sclerites. The axillary apparatus of the final instar nymph of the mayfly presents a clearer picture. Shortly before the molt to the subimago, when the wing is still tightly packed in the wing pad and occupies a typical backward position, and the basalar and subalar sclerites are not developed, the axillary apparatus is represented by five elements (Fig. 2). The structure of the axillary apparatus of the most specialized forms (Caenidae) justifies homologization of the sclerite A with the anterior wing process (Bekker calls it the anterior axillary sclerite). Morphologically and functionally the sclerite B corresponds to the first axillary sclerite. Throughout the length of its larger side it is connected with the sclerite which lies on the pleural wing process. The state of the second axillary sclerite in a mayfly nymph gives an objective representation of its shape (boomerang-shaped) and its connection with the remaining sclerites. In the imago the second axillary sclerite is fused with the median plate into a morphologically unified system, as a result of which Bekker incorrectly takes the hemispherical thickening at the base of the radial vein to be the second axillary sclerite. The following roof-like sclerite is identified by Bekker with the third axillary sclerite. This is morphologically true. Proof is provided by the provision of a pleuroalar muscle to the third sclerite. The sclerite E taken by Bekker to be the fourth axillary sclerite is the posterior wing process.

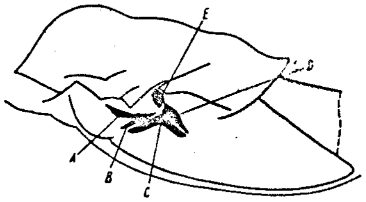

Fig. 2. Mesothorax of final instar mayfly nymph, left side.

In the axillary apparatus of E. vulgata (Fig. 3) the anterior wing process is articulated to the flexible parascutellar process. The rigidity of the articulation is slight and insufficient to ensure transmission of movement of the dorsum to the wing provided that the joint angle is 90° (the angle of the articulated planes clockwise from the parascutellar process), but the whole system is lowered under the action of the dorsoventral muscles at smaller angles of the joint. Articulation: anterior wing process -- first axillary sclerite provides limited freedom of movement around two mutually perpendicular axes in the horizontal plane. The connection between the first and second axillary sclerites permits only of a certain amount of motion around the longitudinal axis. The second axillary sclerite is immobilely fused with the hemispherical thickening at the base of the radial vein. The arm of the second axillary sclerite, perpendicular to the longitudinal axis of the body, is rigidly connected to the third axillary sclerite. Articulations: posterior wing process -- third axillary sclerite and shoulder of scutellum -- posterior wing processes form complex joints so that when the shoulder of the scutellum is raised upward and laterally the plane of the posterior wing process becomes practically horizontal from vertical. Twisting takes place with the anterior margin of the posterior wing process inward. The operational principle is one of the transmission of mechanical effort along the chain:

$$\begin{tikzcd}
 & & & & SC \\
 & & & 2Ax \arrow[ur] \arrow[dr] & \\
\text{Shoulder } Sct \arrow[r] & PWP \arrow[r] & 3Ax \arrow[ur] \arrow[dr] & & R \\
 & & & An &
\end{tikzcd}$$

The hemispherical thickening at the base of the radial vein and the sharp bend of the base of the anal vein are a result of the fact that the movement of the dorsum is imparted to the wing through the posterior wing process. There is therefore a need for firm connection at the wing base, since the main aerodynamic pressure occurs at the leading edge of the wing (SC and C).

Muscles. 1. First longitudinal dorsal muscle ($\mathrm{DLm}_1$). The main muscle producing the downbeat energy (Fig. 4, A). The effort of contraction is transmitted through the phragma of the mesothorax to the scutellum, which is joined to the

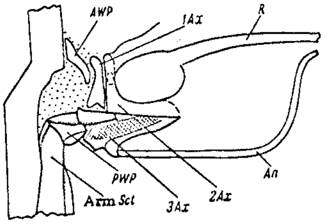

Fig. 3. Right axillary apparatus of Ephemera vulgata L. seen from above; the dashed line indicates the second axillary sclerite and the location of the pleural wing process.

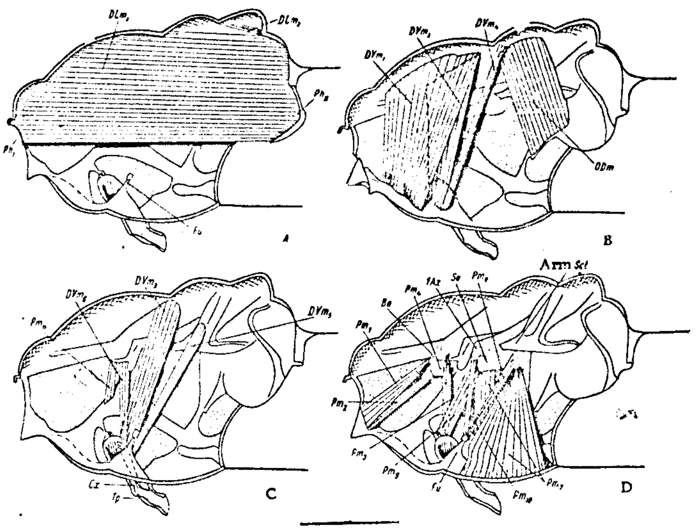

Fig. 4. Mesothoracic muscles of *Ephemera vulgata* L., longitudinal section, right side, viewed from within. A, B, C, D, various groups of muscles.

scutum by the rotating joint at the point E (Fig. 1, A), and it sets in motion the shoulder of the scutellum, which shifts from the point C to the point $C_1$, i.e. upward and sideways. Simultaneously the scutum is shifted caudad, as a result of which the anterior and posterior wing processes are strongly converged, which causes rotation of the second axillary sclerite around the transverse axis. The wing, which is jointed at the point B (anterior wing process) is lowered and at the same time twists with the leading edge downward, i.e. is pronated.

2. Second longitudinal dorsal muscle ($DLm_2$). This muscle has not previously been described in any flight system, although its function may be considerable (Fig. 4, A). It is in a state of tonic contraction when the wings are in use. It probably modifies the elastic characteristics of the scutellum and thus "makes ready" the shoulder of the scutellum.

3. Oblique dorsal muscle (ODm). The ventral articulation is on the postnotum, the dorsal articulation on the scutum. It is difficult precisely to establish the function since ODm will appear as a wing depressor when the postnotum moves and as a levator when the scutum moves (Fig. 4, B).

4. Dorsoventral muscles ($DVm_1$, $DVm_2$, $DVm_3$, $DVm_4$, $DVm_5$, $DVm_6$). The tergosternal muscle ($DVm_1$) is the main muscle producing the upbeat energy, and is correspondingly strongly developed (Fig. 4, B). The ventral articulation is on the sternite and the dorsal articulation on the scutum laterad of the first parapsidal fold.

The three tergocoxal muscles ($DVm_2$, $DVm_4$, $DVm_5$) have no bifunctional significance. The fulcrum of the leg, the pleural articulation of the coxa, has been shifted above the point of insertion of the muscle, so that all three muscles can act only as adductors of the coxa and are antagonists of the elastic strain forces of the pleural articulation. In relation to the wing the muscles $DVm_2$, $DVm_3$ and $DVm_4$ are synergists of the tergosternal muscle. The muscle $DVm_5$ regulates the degree of closing of the scutellar slit by the shoulder of the scutellum and may therefore hold up the natural pronation of the wing plate when the wing moves downward. The tergotrochanteral muscle $DVm_6$ (Fig. 4) drives back the wing, i.e. emerges in a somewhat unusual role as a synergist of the anterior tergopleural muscle.

5. Basalar muscles ($Pm_1$, $Pm_2$, $Pm_3$, $Pm_4$). The basalar sclerite occupies its usual place and is morphologically represented by a three-armed lever (Fig. 4, D) equipped with two pairs of slender muscles. The role of the basalar complex differs strongly from its role in the usual scheme of a wing-bearing segment. It was this apparently which led Bekker to take the basalar sclerite as the tegula. In fact, the basalar sclerite is connected with the wing through the humeral plate (Fig. 1, B), one end of which is articulated to the distal arm of the basalar sclerite and the other to the wing brace (Bekker's B-c). Both articulations have freedom of rotation in opposite directions. This connection between the basalar sclerite and the wing is incapable of transmitting effort to the costal and subcostal veins of the wing, but limits the movement to the longitudinal axis of the wing. The position of the elements of the three-unit chain (Ba-H-B) is depicted in Fig. 1, B and Fig. 1, C with the wing raised and lowered respectively. As is noted by Bekker, it provides for shortening of the leading edge of the wing as it moves downward. The effect of contraction of the basalar muscles is manifested in the movement of the distal arm of the basalar sclerite. The first basalar muscle $Pm_1$ (Fig. 4, D) turns back the distal arm, the fourth $Pm_4$ (Fig. 4, D), a partial synergist, partly draws back and rotates the distal arm forward. The second $Pm_2$ and the third $Pm_3$ basalar muscles rotate it backward. The contribution of these muscles is probably to modify the position of the wing when raised and at rest.

6. Subalar muscles ($Pm_7$, $Pm_8$, $Pm_9$). Posteriorly located on the subalar sclerite there is a digitiform process (main arm), to which the third subalar muscle $Pm_8$ is articulated (Fig. 4, D) and one of the heads (insertion$_1$, Fig. 5, B) of the first subalar muscle $Pm_7$ (Fig. 4, D). The second

head of the first subalar muscle (insertio$_2$) is articulated to the anterior margin of the plate. The second subalar muscle $Pm_9$ is articulated in front to the semicircular apodeme (forearm) (Fig. 4, D). Beneath the sclerite lies a region of fine membrane covered by the plate of the sclerite when the posterior margin of the sclerite is shifted downward; the anterior-superior margin of the plate is rigidly fastened to the pleurite (point 3, Fig. 1, B). When the first subalar muscle is contracted the main arm is lowered and simultaneously rotates with its proximal end downward. In its turn it rotates the apex of the third axillary sclerite by its distal end and by means of a ligament (Fig. 5, A). The longitudinal axis of the wing is strongly deflected caudad. Simultaneous contraction of the third subalar muscle places the plane of the subalar sclerite perpendicular to the major axis of the body. The second subalar muscle apparently balances the first.

7. Muscle of the first axillary sclerite ($Pm_{10}$). A slender muscle articulated to the proximal process of the first axillary sclerite (Fig. 4, D). This muscle may possibly contribute to control of the angle of incidence.

8. Anterior tergopleural muscle ($Pm_{11}$). A weak muscle (Fig. 4, B) which is a wing abductor.

9. Pleuroalar muscle ($Pm_{14}$). The origin is on the pleural process (pt. C in Fig. 1, B and Fig. 5, A), although it corresponds morphologically to the insertion which is on the third axillary sclerite. The muscle helps to control the plane of impact. The insertion is below the origin when the wing is at rest, above it when the wing is lowered and on the same level when the wing is raised.

Discussion. From analysis of the mesothoracic elements of *E. vulgata* it is possible to comprehend the functional contribution of the individual parts in the creation of lift and traction. The contractile energy of the first longitudinal dorsal muscle, which is transmitted through the shoulder of the scutellum and the posterior wing process, lowers the wing; this corresponds to alteration of the angle of attack which is dependent in this case on the mechanical properties of the system and is in no sense optimum. Upward movement of the wing is produced by the dorsoventral muscles acting through the anterior wing process. The muscle of the first axillary sclerite and the tergocoxal muscle $DVm_5$ have the function of controlling the angle of incidence when the wing moves downward, i.e. they vary it in such a way as to produce the optimum angle of attack for each specific phase in the motion of the wing. These muscles cannot effect supination of the blade of the wing as the wing moves upward. Supination, which in this case means slowing down of the trailing edge of the wing may be effected by contraction of the oblique dorsal muscle in phase with the dorsoventral muscles. The plane of impact is controlled by the pleuroalar muscle, which alters the position of the third axillary sclerite. This muscle is so weak that it is probably capable only of controlling balance whereas active modification of the plane of impact is the task of the first subalar muscle, upon whose complete contraction the longitudinal axis of the wing is deflected backward. This may be of significance in vertical flight in the nuptial dance, since otherwise the aerodynamic resultant would tend to overturn the insect.

Partial experimental verification of this picture is possible. We recorded the electrical activity of the mesothoracic muscles of *E. vulgata* males in fixed flight at the base of the entomological laboratory of the Peterhof Biological Institute. The thickness of the tungsten electrodes used to lead off the action potentials made it possible to record potentials from a single motor unit. The amplification of the potentials was calculated so as not to record respiratory contractions.* The muscles $DLm_1$, ODm, $DVm_1$ and $Pm_7$ revealed rigid joints, whose frequency coincided with the vibratory frequency of the wings (25/sec). In any case the magnitude of the action potentials recorded from $DLm_1$ correlates with the vibratory amplitude of the wings, whereas the magnitude of the action potentials of $Pm_7$ is not correlated with it but is dependent on the sector in which movement of the wings occurs. Thus, if the wings vibrate in the upper sector the magnitude of the action potentials of $Pm_7$ is slight, if they vibrate in the middle sector it is greater, and in the lower sector it is maximum. When tests were carried out in a wind tunnel with a mayfly from which the subalar sclerities had been removed the wing sweep was found to be large, but the lift was only half the body weight. All this suggests that the first subalar muscle blocks the third axillary sclerite via the subalar sclerite and in so doing blocks the entire wing in its downward movement. Therefore, $Pm_7$ has the function of controlling the amplitude of the wing beat. It is most probable that the first subalar muscle may initially have emerged successfully in the role of the main depressor of the wing, but that such use of it was confined to nuptial dances which are possibly the oldest flight regime of this insect order.

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*The experimental electrophysiological and aerodynamic methods will be described in another paper.

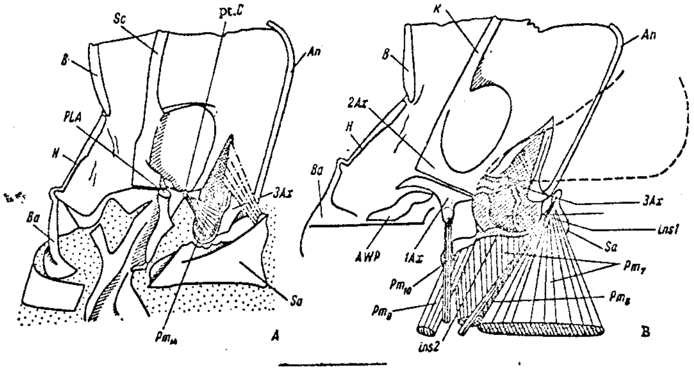

Fig. 5. Base of raised wing of *Ephemera vulgata* L.

A) left side (anterior-superior margin of subalar sclerite removed); B) right side, seen from the inside, the dashed line indicates the shoulder of the scutellum.

It is a significant feature of the mesothorax of E. vulgata that it is incapable of creating a significant store of energy in the elastic structures because of the fused parts of the thorax. Elastic strain energy may, however, be stored in the subalar sclerite. This occurs when the wing is raised, when the third axillary sclerite bends the plate of the subalar sclerite. The subalar sclerite may thus control the energy of the wing at the beginning of its downward movement.

The third subalar muscle contracts tonically and may have the function of fixing the wing when the mayfly descends in the nuptial dance.

## CONCLUSIONS

1. The distinctive features of the mesothorax of E. vulgata as a flight system are:

a) the structural plan of the axillary apparatus differs from the plan in other insect orders; the main difference is due to the transmission of effort from the wing muscles to the wing via the posterior rather than the anterior wing process;

b) the basalar sclerite plays an insignificant role in the movement of the wing;

c) the function of the subalar sclerite is active alteration of the impact plane of the wing and also control of the energy released, which is possibly regulated by the amplitude of the sweep, and in control of the elastic properties of the skeleton.

2. The motive energy of the wing is produced by the indirect wing muscles. The powerful development of the first subalar muscle may be explained by the distinctive features of the behavior of mayflies in the air.

3. On the basis of the type of muscles producing the energy of wing movement, the order Ephemeroptera should be placed among the other Neoptera. The position of the wings at rest does not apparently play a significant role in the evolution of winged insects but is merely a special ecological adaptation which is not related to the general course of insect evolution. All the elements needed for folding of the wings on the tergite are present on the mesothorax of E. vulgata: a third axillary sclerite, a pleuroalar muscle, and an anal-jugal wing fold. However, the function of these formations differs from their function in insects of other orders which may fold the wings on the tergite.

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# ENTOMOLOGICAL REVIEW

Vol. 49, Number 2
April-June 1970

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