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## EVOLUTION OF THE WING APPARATUS IN THE EPHEMEROPTERA

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In a study of the ways in which the wing apparatus of insects formed and evolved authors frequently consider the structure of the thorax of mayflies (Durken, 1907; Bekker, 1954, 1956; Bocharova-Messner, 1965, and others). Nevertheless, there are comparatively few works that give a complete description of the morphology of the thorax of these insects (Knox, 1935; Maki, 1938; Matsuda, 1956; Tsui, 1970). The use of different species that occupy different positions in the system of the order as the object of research has led to contradictory views on certain aspects of the organization of the wing apparatus of mayflies. Thus, there is at present no consensus on the structure of the axillary apparatus, the homology of a whole series of wing muscles and the operational principle of the entire wing apparatus. In this connection it has become essential to make a comparative morphological study of the ephemeropteran pterothorax with the object of establishing a common pattern for the order and of clarifying the ways in which it evolved.

In the course of the present study we investigated the morphology of the wing apparatus in seventeen species of Ephemeroptera drawn from the following families: Ametropodidae, Baetidae, Behningiidae, Caenidae, Ephemerellidae, Ephemeridae, Heptageniidae, Metretopodidae, Oligoneuriidae, Palingeniidae, Polymitarciidae, Siphonuridae. The nomenclature devised by Snodgrass (1935) and refined by Matsuda (1970) has been used to designate the parts of the skeleton. An original nomenclature based on muscle topography has been devised to designate the musculature.

### AXILLARY APPARATUS

In the usual outline of the axillary apparatus (Snodgrass, 1935) the 1st axillary sclerite carries the main load in transmission of the motion of the tergite to the wing: from the anterior notal process of the tergite to the 2nd axillary sclerite and the subcostal vein. The 3rd axillary sclerite has its long axis oriented perpendicularly to the longitudinal axis of the body. This sclerite lies between the posterior notal process of the tergite and the anal vein system. In addition, the 3rd axillary sclerite is in contact with the 2nd axillary sclerite lying on the pleural process.

Having taken this principle of the structure of the axillary apparatus as a basis, it may be shown that there are three typical axillary sclerites in mayflies in the region of the articulation of the wing and the mesothoracic tergite which are homologous to the sclerites in the usual scheme of the axillary apparatus (Fig. 1). What is specific to mayflies is the loss of connection between the 1st axillary sclerite and the subcostal vein. The 3rd axillary sclerite, which bears the main load in transmission of the motion of the tergite to the wing in these insects (Brodskiy, 1970), is fused with the basal plate and has lost its connection with the 2nd axillary sclerite.

A further sclerite has been found in the axillary apparatus of some species between the shoulder of the scutoscuteillum and the proximal process of the 2nd axillary sclerite (Grandi, 1947; Matsuda, 1956). On the basis of the topography of this sclerite in *Siphonurus columbianus* McDunn., Matsuda (1956) homologizes it with the 3rd sclerite in the usual scheme of the axillary apparatus. If this is in fact so, the sclerite should additionally be in contact with the anal vein system and with the posterior notal process of the tergite or with at least one of these elements. However, this has not been observed in any of the species investigated. In addition, it is of significance that this sclerite is present in the axillary apparatus of species belonging to the most generalized genera: *Siphonurus* Etn., *Parameletus* Egt., etc. Among species of the family Leptophlebiidae this sclerite has been found in the mesothoracic axillary apparatus of *Aprionyx tricuspoidatus* Crass (Tsui, 1970). It is characteristic that the genus *Aprionyx* Barn. is one of the most primitive in the Leptophlebiidae (Peters and Edmunds, 1970). Therefore, the sclerite occurs in the axillary apparatus of the most primitive Ephemeroptera.

The formation of the sclerite may be depicted in the following way on the basis of what has been said. We know that the tergite of the thysanuriform ancestors of the winged insect was represented by an undivided plate with two sutures on the anterior margin (Matsuda, 1970). In connection with the acquisition of wings a number of additional sutures appear on the tergite, one of which is a paired posterolateral scutal suture (Fig. 2). This suture acquires particular importance in the evolution of the ephemeropteran wing apparatus, since it makes possible rotation of the part of the tergite located behind the suture and laterally bearing the posterior notal processes relative to the anterior part. The vertical vibration of the anterior part of the tergite is effected without involving the posterior part in this motion. Further increase in the mobility of the parts of the tergite is brought about by the formation of a slit on the site of the posterolateral scutal suture. This is connected in its turn with membranization of the divisions of the tergite in the distal parts of this suture. Therefore, the sclerite under consideration, located in precisely this place, is the portion of the tergite remaining on the site of the previously uniformly sclerotized division. In view of the position of this portion of the tergite, it may be designated the median notal process. The connection of each of the axillary sclerites with the corresponding notal process of the tergite would seem to us to be a state close to the original state in the development of the insect wing apparatus. It should be noted that the median notal process of mayflies is not homologous to the "median notal process" of insects of other orders (La Greca, 1947), since the latter is articulated with the 1st axillary sclerite.

For those Ephemeroptera in which the median notal process is retained the connection of the skeletal elements in the horizontal plane may be outlined as follows:

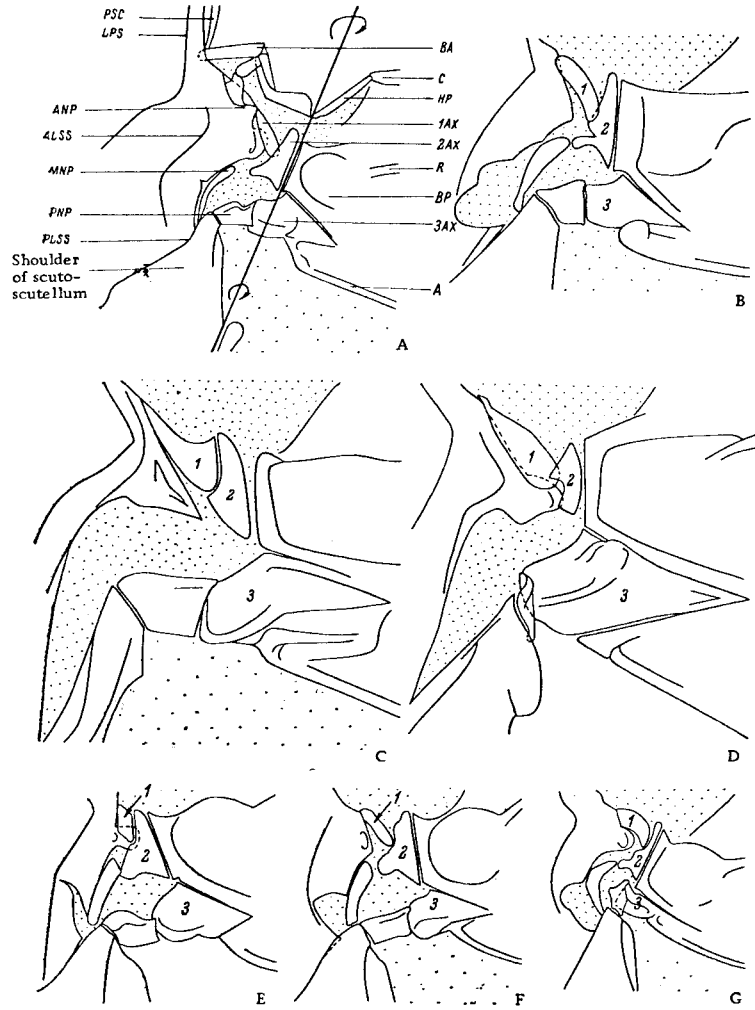


Fig. 1. Right axillary apparatus of the mesothorax in various species of the Ephemeroptera.

A) *Metretopus norvegicus* Etn. (A--anal vein; ALSS--antero-lateral scutal suture; ANP--anterior notal process; AX--axillary sclerite; BA--basalar sclerite; BP--basal plate; C--costal vein; HP--humeral plate; LPS--lateral parapsidal fold; MNP--median notal process; PLSS--posterolateral scutal suture; PNP--posterior notal process; PSC--prescutum; R--radial vein rotational axis of wing indicated by a thick line); B) *Rhithrogena tianschanica* Br.; C) *Palingenia longicaudata* Oliv.; D) *Behningia lestagei* Mot. et Bac.; E) *Ametropus eatoni* Br.; F) *Parameletus chelifera* Bgtn.; G) *Heptagenia fuscogrisea* Retz.; H) *Baetis vernus* Curt.; I) *Leptophlebia pacifica* McDunn. (from Tsui, 1970, with alterations); J) *Ephemerella ignita* Poda; K) *Caenis undosa* Tiens.; L) *Oligoneuriella rhenana* Imh.; M) *Polymitarcys nigridorsum* Tshern. The numbers on Figs. B-M correspond to the axillary sclerites.

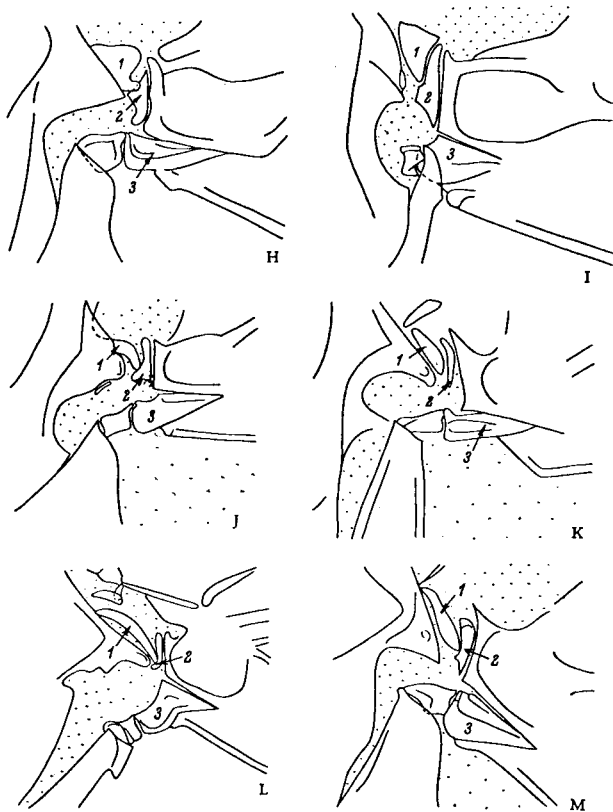
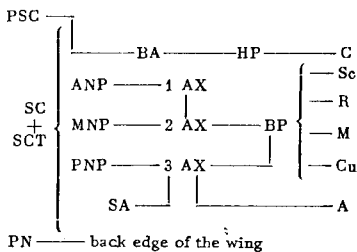


Fig. 1 (Continued).



muscle of *Siphonurus linnaeanus* Eln., with the exception of the muscle Tm3, for which the extent of development was compared with the corresponding muscle of *Ephemera vulgata* L. Only muscles involved in the movement of the wings, i. e. directly and indirectly acting muscles, and muscles modifying the elastic characteristics of the skeleton have been included in the tables. The pleurocoxal muscle, which it has been suggested by Bocharova-Messner (1965) is an indirectly acting muscle, has not been included in the tables in view of its identical development in all the species investigated.

Retention of the median notal process in some species of the Ephemeroptera is to be explained by the influence which it has on the nature of deformation of the tergite produced by contraction of the longitudinal dorsal musculature. Reduction of the median notal process does not modify the general principle of the connection and functioning of the elements of the axillary apparatus, but it is reflected in the shape of the lumen of the posterolateral scutal slit.

A detailed account of the topography of the muscles is not given since the sites of their insertion are indicated on the diagram of the muscles of a generalized wing-bearing segment of a mayfly (Fig. 2). We need to consider only those muscles concerning whose sites of insertion there are differences that lead to different interpretations of their functional significance. In indicating the sites of insertion of the muscles enumerated below we give the mobile end first.

p. 295

### MUSCULATURE

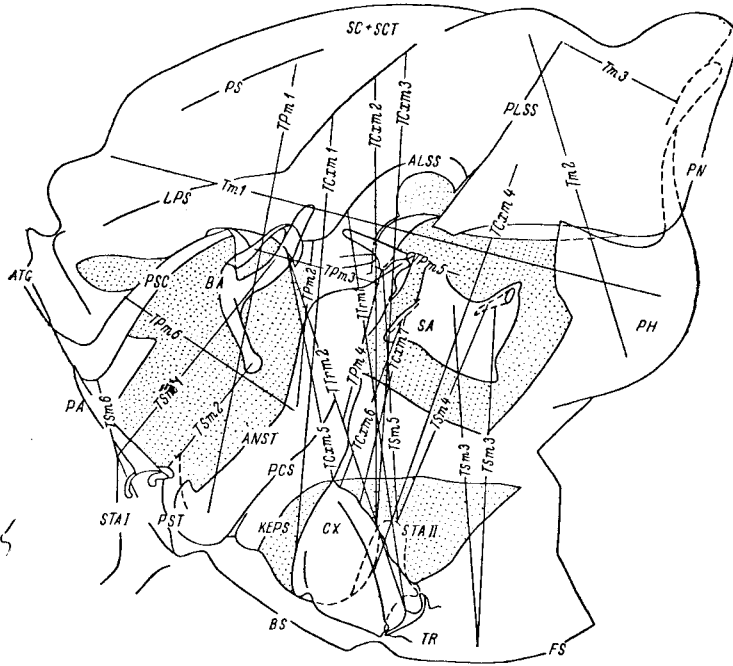
Data relating to the mesothoracic muscles are set out in the first table and those pertaining to the postthoracic muscles in the second. Strong development (rs) or weak development (rw) of any given muscle was evaluated in relation to the corresponding

(p. 296 not used) p. 297

TFm2: scutoscutellum in the region of the anterior third of the anterolateral scutal suture—anepesternum.

TFm3: articulation of the basalar sclerite with the scutoscutellum and the prescutum—pleural notal process.

TFm5: 3rd axillary sclerite—pleural notal process.



p. 295

Fig. 2. Diagram of the muscles of a generalized wing-bearing segment of a mayfly.

ANST—anepisternum; ATG—acrotergite; BS—basisternum; CX—coxa; FS—furcasternum; KEPS—katepisternum; PA—prealar bridge; PCS—paracoxal suture; PH—posterior phragma; PN—postnotum; PS—parapsidal fold; PST—presteronite; SA—subalar sclerite; SC + SCT—scutoscuteum; STAI—sternal apophysis of prothorax; STAI.II—sternal apophysis of mesothorax; TR—trochanter; otherwise as in Fig. 1.

Table 1

Mesothoracic muscles of various species of the Ephemeroptera

Muscle	<i>Siphonurus columbus</i> (Malsaud, 1955)	<i>Siphonurus tinacens</i> Esh.	<i>Parameletus cheitjer</i> Bgtn.	<i>Ametropus eatoni</i> Br.	<i>Metropus norvegicus</i> Esh.	<i>Ephemereilla ignita</i> Poda	<i>Leptohlebia pacifica</i> McDunn. (Tsui, 1970)	<i>Baetis ternus</i> Curt.	<i>Centroptilum luteolum</i> Müll.	<i>Ephemerus hucianus</i> Ume. (Maki, 1958)	<i>Ephemerus peterseni</i> Loeb.	<i>Hapligenia fusco-grisea</i> Reft.	<i>Rithrogena fian-schanica</i> Br.	<i>Hazegesia recurvata</i> Morg. (Knox, 1955)	<i>Ephemera vulgata</i> L. (Brodskiy, 1970)	<i>Polymitarcus nigridorsum</i> Tsherna.	<i>Polisarcia longicauda</i> Ollv.	<i>Robingia testagel</i> Höt. et Bac.	<i>Oligoneuriella rhinana</i> Imh.	<i>Cerenis undosa</i>
Tm1	30	+	+	+	+	+	4	rs	+	20	+	+	rs	DLm	DLm1	+	+	+	+	+
Tm2	31	+	+	+	+	+	1	+	+	21	+	+	+	Dm	ODm	+	+	+	+	+
Tm3	—	—	—	rw	—	+	—	—	—	—	—	—	rw	—	Dlm2	—	rw	—	—	—
TPm1	43	+	+	+	+	+	6	+	+	25	+	+	+	Dvm1	Dvm1	+	+	+	+	+
TPm2	45	+	+	+	+	+	13	+	+	29	+	+	+	Pm11	Fm11	+	+	+	+	+
TPm3	42	+	+	+	+	+	10	+	+	30	+	+	+	Pm5	Fm4	rs	rs	+	+	+
TPm4	51	+	+	+	+	+	—	+	+	—	+	+	+	—	—	+	+	+	+	+
TPm5	53	+	+	+	+	+	22a	+	+	32	+	+	+	Pm6	Pm14	+	+	+	+	+
TPm6	44	+	+	+	+	+	7	+	+	—	+	+	+	—	—	+	+	+	+	+
TCxm1	32	+	+	+	+	+	11	+	+	36	+	+	+	DVm2	DVm2	+	+	+	+	+
TCxm2	33	+	+	+	+	+	19	+	+	39	+	+	+	DVm3	DVm3	+	+	+	+	+
TCxm3	34	+	+	+	+	+	—	+	+	40	+	+	+	DVm4	DVm4	+	+	+	+	+
TCxm4	35	+	+	+	+	+	21	+	+	—	+	+	+	DVm5	DVm5	+	+	+	+	+
TCxm5	50	+	+	+	+	+	18	+	+	31	+	+	+	Pm3	Pm3	+	+	+	+	+
TCxm6	37	+	+	+	+	+	23	rw	rw	41	+	+	+	Pm9	Pm9	+	+	+	+	+
TCxm7	—	+	+	+	+	+	22	—	—	—	+	+	+	—	—	+	+	+	+	+
TSm1	40	+	+	+	+	+	8	+	+	33	+	+	+	Pm1	Pm1	rs	rs	rs	rs	rs
TSm2	41	+	+	+	+	+	9	+	+	34	+	+	+	Pm2	Pm2	—	rw	rw	rw	+
TSm3	38	+	+	+	+	+	5	+	+	26	+	+	+	Pm7	Pm7	+	+	+	+	+
TSm4	39	+	+	+	+	+	20	+	+	27	+	+	+	Pm8	Pm8	+	+	+	+	+
TSm5	52	+	+	+	+	rs	17	+	rw	8, 24	rw	rw	+	Pm10	Pm10	+	+	+	+	+
TSm6	—	+	+	+	+	+	2	+	+	—	+	+	+	rw	rw	+	+	+	+	+
TTm1	48	+	+	+	+	+	14	+	+	44	+	+	+	DVm6	DVm6	+	+	+	+	?
TTm2	—	—	—	—	—	—	—	—	—	—	—	—	—	Pm3	—	—	—	—	—	—

p. 296

Table 2

## Postthoracic muscles of various species of the Ephemeroptera

Muscle	<i>Siphonura cecidomyia</i> McDunn. (Matsuda, 1956)	<i>Microtopus norvegicus</i> Ehn.	<i>Lepidostibia rhenana</i> McDunn. (Taul, 1970)	<i>Baetis ternus</i> Curt.	<i>Cloeon dipferum</i> L.	<i>Ecdyonurus hyalinus</i> Ulm. (Maki, 1933)	<i>Ecdyonurus peterseni</i> Lest.	<i>Hapligenia fusca</i> Reitz.	<i>Hexagenia recurvata</i> Morg. (Knox, 1935)	<i>Ephemerella vulgata</i> L.	<i>Palisagenia longicauda</i> Oliv.	<i>Oligoneuriella rhenana</i> Imb.
Tm1	63	+	1	+	+	47	+	+	DLm	+	+	+
Tm2	64	+	—	—	—	—	—	—	—	+	+	—
Tm3	—	—	—	—	—	—	—	—	—	—	—	—
TPm1	71	+	2	+	+	51	+	+	DVm1	+	+	+
TPm2	72	+	6	+	—	54	+	+	Pm2	+	+	+
TPm3	—	—	20	—	—	55	—	—	Pm3	+	+	+
TPm4	76	—	—	—	—	—	—	—	Pm6	+	—	—
TPm5	—	—	—	—	—	57	+	+	—	—	—	—
TPm6	—	—	5	—	—	—	—	—	—	—	—	—
TCxm1	65	+	4	+	—	59	+	+	DVm2	+	+	+
TCxm2	66	+	12	+	+	62	+	+	DVm3	+	+	+
TCxm3	—	—	—	—	—	63	—	—	—	—	—	—
TCxm4	67	+	17	—	—	—	+	+	—	+	+	+
TCxm5	78	+	15	+	—	56	+	+	Pm1	+	+	+
TCxm6	69	+	16	+	—	—	+	+	Pm5	—	—	—
TCxm7	—	—	—	—	—	—	—	—	—	—	—	—
TSm1	—	—	—	—	—	50	+	+	—	—	—	+
TSm2	—	—	—	—	—	—	+	+	—	—	—	—
TSm3	—	+	8	—	—	52	+	+	—	—	+	—
TSm4	70	+	9	+	+	—	—	—	DVm4	+	+	+
TSm5	77	+	11?	—	—	—	—	—	Pm4	+	+	+
TSm6	—	—	—	—	—	—	—	—	—	—	—	—
TTrm1	74	+	13	+	+	—	+	+	DVm5	+	+	+
TTrm2	—	—	—	—	—	66	—	—	—	—	—	—

TCxm5: articulation of basalar sclerite with scutoscuteUum in front of the anterior notal process—coxa at its articulation with the pleurite.

TCxm7: anterior apodeme of subalar sclerite—posterior margin of coxa. The muscles TCxm6 and TCxm7 formed as a result of the splitting of a single muscle into two. When only one of the two muscles is present it is not always clear which.

TSm1: basalar sclerite—sternal apophysis of prothorax. In the opinion of Matsuda (1970), the muscles TSm1 and TSm2 are homologous to the tergo-sternal muscles of *Lepisma saccharina* L. On this basis, and also having regard to the fact that these muscles have not been found in any other insect order, they are placed in the tergo-sternal muscles and not in the pleurosternal muscles, as is done by Matsuda. In a number of species the ventral articulation is shifted to the apodeme of the presternite.

TSm6: anterior end of prescutum—sternal apophysis of prothorax. The articulation is on the prealar bridge in *Polymitarcys nigridorsus* Tshern. and *Oligoneuriella rhenana* Imb. In *Ecdyonurus peterseni* Lest. this muscle is articulated ventrally to the apodeme of the presternite and dorsally to the prescutum at two points.

#### FUNCTIONAL SIGNIFICANCE OF THE MUSCLES OF THE GENERALIZED WING-BEARING SEGMENT

The wing apparatus of mayflies functions in the following manner. Contraction of muscle Tm1 causes an abrupt rearward movement of the part of the scutoscuteUum located before the posterolateral

scutal sutures. The posterior part of the scutoscuteUum, which is mobile articulated to the anterior part, rotates as this happens, as a result of which the shoulders of the scutoscuteUum are raised upward and sideways. The wings, which are hinged at the size of the anterior notal processes, are lowered. When the wing tip is lowered to below the level of the pleural notal process the muscles of the subalar sclerite are brought into play. These muscles (TSm3, TCxm6 and TCxm7) were previously unable to lower the wing owing to the inadequate length of the lever formed by the connection between the tip of the subalar sclerite and the wing base.

Upward movement of the wing is effected by contraction of the levator muscles, which are all the dorsoventral muscles dorsally inserted on the scutoscuteUum medially form the anterolateral scutal suture; Tm2, TPm1, TPm2, TCxm1, TCxm2, TCxm3, TTrm1.

Forward movement of the wing is governed by rotation of the distal shoulder of the basalar sclerite inward and forward. Consequently, the wing promoters are the muscles TSm1, TCxm5 and TTrm2, while the remoters are TSm2 and TPm3, as well as the elastic forces of deformation of the skeleton.

Pronation of the wing is achieved mainly by the difference in the lift of the anterior and posterior notal processes on contraction of the muscle Tm1: when the wing moves downward the posterior notal process is considerably above the anterior one. In addition, pronation is assisted in a number of species by muscles TCxm5 and TTrm2, which cause inclination of the wing by means of the connection between the 2nd articulation of the basalar sclerite with the scutoscuteUum and the anterior margin of the basal plate.

Supination presents a serious problem to Ephemeroptera, since when the wing is in the lowest position it is completely pronated. The first stage of supination is effected by the muscle TSm3, which is in a contracted state at the start of the upward movement of the wing. After relaxation of this muscle the contraction of Tm2 governs the second stage of supination.

Control of the movement of the wing not requiring appreciable alteration of the parameters of the wing beat\* is effected by the muscles regulating the elastic properties of the sclerite and also modifying the relative orientation of its elements: Tm3, TPm5, TPm6, TCxm4, TSm6. The beat plane is controlled by the muscles TPm5, which is contracted in the downbeat phase of the wing. The angle of incidence may be regulated by the muscle TCxm4, which opposes the natural twisting of the wing.

The complexity of functional interpretation of the muscles TPm4 and TSm5 is connected with the relatively slight mobility of the 2nd axillary sclerite. The function of the muscle TSm5 is variously explained even when similar species are considered: *Ephemeradanica* Mull. (Grandi, 1947) and *E. vulgata* L. (Brodskiy, 1970).

The muscles TSm4 and TSm5 were found in all the species investigated except *Behningia lestagei* Mot., Bac. and *Oligoneuriella rhenana* Imh. The flight of all the Oligoneuriidae is distinguished by high speed and the lack of gliding elements (Brodskiy, 1973). There are no data on the flight of members of the family Behningiidae. However, in view of the wing structure in species of the genus *Behningia* Lest., it may be assumed that they also have rapid flight and that their swarming behavior is similar to that of the Oligoneuriidae. On this basis, and also considering the tonic nature of the contraction of these muscles, it may be considered that the ability to lock the wings in the gliding position is connected with the existence of at least one pair of these muscles (TPm4, TSm4, TSm5).

Finally, active control of the power developed by mayflies in flight presupposes the existence of a special mechanism. We have already explained that an increase in the power developed takes place by an increase in traction (Brodskiy, 1971). The creation of greater traction than in trivial flight is achieved by the earlier incorporation of the muscle TSm3 in the downbeat phase, which moves the wing rearward by means of the connection between the subalar and 3rd axillary sclerite.

## DISCUSSION

It is evident from our comparative morphological analysis of the wing apparatus in members of various families of the Ephemeroptera that the most specific feature of the wing apparatus in the order is the presence of a large number of tergo-sternal muscles. With the exception of TSm6, none of these muscles has been found in insects of other orders (Matsuda, 1970). This author regards the presence of a large number of tergo-sternal muscles as a primitive feature of the Ephemeroptera, since the same muscles are abundantly represented in the Apterygota. The same

\*We are not here discussing the mechanism of active control of the flight path in mayflies.

idea was stressed by Bekker (1956) when he homologized the muscles of the subalar sclerite with the pleural muscles of the wing-like formation of *Symphyla*.

At the same time, another assumption is possible, namely that the presence of tergo-sternal muscles indicates specialization of the wing apparatus in the Ephemeroptera. In fact, we find all the principal elements peculiar to the wing apparatuses of insects of other orders (tergal, tergo-pleural, tergo-coxal and tergo-trochanteral groups of muscles, three typical axillary sclerites etc.) in the mesothorax of different species of the Ephemeroptera. The most primitive species additionally have a pleural suture and a typical muscle, the wing flexor (TPm4). The distinctive, specialized structure of the wing muscle fibers of mayflies also supports this assumption (Pipa, 1955). In addition, if we turn to the morphology of *Lepisma saccharina* L. (Barlet, 1953), an insect similar to the hypothetical ancestor of the Pterygota, it is found that a more or less probable homolog may occur only for the muscle TSm5, and that it is not in general possible to establish homologs for TSm3 and TSm4.

The formation of the wing apparatus in the Ephemeroptera may be represented as follows on the basis of secondary acquisition of tergo-sternal muscles. Winged insects most probably inherited pleuro-coxal, tergo-coxal and tergo-trochanteral muscles from wingless ancestors. Pleural and tergo-pleural muscles developed in the first stage of the formation of the insect wing apparatus. These muscles gave rise to the directly acting muscles: basalar, subalar and axillary. According to Matsuda (1970), the overwhelming majority of the tergo-pleural muscles first appeared in winged insects. The basalar and subalar muscles were probably established at the expense of the tergo-coxal muscles, and the axillary muscles at the expense of the small tergo-pleural muscles referred to by Bocharova-Messner (1968) as positional muscles. The wing apparatus of the Polyneoptera formed at this level in the development of the wing muscles.

The essence of the second stage in the formation of the wing apparatus is involvement of the tergal muscles in the work of the wings. The wing apparatuses of the Oligoneoptera and the Paraneoptera formed at this level.

Establishment of the tergo-sternal muscles occurred in the third stage. Only a considerable alteration in the nature of the dominant behavior in the air could have provided a basis for the development of a whole series of muscles in the excellently flying ancestors of that Ephemeroptera. We relate such a behavioral change to the commencement of the ecological divergence between the larval and imaginal stages. This led to the selection of forms capable of distinctive flight in a limited space. In other words, formation of the wing apparatus in the Ephemeroptera was connected with the establishment of the swarming mechanism.

It is noteworthy that all the tergo-sternal muscles except for TSm6 are directly acting muscles. The loss of normal swarming behavior at the present time entails an alteration in most of these muscles. Some of the tergo-sternal muscles (TSm2, TSm4, TSm5) are manifesting a tendency to reduction. The function of the most powerful of the tergo-sternal muscles (TSm3) is closely connected with execution of the nuptial dance. It may be suggested on this basis that specialization of the wing apparatus for swarming behavior of the first type in the ancestor of the Ephemeroptera (Brodskiy, 1973) was reflected in the development of the tergo-sternal muscles.

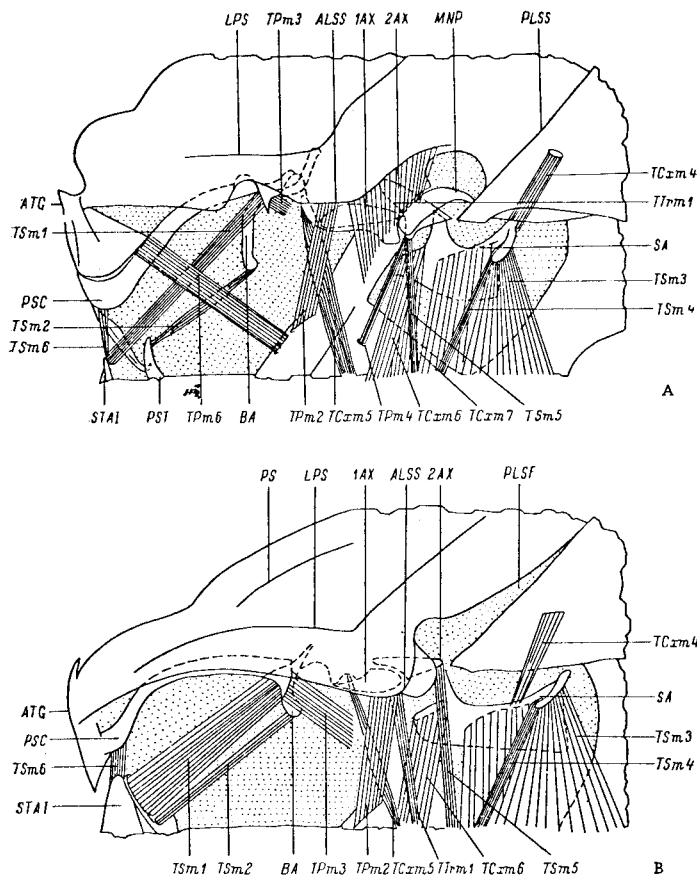


Fig. 3. Parasagittal section of the mesothorax in two species of Ephemeroptera; right side—internal view; muscles partly removed.

A) *Siphonurus linnaeanus* Etn. ; B) *Palingenia longicaudata* Oliv. ; PLSF—posterolateral scutal slit; otherwise as in Figs. 1 and 2.

A number of significant changes in the organization of the flight system are closely connected with the establishment of these muscles. In the first instance there was an increase in the role of the subalar sclerite in the movement of the wing, which led to strengthening of the posterior notal contact between the dorsum and the wing: fusion of the 3rd axillary sclerite with the basal plate, separation of the posterior notal process, formation of the anal bracket, etc. The simultaneous development of the palaeopterous state, which made it possible to restrict the mobility of the 3rd axillary sclerite, was conducive to the specialization of the posterior notal process solely for transmission of the motion of the tergite to the wing. As a result one of the two pairs of muscles of the 3rd axillary sclerite (TPm4) remains at the present time in the mesothorax of the most generalized species, while the other (TPm5) has considerably altered its function.

Such is the way in which the "generalized wing apparatus" of the Ephemeroptera may have formed. The flight of mayflies has changed little during the long history of the order. In the early stage of evolution a branch, in which the wing apparatus lacked a

median notal process and the muscle TPm4, separated from the type of organization of the wing apparatus which we treat as generalized. Such a state of the wing apparatus is to be found at the present time in members of the families Baetidae, Leptophlebiidae and Ephemerellidae.

The wing apparatus that was the starting point in the evolution of mayflies of the superfamily Ephemeroidae Leach formed subsequently as a result of reduction of the muscle TPm6. The separation of this branch and of the previous branch was not connected with an alteration in the nature of flight, since no significant differences in flight behavior are to be noted in present day species.

The next stage in the evolution of the wing apparatus of the Ephemeroptera was determined by deviation in the dominant behavior in the air from ordinary swarming behavior (Brodskiy, 1973). Thus, there was strengthening of the muscle TPm3 in members of the families Palingeniidae and Polymitarcidae compensating the reduction or weakening of TSm2. Movement of the wing in the horizontal plane is effected in these mayflies by

two antagonist muscles: TPm3 and TSm1 (Fig. 3). The last of these muscles is appreciably developed and emerges as a direct promoter of the wing. The function of the muscle TCxm5 is limited to pronation of the wing in its downward movement.

The deviation from ordinary swarming behavior reaches its greatest significance in members of the families Oligoneuriidae and Behningiidae, in which there is reduction of the muscles of the mesosternal apophyses (TSm4, TSm5), in addition to such changes.

A number of features such as the considerable weakening of the tergoxal muscles and the reduction of TPm2 makes the wing apparatus of the Oligoneuriidae the most specialized.

In addition, members of the family Caenidae have a specialized wing apparatus. The most characteristic organizational feature of the pterothorax in these mayflies is reduction of TSm3. Tm2, the fibers of which run parallel to those of the dorsoventral muscles, attains considerable development. The point of dorsal insertion of TCxm4 was shifted to the apex of the shoulder of the scutellum, which made for greater efficiency in regulation of the lumen of the posterolateral scutal slit. TPm2 emerged as a wing abductor.

Adaptation to flight at low Reynolds numbers is one cause of the specialization of the wing apparatus in these mayflies. Vogel (1967) has shown in a study of the flight of the fruit fly *Drosophila virilis* Sturt. that the organization of the flight system is simpler in this species than in larger insects. Insofar as *Drosophila virilis* Sturt. and *Caenis undosa* Tiens. operate at approximately the same Reynolds numbers, the observable simplification in the wing apparatus of the Caenidae should be regarded as a result of reduction in body size.

At the same time it must be noted that the phylogenetic branch that gave rise to the family Caenidae separated early from the common trunk (Edmunds, 1962; Chernova, 1970). This, taken in conjunction with the reduction of body size, was conducive to segregation of the wing apparatus of the Caenidae from the more generalized type to be found in most of the Ephemeroptera.

The original branch with the generalized type of wing apparatus gave rise to the families Siphonuridae, Ametropodidae, and Metretopodidae. The family Heptageniidae, in which the wing apparatus is appreciably modified in connection with deviation from the usual pattern of behavior in the air (Brodskiy, 1973), subsequently separated from this branch. Thus, the posterior half of the prescutum was reduced and the muscle TPm3 weakened. Despite the retention of the median notal process, reduction of TPm4 and weakening of TSm5 is to be observed, the result of which was to increase tension in the axillary apparatus. There was also reduction of TPm6.

The reduction of the metathorax observed to varying degrees in all members of the order occurred independently in the different phylogenetic branches. The metathoracic axillary apparatus was simplified in connection with the loss of independence of the hind wings. Reduction of the 1st axillary sclerite is most often noted, but the posterior notal process is reduced in the Leptophlebiidae and the shoulder of the scutoscutellum loses contact with the wing.

Changes in the metathoracic muscular apparatus are determined by the reduction of a part of the

muscles and also, in connection with changes in the skeleton, by the loss of their former function. Thus, the powerful development of Tm1 in the metathorax is to be explained primarily by the need to compensate the deformation of the posterior phragma on contraction of the corresponding mesothoracic muscle.

The muscles TSm3, which is important in the mesothorax, is reduced in many species. However, even when preserved, this muscle frequently loses its connection with the movement of the wing (Leptophlebiidae, Palingeniidae).

The muscles of the mesosternal apophyses are reduced in the metathorax of members of the family Heptageniidae, as a result of which fixation of the hind wings in gliding becomes impossible. At the same time it is only in these mayflies that the hind wings remain capable of movement in the horizontal plane.

The process of reduction of the hind wings apparently began earlier in members of the family Oligoneuriidae than the alteration in the nature of the dominant behavior. This explains the retention in the metathorax of muscles lost from the mesothorax.

#### SUMMARY

1. Mesothoracic structure is considerably more uniform in different members of the order Ephemeroptera than it is in other insect orders.
2. It is assumed that formation of the "generalized wing apparatus" of the Ephemeroptera took place in connection with the adaptation of these insects to distinctive swarming flight.
3. The basic features to the evolution of the wing apparatus in the Ephemeroptera are determined by deviation from the usual pattern of dominant behavior in the air, by development of functional and morphological "dipterousness" and by reduction in the size of the body.
4. Modification of the skeleton and the metathoracic muscles is connected with the different degree of subordination of the hind wings to the fore wings. There are several possible ways in which the metathoracic muscles could have been reduced.

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