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MORPHOLOGY OF THE THORACIC EXOSKELETON AND MUSCULATURE OF A MAYFLY *SIPHLONURUS COLUMBIANUS* McDUNNOUGH (Siphlonuridae, Ephemeroptera), A contribution to the subcoxal theory of the insect thorax[1]

RYUICHI MATSUDA

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INTRODUCTION

So far as the writer is aware the first noteworthy morphological work on the thorax of an adult mayfly is that of Dürken. Dürken, in his attempt to homologize the muscles of the abdominal gills with the wing muscles of the pterothorax, worked on the external structure and musculature of *Centroptilum luteolum* and *Ephemerella ignita.* Dürken's work was immediately refuted by Börner (1908). Börner, applying his theory of the subcoxal origin of the leg base in the Arthropoda (1904), came to the conclusion that the abdominal gills are homologous to the thoracic legs which is contrary to Dürken's conclusion that the abdominal tracheal gills in the mayfly are of tergal origin. This controversy lasted until Dürkin published his work on the postembryonic development of the tracheal gills in the mayfly abdomen (1923). Börner succeeded in pointing out, at least, the insufficiency of Dürkin's data as to the ventral attachement of one morphologically important dorso-ventral muscle.

Later, Takahashi (1932), Knox (1935), and Maki (1938) worked on the thorax of the adult mayflies, but their works do not touch the problem of the subcoxal origin of the pleuro-sternal region of the thorax with which the present study is primarily concerned. Knox's work on *Hexagenia recurvata* and Maki's work on *Ecdyonurus hyalinus* are, however, referred to in this study for their apparent reliability in anatomical data.

Grandi (1941, 1942) briefly described the external structure of *Caenis macrura* and *Choroterpes pictei.* Grandi (1947) further studied the muscles associated with the axillary sclerites in a series of species of Ephemeroptera and came to the conclusion that the axillary sclerites in this order are not homologous to those in other orders of pterygote insects.

As already noted, Börner was the first to apply the concept of the subcoxal origin of the pleuro-sternal region of the insect thorax to this order, but his interest was apparently in the origin of the abdominal tracheal gills, and what he actually worked out and interpreted by himself was the thorax of the nymph. Moreover, the subcoxal theory has undergone changes in its details since Heymons (1899) first postulated the theory on the basis of embryological evidence as was recently reviewed by Matsuda (1956).

The present study is, primarily, an attempt to interpret the pleurosternal region of the adult thorax of this more or less strongly divergent group, the order Ephemeroptera, in terms of the subcoxal theory as interpreted by Ferris (1939) which is being steadily accepted in recent years.

[1] Contribution No. 922, Department of Entomology, University of Kansas.

The genus *Siphlonurus* on which the present study is based is admittedly the most primitive group existing in the order Ephemeroptera. This excellent material will provide more authentic anatomical data for morphological consideration than any other groups that have been worked out by previous workers.

The specimens were collected at Tuolumne Meadow, Yosemite National Park, California by the writer during his stay in that park from June to August, 1955.

ACKNOWLEDGMENTS

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EXTERNAL MORPHOLOGY

THE PROTHORAX

(Plate 1, A, B)

The pronotum: The pronotum is a transverse simple plate hanging laterally over the subcoxa, and connected with the latter by a folded membranous area. There is an elongate strongly sclerotized area on either side of the median longitudinal axis for the attachment of muscles.

The subcoxa: The subcoxa is distinctly divided into anterior episternal and posterior epimeral regions by the pleural suture. The episternal region exposed outwardly is the anepisternum. There is also a narrow sclerite along the inner margin of the coxal base. This sclerite is the katepisternum, and is articulated with the coxal margin. No previous authors described this narrow sclerite. This is apparently the ventral part of the inner ring of the subcoxa homologous to the katepisternum in the pterothorax of this species and in Neuroptera. The validity of this interpretation is further demonstrated by the attachment of the homologous muscle with the notokatepisternal muscle in the pterothorax on this sclerite. There is present no trochantin in the prothorax. The procoxa has, thus, dicondylar articulation with the subcoxa, namely, with the ventral end of the pleural suture and with the apex of the katepisternum.

The prosternum: The basisternum is well developed antero-laterally extending almost to the ventral end of the anepisternum; laterally the basisternum is clearly separated from the subcoxa by membranous area; posteriorly the basisternum is indistinguishably fused with the furcasternum. The sternal apophysis is vertically erected and its presence is recognizable externally by the presence of a pit, the sternal apophyseal pit. There is no differentiation into the presternite and postfurcasternite in this species.

The cervical sclerites: The cervical sclerites are composed of a pair of narrow plates, which are articulated posteriorly with the antero-lateral angle of the anepisternum, and anteriorly with the lower lateral angle of the postoccipital ridge.

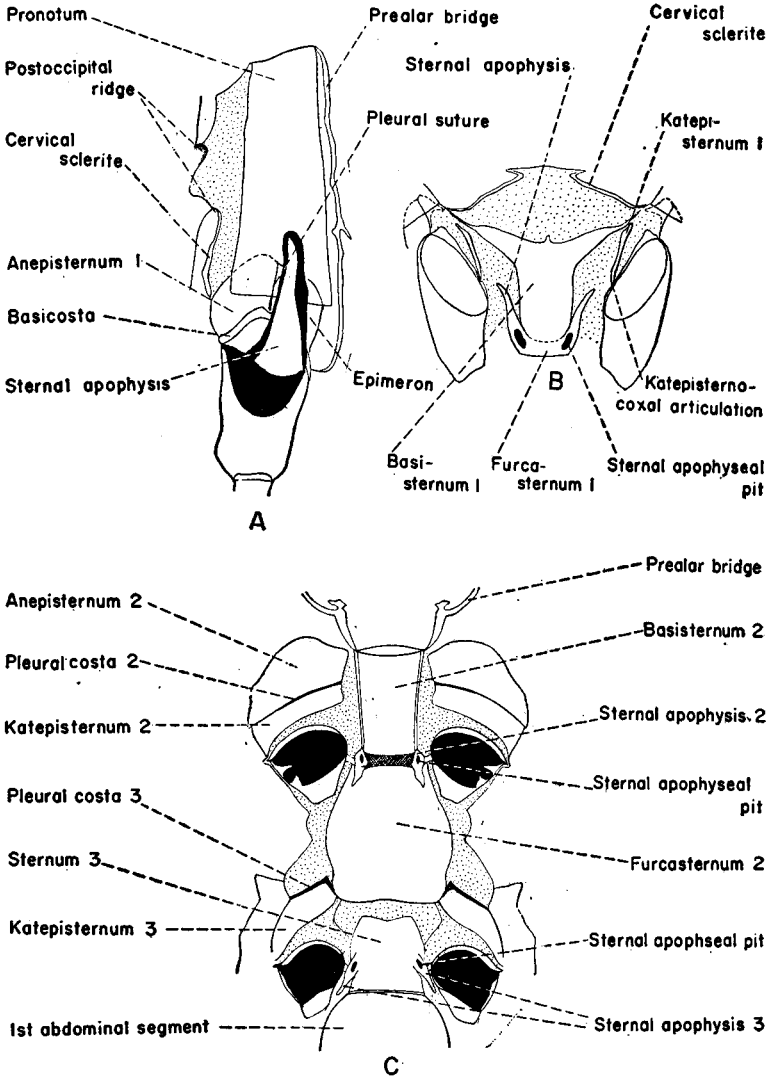

PLATE 1

A. Prothorax, lateral view.
B. Prothorax, ventral structure, seen from above (notum removed).
C. Pterothorax, ventral structure, seen from above (notum removed).

THE MESOTHORAX

(Plate 1, C; Plate 2, A, B)

The mesonotum: The mesonotum is divided into the following regions: The acrotergite, the prescutum, the scutum, the scutellum, and the postnotum. The acrotergite extends latero-ventrally to form the prealar bridge. The prealar bridges are united ventrally foming a complete ring in the anteriormost region of the mesothorax. The prescutum is anteriorly united with the antecosta at the point where the prealar bridge differentiates latero-ventrally, and forms an inflection for the attachment of the dorsal longitudinal muscle. The scutum is the largest part of the mesonotum forming a characteristic round protuberance. The posterior parapsidal suture extends anteriorly to fuse with the prescutal suture. The lateral margin of the scutum bears a narrow and concave anterior notal process to articulate with the first axillary sclerite. The scutellum is marked off from the lateral margin of the scutum by the scuto-scutellar suture which makes a curve upward close to the midline, the suture does not entirely set off the scutellum from the scutum in the mid-dorsal region. Laterally the scutellum bears the posterior notal process. The postnotum is represented by a narrow transverse sclerite lying beneath the scutellum. The large phragma arising from the postnotum projects downwardly into the thoracic cavity and fuses laterally with the mesepimeron; posteriorly the phragma arising from the postnotum is continuous with the phragma arising from the anterior margin of the metanotum. No development of well sclerotized postnotum is seen in this order.

The subcoxa: In the mesothorax of this primitive species two subcoxal rings, namely the ana- and katapleural rings are clearly recognized. The well sclerotized, depressed suture running dorso-posteriorly from the ventral surface in front of the coxal base is apparently the pleural costa of Ferris which demarcates the katapleural ring from the anapleural ring. The pleural costa ventrally reaches near the middle of lateral margin of the basisternum, it dorsally extends into the epimeral region after it meets with the pleural suture arising upwardly from the point of articulation between the subcoxa and the coxa, thus the mesepimeron is divided into the upper anepimeron and lower katepimeron. The pleural suture which Knox (1935) failed to recognize in *Hexagenia recurvata* is fine but distinct in this species. The anapleural ring in the episternal region which is represented by the area above and anterior to the pleural costa is not divided into the upper and lower areas by a suture as in Neuroptera. The basalar sclerite is well marked and located in front of the pleural wing process. It is articulated with the tegula, and the tegula, in turn, is articulated with the humeral plate of the wing. There is no trochantin in the katepisternal region in this order. The katepisternum extends ventrally near to the lateral margin of the basisternum. The subcoxa, both ana- and katapleural rings, is clearly separated from the sternum ventrally. The epimeral region is largely membranous, but the well sclerotized large subalar sclerite is present above the pleural costa. The subalar sclerite is provided with an apodeme inwardly, the presence of this apodeme is externally recognizable

by the presence of a pit. The totally membranized postcoxal bridge borders ventrally the furcasternum. There is, thus, only one point of articulation between the subcoxa and the coxa in the mesothorax.

The ordinary three axillary sclerites are clearly recognizable, each sclerite maintains the typical topographical position in relation to the other axillary sclerites and to the anterior and posterior notal processes as is exemplified by Snodgrass (Principles of insect morphology, p. 219). The first axillary sclerite is articulated with the anterior notal process and the second axillary sclerite. The third axillary sclerite is anteriorly articulated with the second axillary sclerite and posteriorly with the base of the posterior notal process. Each sclerite, however, has no particular relationship with the base of a particular wing vein due to the strong development of the region corresponding to the median plate in other orders of pterygote insects as Grandi (1947) contends. Grandi apparently failed to recognize the presence of the third axillary sclerite in a series of species she examined, and she proposed the names Pseudopteralia 1, 2, 3, referring each to the first, second sclerites and the basal part of the median plate. The present writer will again discuss this problem in the discussion of the musculature associated with these sclerites.

The mesosternum: The mesosternum is clearly divided into two regions, the furcasternum and the basisternum. The division of these two regions is marked by the position of the sternal apophysis and the suture connecting both apophyses. The furcasternum is well developed and concave to receive the subalar-furcasternal muscle. The pleural costa of the metathorax reaches the posterolateral angle of the furcasternum. The basisternum is the region anterior to the sternal apophyses, elongate and much narrower than the furcasternum. The sternal apophyses are well marked externally by small pits (sternal apophyseal pit). The apophysis is connected with the inner margin of the coxa by a weak membrane. The pleural apophysis is absent in this species.

THE METATHORAX

(Plate 1, C; Plate 3, A, B, C)

The metanotum: In the metanotum a recognizable prescutum is not differentiated on the anterior margin. The phragma directly develops from the anterior margin of the scutum, the phragma goes first upwardly then abruptly downwardly to connect with the phragma arising from the postnotum beneath the mesothoracic scutellum. The scutum is not subdivided by ridge or the parapsidial suture as in the mesothorax; the anterior notal process on the lateral margin of the scutum is represented by a small concave sclerite. The scutellum is the region posterior to the scutum, the division between the scutum and the scutellum is rather obliterated. A concave postnotal process arises from the anterior end of the lateral margin of the scutellum. The postnotum is attached on the undersurface of the scutellum and is developed laterally so that it fuses with the epimeron, posteriorly it is inclined and distinctly bordered by the anterior margin of the first abdominal segment.

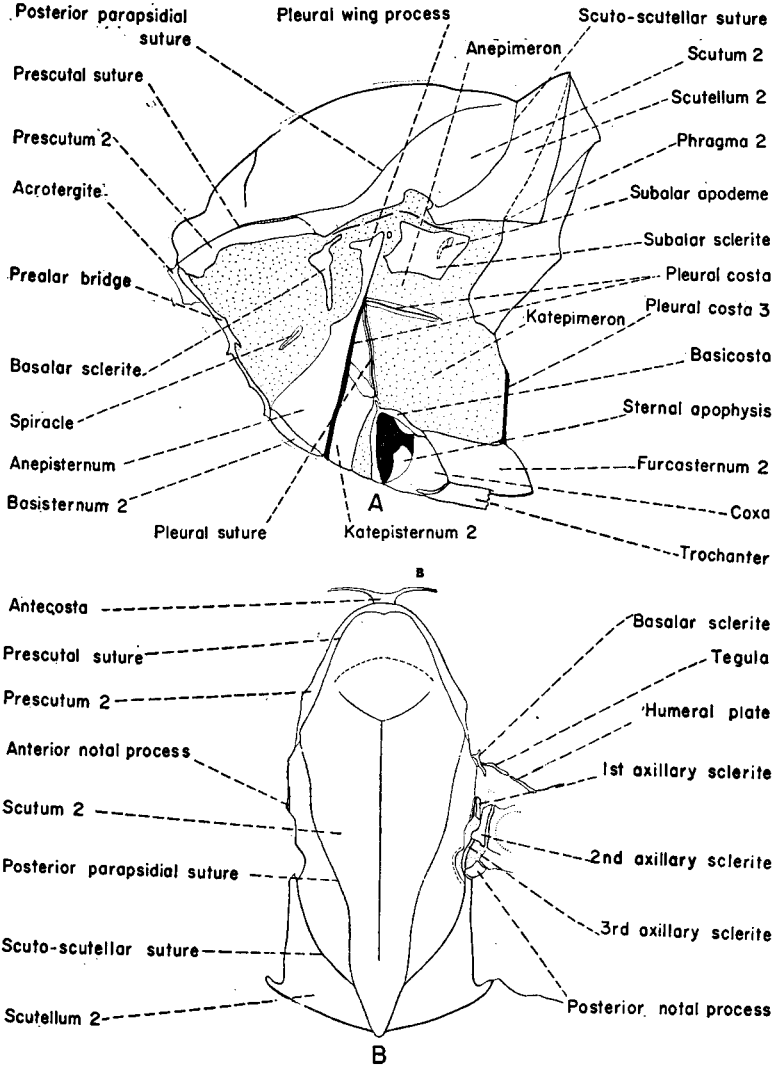

PLATE 2

A. Mesothorax, lateral view.
B. Mesothorax, dorsal view.

The subcoxa: The subcoxal region in the metathorax is characterized by its strong reduction of the anapleural ring. Otherwise the organization of the subcoxal wall is essentially the same as in the mesothorax. The pleural costa ventrally reaches the postero-lateral angle of the mesothoracic furcasternum, dorsally the suture meets with the pleural suture which is represented by a rather weak suture arising from above the coxal condyle. The area bounded by the pleural costa, the pleural suture, and the anterior margin of the coxa is apparently homologous to the katepisternum in the mesothorax. The katepisternum, as in the mesothorax, lacks the trochantin and the area along the anterior coxal margin is widely membranized. The anapleural ring is represented by the membranized region enclosing the spiracle anterior to the pleural costa and the upper part of the pleural suture. There is no development of the postcoxal bridge in the metathorax. The epimeron is indistinguishably fused with the postnotum. There is no sclerotized basalar sclerite in the metathorax. The subalar sclerite is small and oblong, located behind the pleural process. The hind wing is articulated anteriorly with the membranous area in front of the sclerotized antero-lateral angle of the scutum. There is only one well sclerotized axillary sclerite which is apparently homologous to the second axillary sclerite judging from the muscle attachment and from the position in relation to the median plate. This sclerite, however, is articulated with the anterior notal process which is small and concave.

The metasternum. The metasternum is represented by a single plate located posterior to the mesofurcasternum with the intervention of the membranous region between them. There is no clear subdivision of this plate into the basi- and furcasternum. The location of the sternal apophyses are recognizable externally by the presence of the sternal apophyseal pits. The metasternum is posteriorly bordered by the sternum of the first abdominal segment.

THE COXA

The basicoxite in all three thoracic segments is well developed on outer margin of the coxa. There is no development of the secondary meron (Larsen, 1945) in this species. Also there is no conspicuous development of the trochanteral apodeme intruding into the coxa seen in other orders of insects.

THE MUSCULATURE

THE PROTHORAX

(Plate 4, A, B, C; Plate 7, B)

Muscles inserted on the cervical sclerites: There are three muscles that are inserted on the cervical sclerite. The first one is an oblique thick muscle arising from the heavily sclerotized portion of the pronotum and is inserted on the upper tip of the cervical sclerite (1). The second thin muscle connects the upper lateral angle of the postoccipital ridge and the lower tip of the cervical sclerite (2). The third fine muscle extends between the sternal apophysis near tip and the cervical sclerite near tip (3). Knox (1935) shows five muscles attached on the cervical sclerite.

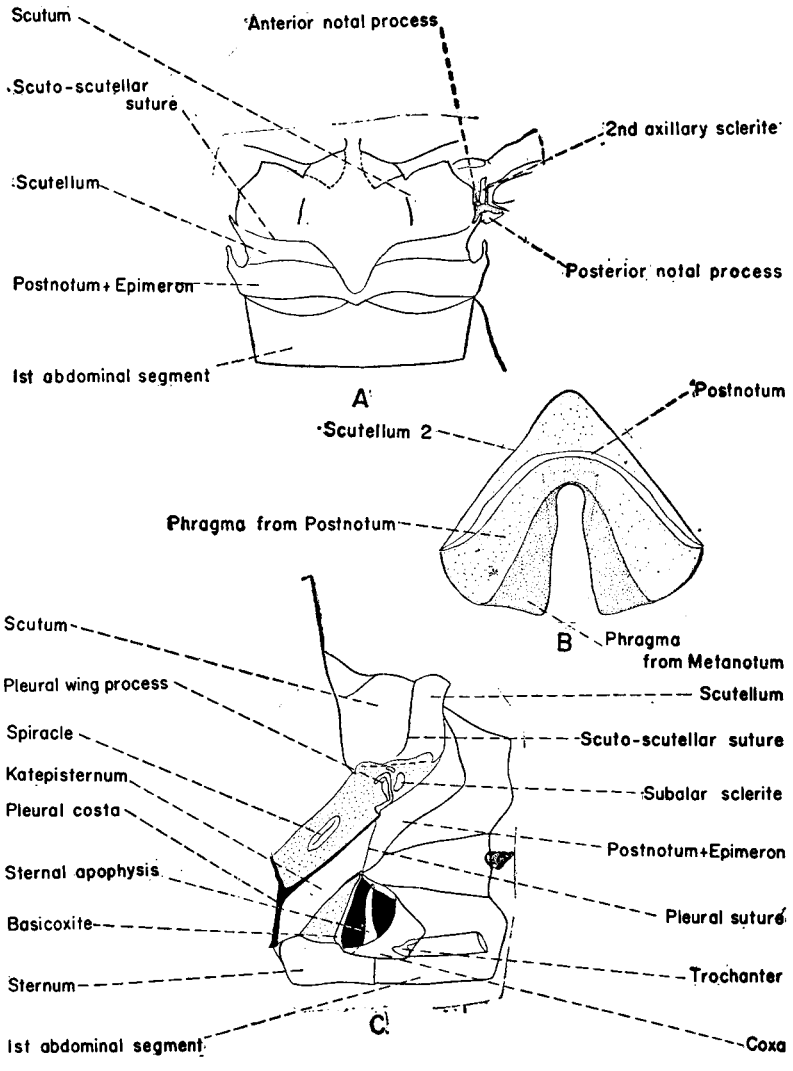

PLATE 3

A. Metathorax, dorsal view.
B. Phragma between the meso- and metathorax.
C. Metathorax, lateral view.

Dorsal muscles: There are seven dorsal muscles. Three of them are attached on the upper lateral angle of the postoccipital ridge, one coming from the pronotum on anterior margin at middle (4), one from the pronotum near posterior margin at middle (5), and the third from the prealar bridge at base (6). The fourth thick and oblique muscle extends between the antecosta of the mesothorax and the pronotum near median longitudinal axis (7). The fifth rather slender muscle extends between the posterior end of the oblong strongly sclerotized region of the pronotum and the prealar bridge above the middle (8). The sixth very short muscle is superposed on the preceding muscle between the prealar bridge and near posterior margin of the pronotum (9). The seventh slender oblique muscle stretches between the prealar bridge above the attachment of the preceding muscle and the anterior margin of the pronotum at middle (10). Both Maki (1938) and Knox (1935) have described only three muscles.

Longitudinal muscles attached on the postoccipital ridge: There is one very fine muscle extending between the upper lateral angle of the postoccipital ridge and the anterior angle of the anepisternum (11). Another fine longitudinal muscle extends between the postoccipital ridge and the antero-lateral margin of the basisternum (12).

Noto-subcoxal muscles: There is one wide but very thin muscle which arises from near the lateral margin of the pronotum and is inserted on the upper margin of the subcoxa including both the episternal and epimeral regions (13). There is another muscle originating from the pronotum below the oblong heavily sclerotized area which is inserted on the anterior margin of the katepisternum (14). Knox (1935) did not show either one of these muscles. Maki's (1938) first tergal abductor of the coxa (16) is probably the noto-katepisternal muscle in this species.

Noto-coxal muscles: Two slender muscles originating from near the lateral margin of the pronotum insert on the posterior basicosta near posterior angle (15, 16). The third slender, oblique muscle originating from above the origin of the preceding muscles are inserted on the basicosta beneath the insertion of the preceding muscles (17). The fourth slender muscle originating from the pronotum anterior to the origin of the preceding muscle (17) goes obliquely cephalad to insert on the anterior angle of the basicosta (18).

Subcoxo-coxal muscle: One rather broad but thin muscle originating from near the upper margin of the anepisternum is inserted on the antero-lateral part of the basicoxite (19).

Trochanteral muscles: One slender muscle originating from near the origin of the posterior noto-coxal muscles is inserted on the anterior tip of the trochanter (20). Another muscle originating from the subcoxa in the epimeral region inserts on the trochanter (21). Another muscle arising from the coxal margin beneath the coxal muscle inserts on the trochanter (22). Maki (1938) does not give the noto-trochanteral muscle.

Sterno-coxal muscles: One fine muscle connects the base of the sternal apophysis and the coxal margin beneath the point of insertion of the

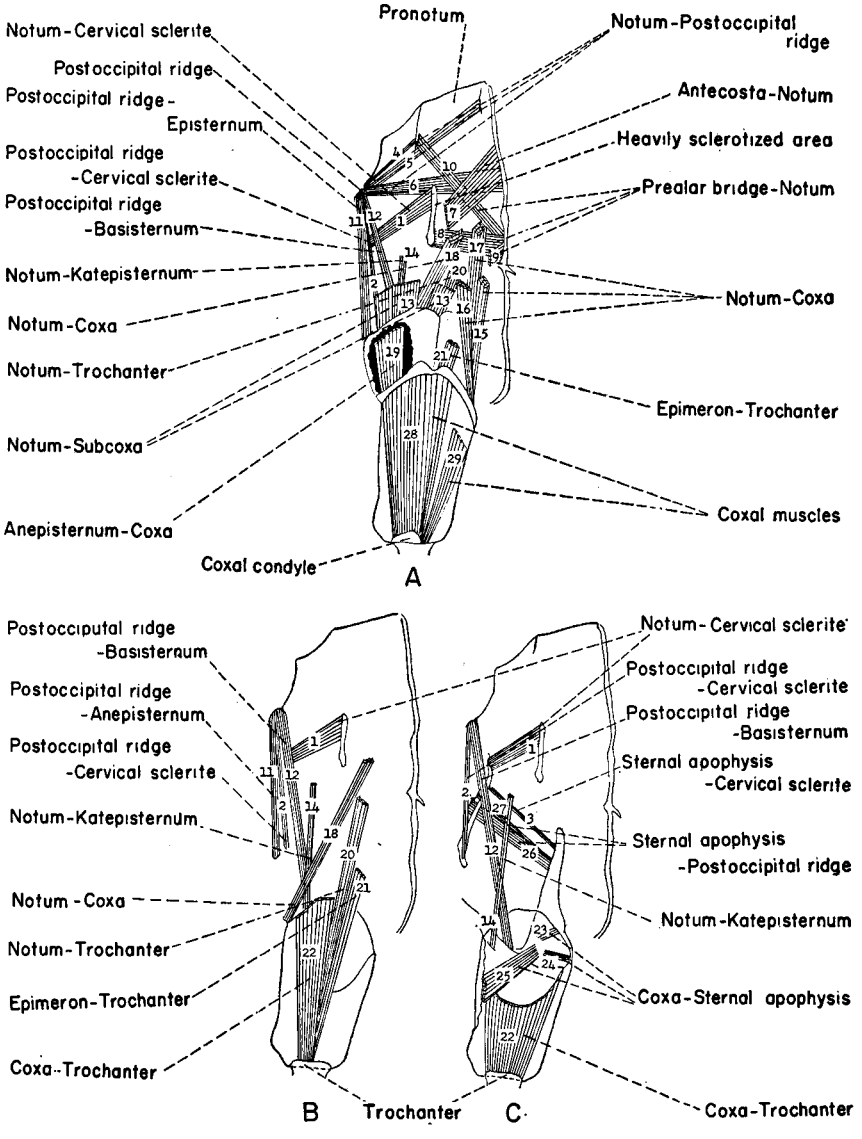

PLATE 4

Muscles of the prothorax.

posterior noto-coxal muscles (23). Another small muscle connects the inner posterior margin of the coxa and the base of the sternal apophysis (24). A rather strong muscle originating from near outer anterior margin of the coxa attaches on the base of the sternal apophysis (25).

Ventral muscles: There are two fine muscles connecting the sternal apophysis and lower postoccipital ridge inside the point of articulation with the cervical sclerite (26, 27). One of them is thicker and superposed on the other.

Coxal muscles: Two muscles arising on the coxal wall insert on the coxal condyle. The anterior one arises from the anterior upper coxal margin (28), and the posterior small one from near the postero-lateral angle of the coxa (29).

THE MESOTHORAX

(Plate 5, A, B; Plate 6, A, B; Plate 7, A, B)

Dorsal muscles (Plate 5, A ,B): The median dorsal muscle is a huge muscle occupying two thirds of the median axis of the mesothorax when viewed laterally (30). The oblique dorsal muscle originates from the scutum in front of the scutoscutellar suture and inserts on the mesophragma (31).

Noto-coxal muscles (Plate 5, A and Plate 6, B): One thick muscle arising from the scutum anterior to the posterior parapsidal suture inserts on the anterior coxal margin (32). Two other vertical muscles arising along the posterior parapsidal suture insert on the posterior coxal margin (33, 34). A fine muscle coming from the scutellum near its lateral margin is continuous with the connective tissue arising from the inner posterior angle of the coxa (35).

Pleural costa-coxal (Katapleuro-coxal) muscle (Plate 5, B): The katapleuro-coxal muscle arises from the pleural costa and inserts on the anterior basicoxite (36).

Subalar muscles (Plate 5, B and Plate 6, B): There are three muscles originating from the subalar sclerite. The subalar-coxal muscle arises from the anterior portion of the subalar sclerite and inserts on the posterior basicoxa (37). The subalar furcasternal muscle is a robust muscle arising from almost the entire surface of the subalar sclerite. It is twisted posteriorly and is inserted ventrally practically on the entire surface of the furcasternum (38). The third muscle is fine, coming from the apodeme of the inner wall of the subalar sclerite and inserts on the tip of the sternal apophysis (39). Dürken (1907) describes a muscle between the apodeme of the subalar sclerite (?) (Zapfen des Epimerum) and the mesonotum in *Ephemerella ignita.*

Basalar muscles (Plate 6, B): There are three muscles that are attached on the basalar sclerite. One muscle goes obliquely between the upper margin of the basalar sclerite and the upper anterior margin of the prothoracic sternal apophysis (40). Another slender muscle connects the lower tip of the basalar sclerite and the prothoracic sternal apophysis on posterior margin near tip (41). The last muscle is a fine muscle coming from the

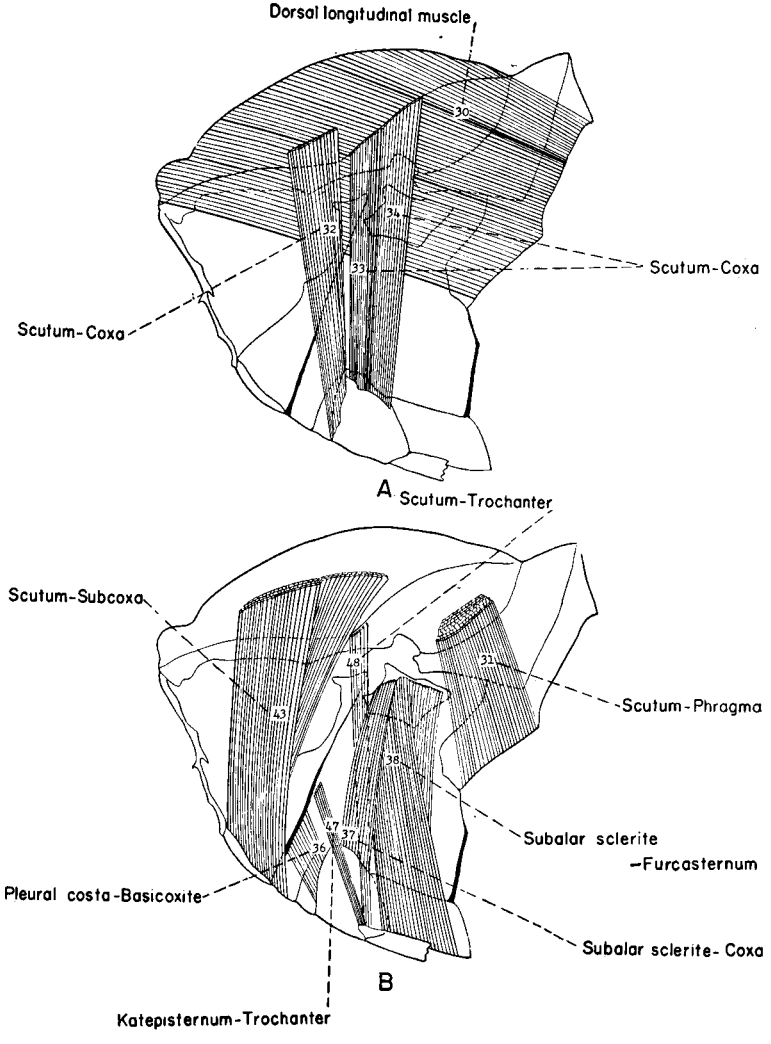

PLATE 5

Muscles of the mesothorax.

pleural wing process and attaches on the basalar sclerite at the point where this sclerite is articulated with the tegula (42).

The first two muscles are Grandi's *muscolo prosterno-basalare dorsale* and *muscolo prosterno-basalare ventrale*. These two muscles seem to be different in the ventral point of attachment in different species. Grandi (1947) says, *"Essi si dirigono parallelemente in avanti e raggiungono la regione posteriore laterale del prosterno ove si attacano a due piccole prominenze piu o meno sclerificate e distinte nelle diverse specie."* Knox (1935) describes the homologous muscle as attaching ventrally on the furcilla of the prothoracic postfurcisternum. Maki (1938) says that they are attached on the antero-lateral corner of the sternum. The last mentioned muscle (42) is very probably Grandi's *muscolo pleurocondilo-scutale*. If so, this muscle also shifts its dorsal point of attachment in different species within the same order. Maki (1938) describes the basalar-coxal muscle. The present writer did not find this muscle.

Noto-subcoxal muscles (Plate 5, B and Plate 6, B): A very robust muscle arising from the lateral area of the scutum before the posterior parapsidial suture inserts on the ventral margin of the anepisternum and the katepisternum (43). The second muscle is a slender one connecting obliquely the lateral margin of the sclerotized part of the anepisternum and the prescutum near the anterior end (44). The third muscle is also a slender muscle connecting the anterior margin of the anepisternum above the attachment of the preceding muscle and the scutum anterior to the anterior notal process (45).

The first muscle (43) is usually called the anterior tergo-sternal muscle. The primitive point of ventral attachment of this muscle in insects was already discussed by Matsuda (1956), and it was considered to be secondary when this muscle is attached to the basisternum. Knox's data (1935) on the ventral attachment of this muscle is obscure. Judging from his description and figures of mesosternum (Plate 23, fig. 2), the area he designates as the ventral point of insertion is not necessarily the basisternum. The same thing happened when Börner (1908) pointed out the imprecision of Dürken's data as to the ventral attachment of this muscle. Börner confirmed that this muscle was the tergo-subcoxal muscle (Noto-subcoxal muscle). Maki gives two anterior tergo-sternal muscles and he says that their ventral point of attachment is the sternum, but as the present writer (1956) already pointed out and cautioned, Maki very often was confused as to the morphological assignment of the ventral sclerites when he wrote his big monograph. Anyhow this muscle is clearly inserted on the ventral end of the subcoxa, at least, in *Siphlonurus columbianus*. Knox (1935) does not describe the second muscle (44).

Trochanteral muscles (Plate 5, B and Plate 7, A): A slender muscle arising from the katepisternum anterior to the point of union between the pleural costa and the pleural suture inserts on the tip of the trochanter (47). Noto-trochanteral muscle originates from the scutellum near lateral margin a little behind the posterior parapsidal suture (48). One muscle

arising along the inner coxal margin inserts on the apical region of the trochanter (49).

Knox (1935) describes one muscle from the basalar sclerite to the trochanter. Dürken (1907) describes a muscle from the sternal apophysis to the postero-inner margin of the trochanter in both *Centroptilum* and *Ephemerella.* These muscles were not found in *Siphlonurus columbianus.*

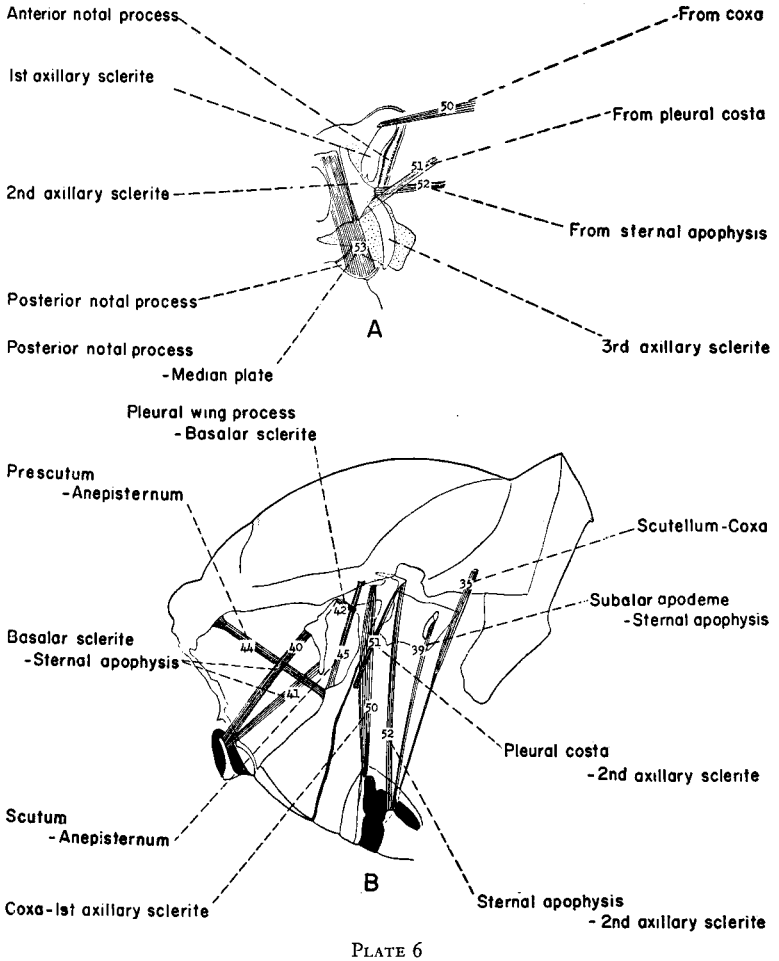

PLATE 6

A. Muscles inserted on the axillary sclerites (Mesothorax).
B. Muscles of the mesothorax.

Muscles of the axillary sclerites (Plate 6, A, B): The first one is a cylindrical muscle extending between the first axillary sclerite and the coxal process (50). Two muscles are attached on the second axillary sclerite. One of them extends between the pleural costa below the point of union with the pleural suture and the posterior margin of the second axillary sclerite where the third axillary sclerite is articulated (51). The other muscle extends between the second axillary sclerite at inner posterior angle and the tip of the sternal apophysis (52). There is a fourth muscle that stretches between the posterior notal process and the base of the median plate (53).

The first muscle (50) seems to vary in its dorsal point of attachment. Knox (1935) says that it dorsally attaches on the basalar sclerite. Maki (1938) found it inserted on the anterior portion of the first axillary sclerite. Grandi (1947) says, "*. . . si inserisce da una parte al meron e dall'altra al limite fra scuto e regione ascellare, davanti all'inflessione ascellare.*"

As to the third muscle extending between the sternal apophysis and the second axillary sclerite (52) Grandi says, "*. . . inserzione dorsale sia il margine dello scuto, subito dietro l'inflessione ascellare, sia il secundo pseudopterale.*"

No previous workers, including Grandi (1947) who has worked on this particular problem in five families of Ephemeroptera, found the muscle extending from the pleural costa to the posterior margin of the second axillary sclerite where the third axillary sclerite is articulated (51). This muscle shows a striking similarity to the wing flexor muscle in other pterygote insects which usually inserts on the third axillary sclerite.

Coxo-sternal muscles (Plate 7, A): Three small muscles arising on the coxal wall insert on the sternal apophysis. One arising from near posterior angle of the coxa inserts on the apical portion of the sternal apophysis (54). One muscle arising from beneath the coxal process inserts on the apex of the sternal apophysis (55). One muscle from the inner anterior angle of the coxa inserts on the basal region of the sternal apophysis (56).

Ventral muscles (Plate 7, A, B): The ventral longitudinal muscle is a slender muscle connecting the prothoracic sternal apophysis and the mesothoracic sternal apophysis at base (57). The ventral transverse muscle is thickened medially. It arises on each side from the outer posterior coxal wall and connects both legs across the sternum in the area of the mesothoracic ganglion (58). Another transverse muscle is fine, connecting the inner margins of the sternal apophyses at their bases (59).

No previous workers have described the transverse muscle that connects the two legs (58).

Coxal muscles (Plate 7, A): Three muscles arising on the coxal wall insert on the coxal condyle. The anterior one arises from the anterior margin (60), the median one from the upper coxal margin (61), and the posterior one from near the postero-lateral angle of the coxa (62).

THE METATHORAX

(Plate 7, B; Plate 8, A, B)

Dorsal muscles (Plate 7, B): The median dorsal muscle is a thick

muscle extending between the mesophragma and the antecosta of the metathorax (63). The dorsal oblique muscle arises from the scutum in front of the scuto-scutellar suture and is inserted on the lateral extension of the postnotum (64).

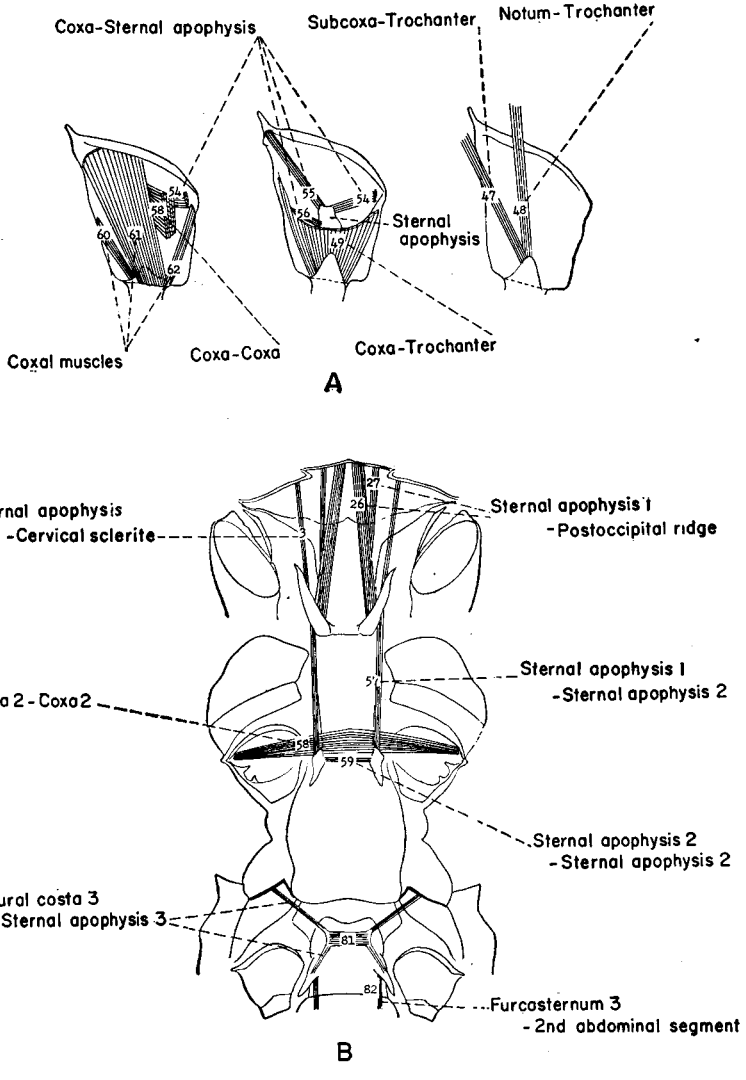

PLATE 7

A. Muscles of mid coxa and trochanter.
B. Ventral muscles.

Noto-coxal muscles (Plate 8, A, B): One muscle arising from near antero-lateral angle of the scutum inserts on the anterior basicosta beneath the insertion of the katapleuro-coxal muscle (65). Another thick muscle originating from near postero-lateral angle of the scutum before the scuto-scutellar suture inserts on the posterior coxal rim (66). A third fine muscle originating on the lateral region of the scutellum right behind the scuto-scutellar suture goes down to connect with the connective tissue arising from the inner posterior angle of the coxa (67).

Pleural costal-coxal (Katapleuro-coxal) muscle: One flat, rather broad muscle originating along the pleural costa inserts on the anterior basi-coxite (68).

Subalar muscles (Plate 8, A, B): There is one muscle going from the subalar sclerite to the basicoxa behind the coxal process above partly on the attachment of the posterior noto-coxal muscle (69). Another muscle homologous to the muscle between the subalar apodeme and the sternal apophysis in the mesothorax arises from the posterior region of the posterior notal process (70). This muscle, on its way down, attaches the anterior margin of the first pleural abdominal segment.

Maki's subalar-sternal muscle ventrally attaches to the posterior sternal region fused with the first abdominal segment. Maki (1938) does not show the subalar-coxal muscle. The homologous muscle arises from the unsclerotized chitin between the epimeron and the scutum in *Hexagenia recurvata* according to Knox (1935).

Noto-subcoxal muscles (Plate 8, A, B): One muscle originating from the antero-lateral angle of the scutum inserts along the ventral margin of the sclerotized katepisternum (71). One small muscle arising from the membrane anterior to the origin of the cylindrical muscle between the first axillary sclerite and the coxal process goes to the antero-lateral angle of the scutum (72). A paired exceedingly fine muscle between the membrane near the spiracle goes to the antero-lateral angle of the scutum (73).

Knox (1935) says that his Dvm 1 (71) attaches ventrally on the antero-lateral portion of the furcasternum. Both Maki (1938) and Knox (1935) do not give the last two muscles.

Trochanteral muscles (Plate 8, A, B): The noto-trochanteral muscle originates from the lateral margin of the scutum at middle and inserts on the trochanter intruding into the coxa (74). The subcoxo-trochanteral muscle originates along the pleural costa between the origin of pleural costa-coxal muscle and the point of union with the pleural suture and inserts on the trochanter (75).

Dürken describes a sternal depressor of the trochanter in both *Centroptilum* and *Ephemerella.* This muscle was not found in *Siphlonurus columbianus.*

Axillary muscles (Plate 8, A, B): From the posterior angle of the second axillary sclerite one fine muscle extends obliquely and is attached on the episternum near the pleural costa at the point of union with the pleural suture (76). Another muscle extends vertically and is inserted on

the tip of the sternal apophysis (77). A third subcylindrical muscle extends from the wing base just anterior to the second axillary sclerite to the coxal process (78).

Knox (1935) describes a muscle between the pleuron anterior to the pleural-coxal articulation and the lateral oblique margin of the scutum which is anterior to the notal wing process, and homologizes this muscle with the dorsal basalar-sternal muscle in the mesothorax. Knox (1935)

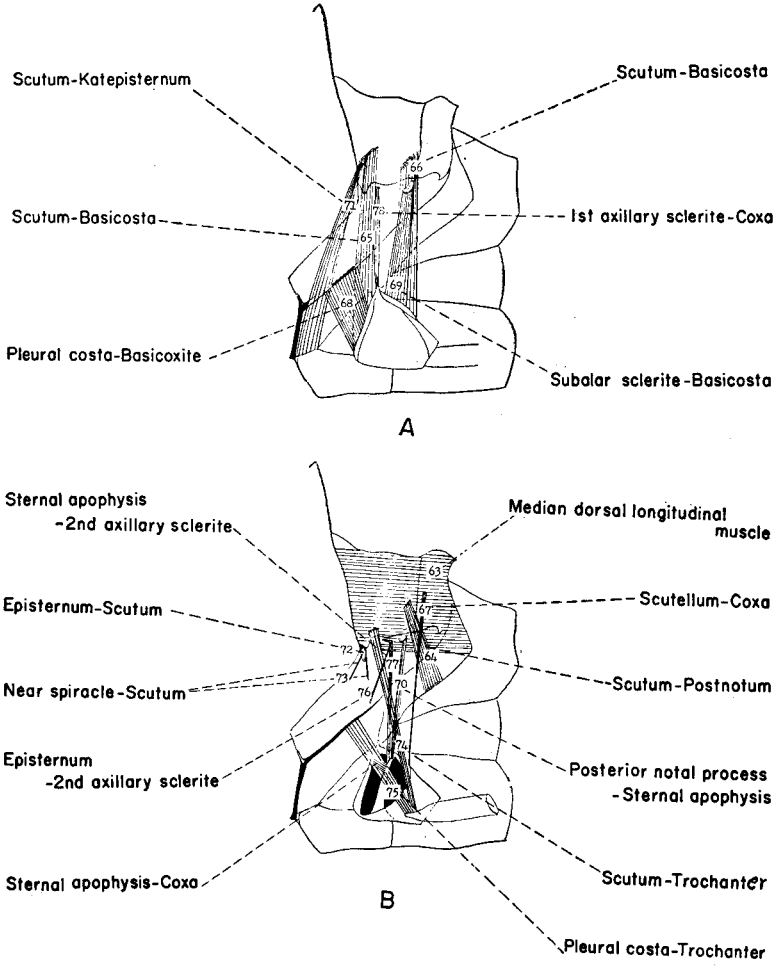

PLATE 8

Muscles of the metathorax.

says that the last muscle (78) attaches on the anterior notal process. This muscle is apparently homologous to the muscle between the first axillary sclerite and the coxal process in the mesothorax of *Siphlonurus columbianus*. Neither Knox (1935) nor Maki (1938) described the muscle from the episternum to the second axillary sclerite in *Siphlonurus columbianus*.

Sternocoxal muscles: Three muscles arising from within the coxa attach on the base of the sternal apophysis as in the proleg.

Transverse muscles (Plate 7, B): A fine transverse muscle coming from the lower portion of the pleural costa and the sternal apophysis is connected with the thicker muscle between the bases of the sternal apophyses.

Ventral longitudinal muscle (Plate 7, B): The ventral longitudinal muscle is thin and connects the posterior margin of the metathoracic sternal apophysis and the antecosta of the second sternal abdominal segment.

Maki (1938) describes a ventral longitudinal muscle connecting the meso- and metathoracic sternal apophyses. Knox (1935) describes a wide muscle attaching to the evagination of the basicoxite at the pleural-coxal articulation which extends caudad to insert to the anterior ridge of the first abdominal segment. The present writer did not see the above two muscles in *Siphlonurus columbianus*.

TABLE I. Thoracic dorso-ventral muscles in *Siphlonurus columbianus* McDunnough

	Prothorax	Mesothorax	Metathorax
Noto-subcoxal muscles			
Noto-katepisternal	1	1	1
Noto-anepisternal	1	2	2
Noto-coxal muscles			
Anterior noto-coxal	1	1	1
Posterior noto-coxal	3	3	2
Subcoxo-coxal muscles			
Katapleuro-coxal	1*	1	1
Subalar-coxal	0	1	1
Subalar-sternal muscle	0	2	1**
Basalar-sternal muscles	0(2)	2	0
Trochanteral muscles			
Noto-trochanteral	1	1	1
Katapleuro-trochanteral	1	1	1
Axillary muscles			
First axillary-coxal	0	1	1
Second axillary-sternal	0	1	1
Second axillary-subcoxal	0	1	1

* Originates from the episternum
** Dorsal point of attachment is posterior notal process

DISCUSSION ON THE THORACIC MUSCULATURE OF THE ORDER EPHEMEROPTERA

From the above description of the thoracic dorso-ventral muscles and the table showing the dorso-ventral muscles of *Siphlonurus columbianus* McDunnough some peculiarities of the musculature are noted.

First, the occurrence in this primitive species *Siphlonurus columbianus* McDunnough of the axillary sclerite which can be homologized with the third axillary sclerite in other orders of pterygote insects and of a muscle inserted on the posterior margin of the second axillary sclerite where the third axillary sclerite articulated to it precludes the acceptance of Grandi's contention (1947) on its face value that the axillary sclerites in this order are not homologous to those occurring in other orders of pterygote insects. The absence of the third axillary sclerite in many other species studied by Grandi is apparently secondary. The occurrence of the muscle here questioned is apparently correlated with the occurrence of the third axillary sclerite. This muscle, though attached to the second axillary sclerite in this species, may be regarded as the muscle of the third axillary sclerite judging from the correlation in the occurrence between the muscle and the third axillary sclerite and the point of attachment of the muscle to the second axillary sclerite. The peculiarity of the axillary sclerites in Ephemeroptera is the loss of relationship between each particular sclerite and the base of each particular vein due to strong development of the area corresponding to the median plate in other pterygote orders.

In connection with the axillary sclerites attention should be directed to the fact that the dorsal points of attachment of axillary muscles which are apparently functionally the point of insertion are subject to specific differences within certain limits. It is generally believed that the origin of the muscle tends to shift, but the above example clearly indicates that the insertion also tends to shift as Matsuda contended (1956). It would be also true of some other muscles attached to the other sclerites beneath the lateral margin of the notum although we are not as sure about their function as we are about the axillary muscles.

The second axillary muscle arising from the sternal apophysis is peculiar to this order.

Another peculiarity of the mayfly thoracic musculature is the presence of the sterno-subalar muscle. No other pterygote insect orders are known to have this muscle. Maki (1938), however, contends that the subalar sclerite in winged insects probably belongs to the tergal region based on the observation of postembryonic development of the coxo-subalar muscle in *Leucophaea surinamensis* L. (Blattidae) and *Locusta migratoria manilensis* (Acridiidae). If so, this muscle can be homologized with the posterior noto-sternal muscle in other pterygote insects. Knox's account (1935) on this muscle in the nymph, however, shows that the subalar sclerite is subcoxal in origin. The occurrence of the huge furcasterno-subalar muscle only in the mesothorax is also a striking feature of the dorso-ventral musculature in the mayfly thorax.

The anterior noto-coxal muscle is known to occur in Ephemeroptera, Odonata, and higher Lepidoptera (Maki, 1938). This muscle is apparently homologous with the noto-trochantinal muscle in other pterygote insects. The occurrence of the anterior noto-coxal muscle is said to be associated with the loss of a visible trochantin (Snodgrass, 1935, Larsén, 1948). This is true of this order.

The sterno-basalar muscle which extends between the prothoracic sternal apophysis and the mesothoracic basalar sclerite in *Siphlonurus columbianus* or area posterior to the prothoracic sternal apophysis and the mesothoracic basalar sclerite in other species of Ephemeroptera are homologous with the sterno-pleural intersegmental pair of muscles of *Locusta migratoria* (Albrecht, 1953). This muscle seems to be common in the orthopteroid insects. In Neuroptera the muscle between the anterior part of the mesothoracic anepisternum and the prothoracic spina in *Agulla adnixa* is probably homologous to this muscle.

The trochanteral muscles occur in the notum and subcoxa as in most other orders. There is no deviation as far as these muscles are concerned.

The basalar-coxal muscle is absent in *Siphlonurus columbianus* although Maki (1938) describes this muscle in *Ecdyonurus hyalinus.*

As already noted, the posterior noto-coxal muscle which attaches on the meral wall in other orders of pterygote insects attaches on the posterior basicosta. The subalar coxal muscle is present in both the meso- and metathorax.

The noto-subcoxal muscle which is usually called the anterior tergosternal muscle was found to be present in all thoracic segments in *Siphlonurus columbianus,* and it was found that this muscle retains its primitive point of insertion without shifting into the sternal region as was already pointed out by Börner (1908).

The katapleuro-coxal muscle originates from the pleural costa of Ferris, the point suggested hypothetically as the primitive point of origin of this muscle in pterygote insects by Matsuda (1956).

The occurrence of a robust transverse muscle which connects both coxae in the mesothorax seems to be, as far as known, peculiar to *Siphlonurus columbianus.* No such muscle in any order is described in Maki's monograph (1938).

The absence of the ventral longitudinal muscle between the meso- and metathoracic sternal apophyses is also characteristic to this order of insects although it was found to occur in *Ecdyonurus hyalinus* by Maki (1938).

SUMMARY

1. The external structure and the musculature of the thorax of a mayfly *Siphlonurus columbianus* were studied.

2. It was found that the subcoxal rings are clearly indicated in the pleuro-sternal region of this species. The pleural costa of Ferris (1939) is represented by a strongly sclerotized depressed costa and it extends posteriorly into the epimeral region.

3. Among the dorso-ventral muscles the presence of the sterno-subalar muscle is most characteristic of the order Ephemeroptera. The points of insertion of the posterior noto-coxal muscle and the noto-subcoxal muscle (anterior tergo-sternal muscle) and the point of origin of the katapleuro-coxal muscle fit the "Hypothetical primitive dorso-ventral musculature of a ptero-thoracic segment" postulated by Matsuda (1956).

4. The presence of three distinct axillary sclerites homologous to those in other pterygote orders and the associated musculature in this primitive species *(Siphlonurus columbianus)* preclude the acceptance of Grandi's concept "Pseudopteralia" (1947) appropriated to this region of the order Ephemeroptera on its face value.

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