

## The comparative morphology of the thorax of selected genera of the *Leptophlebiidae* (Ephemeroptera)\*

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(With 55 figures in the text)

The external thoracic morphology of the nymphs and imagos and the thoracic muscles of the imagos of *Leptophlebia pacifica* are described. Descriptions of the imaginal thoracic exoskeleton are given for five other genera of the *Leptophlebiidae*. A comparison of homologous structures in the imaginal thoraces of these genera and the use of these structures in understanding the taxonomy and phylogeny of the family are discussed.

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### Introduction

The higher classification and phylogeny of the Ephemeroptera are not well understood. Several research laboratories in North America, Europe and Australia are engaged in extensive study concerning these problems on a worldwide basis. The basic purpose of such phylogenetic and classificatory work is to lay a firm foundation for other workers to study in detail regional mayfly faunas. While such a foundation is necessary to gain any level of consistency among regional studies, the task has largely been ignored until recently because the large, worldwide, collections needed for such comparative work have mostly been unavailable.

One of the most diversified families of mayflies is the family Leptophlebiidae which comprises nearly one-half of the world mayfly fauna. This insect family is nearly cosmopolitan in nature, except for some smaller oceanic islands, and is represented by several to many genera in most parts of the world.

Peters & Edmunds (1964) published on the generic classification and phylogeny of the Ethiopian Leptophlebiidae. Later Peters & Edmunds (1970) studied the generic classification and phylogeny of the Eastern Hemisphere Leptophlebiidae. Their work now continues on the generic classification and phylogeny of the Leptophlebiidae in other parts of the world.

Landa (1948, 1959, 1969) has described the comparative internal anatomy of various Ephemeroptera. He has especially studied the tracheal and nervous systems, and the Malpighian tubules. Preliminary data as indicated by Landa (1969) suggest that such research on the internal anatomy might be of use in understanding the phylogeny and relationships of the Leptophlebiidae.

After examining many genera of the Leptophlebiidae, Peters (1966) proposed that the thoraces of the imagos and nymphs, which display a great diversity in structural patterns, should be examined because the thorax could be of significance in further understanding the phylogeny and relationships of the genera. Little research has been conducted on the mayfly thorax, and none has hitherto been used for phylogenetic interpretation. The purpose of the present study is to establish the basic morphology of the leptophlebiid thorax, and based on the study of selected genera, to establish whether such data can be used to further understand the phylogeny and relationships of the leptophlebiid genera. While those genera selected and included for this study are from widely different phyletic lines, detailed studies of some closely related genera have also been completed but are not

included herein. Study of the thoraces of other genera of the Leptophlebiidae is planned for the future.

### Materials and methods

All specimens used in this study were preserved in 75% to 95% alcohol and dissected under a stereoscope microscope. In examining the exoskeletal thoracic structures of the nymphs and imagos, the abdomen was cut off at the second segment and the legs were cut off at the distal end of the coxa. The specimens were boiled in a 10% KOH solution for about 10 min until the soft tissues were dissolved. They were then rinsed in distilled water and further dissected in 75% alcohol. In case of very small and delicate specimens, such as *Isca (Tanycola) serendiba*, the muscles were destroyed by keeping the specimens in 10% KOH at room temperature for 12 h.

In order to study the tergal and sternal sclerites, a frontal section was made across the pleura, producing a tergal and a sternal half. To study the pleural sclerites, a median sagittal section was made. Weakly sclerotized specimens were stained with acid fuchsin.

Permanent mounts were prepared by transferring the prepared dissections directly from 75% alcohol to Canada balsam dissolved in cellosolve (ethylene glycol mono ethyl ether).

In order to study the axillary sclerites a specimen was boiled in 10% KOH to dissolve the soft tissues. The tergal part near the axillary regions and the upper half of the wings were teased off. The specimen was then stained in acid fuchsin and mounted in the xylene-free balsam diluted with cellosolve. Excessive stain was washed in 75% alcohol before mounting.

Musculature studies were completed by sectioning the specimen sagittally. The halves were then embedded in beeswax and dissected in 75% alcohol.

## The thoracic morphology of *Leptophlebia pacifica*

### *Imagos*

#### *The cervical region*

*Cervical region* (Figs 43 and 50). The cervical sclerites are a pair of slender sclerites, curving progressively ventrad towards the posterior ends. Anteriorly they articulate with the lateroventral edges of the postoccipital ridges or the occipital condyles. Posteriorly they articulate with the lateral ends of the basisternum and the proepisterna.

#### *The tergum*

*Pronotum* (Figs 24 and 25). The pronotum is H-shaped, with the anteromedian and posteromedian margins curving inwardly. Medially the short median notal suture divides the pronotum into the right and left halves. Near the anterosubmedian margin, paired concave depressions occur which several prothoracic muscles are attached internally. The pronotum extends laterally and ventrally to cover a greater part of the propleuron. The subanterior edge inflects to form the antecostal suture. Internally this suture forms a ridge to which several prothoracic muscles are attached. Anterior to this suture is the acrotergite. The pro- and mesonotum are connected by a membranous area.

*Mesonotum* (Figs 24 and 25). The mesonotum consists of the following regions: the acrotergite, the prescutum, the scutum, the scutellum, and the postnotum. The acrotergite is a narrow region separated from the scutum by the antecostal suture. This suture forms an inflection giving rise to the anterior phragmata. Laterally, the acrotergite extends ventrally to fuse with the presternite of the mesosternum to form a complete ring, the prealar bridge, at the anterior end of the mesothorax. On each side, the prescutum is separated from the scutum by the membranous prescutal suture. Anteriorly the prescutum

is fused with the acrotergite and posteriorly it articulates with the posterior basalar sclerite and the scutum. The scutum is a large shield-like structure which internally houses the large dorsal longitudinal muscles. On each side, the anterolateral margin is bounded by a deep notal furrow. Posterior to the notal furrow the lateral margin expands outwardly to form the anterior notal wing process, bearing an internal apodeme at the point where the first axillary sclerite articulates with it. Posterior to the anterior notal wing process the lateral margin notches inwardly. The scutal surface is bisected by the median notal suture. Lateral to this suture are the paired inner and outer parapsidal sutures. The scutum is separated from the scutellum by the scutoscutellar suture, except they fuse medially. In each of the fore wing axillary regions there are two distinct axillary sclerites. The first axillary sclerite articulates anteriorly with the posterior basalar sclerite, laterally with the anterior notal wing process, and posteriorly with the second axillary sclerite. The second axillary sclerite articulates with the first axillary sclerites and the median plate (Fig. 31). In addition to these two sclerites in the axillary region there is a third sclerite at the posterior part of the wing base lateral to the scutellum. In specimens that have not been treated with KOH, this sclerite is observed to lie close to the dorsal part of the postalar bridge. The scutellum forms the posterior hump on the mesotergal surface; laterally it projects forward on both sides to bear the posterior notal wing processes at its apices. The posterior margin of the scutellum bears the corrugated hind margins of the fore wings. The postnotum consists of the precosta and the antecosta. The precosta is seen as a transverse sclerite beneath the mesothoracic notum; laterally it bears two triangular projections which lie close beneath the scutellum. Ventral to the precosta is the antecosta which fuses with the infolding of the anterior scutum of the metathorax to form the posterior phragmata. Laterally the antecosta is fused with the postalar bridges of the mesopleura.

*Metanotum* (Figs 24 and 25). In the metanotum the acrotergite and prescutum are absent. Anteriorly, the scutum fuses with the antecosta of the mesothorax to form the posterior phragmata of the thorax. The tergal surface is incompletely divided by a membranous scutoscutellar suture into the anterior scutum, and the posterior scutellum. On each side, the anterior notal wing process forms a small apodeme on the mid-lateral margin of the scutum. Posterior to this is the posterior notal wing process which also bears a small apodeme. Two axillary sclerites are found in the base of the hind wings. The first axillary sclerite is weakly sclerotized. Laterally it articulates with the anterior notal wing process and posteriorly with the second axillary sclerite. The second axillary sclerite is more distinct. It articulates with the posterior notal wing process on one side and the median plate on the other (Fig. 37). Each anterolateral angle of the scutellum forms a projection with which the median plate articulates. The posterior margin of the scutellum bears the posterior edge of the hind wings. The postnotum is similar to that of the mesothorax. It consists of the precosta which also forms two triangular lobes. The precosta attaches closely beneath the scutellum. The antecosta is bisected medially by a short, longitudinal suture and laterally fuses with the epimera of the metathoracic pleura. Posteriorly, the antecosta is fused to the first abdominal tergum.

### *The pleuron*

*Propleuron* (Figs 42 and 43). The propleuron on each side is divided by the pleural suture into the anterior episternum and the posterior epimeron. Dorsal to the pleural

suture the pleural wall forms an internal apodeme. Whether this apodeme is homologous with the pleural apophysis of other insects is yet undetermined. Anteriorly, the episternum becomes a narrow piece of sclerite and fuses with the anterolateral arm of the probasisternum. The epimeron is a simple crescent-shaped sclerite. The degree of sclerotization of the epimeron varies between individuals of the species.

*Mesopleuron* (Figs 42 and 43). On each side of the mesopleuron in the anterior membranous area are the following structures: the anterior basalar sclerite, the posterior basalar sclerite, two spiracular sclerites or peritremes, and the mesothoracic spiracle. The anterior basalar sclerite is triangular in shape; no muscles are attached to it. This sclerite is characteristic of the genus *Leptophlebia*. It is absent from all the other genera of Leptophlebiidae studied and also from primitive genera such as *Siphonurus* (Siphonuridae). It is possible that the anterior basalar sclerite is secondarily formed and the exact function of this sclerite is not known. The posterior basalar sclerite is irregular in shape and consists of three arms: slender anterodorsal and posterodorsal arms and a thicker ventral arm. The anterodorsal arm articulates with the prescutum and forms a small apodeme onto which the basalar-pleural arm muscles are attached. The posterodorsal arm forms the tegula which articulates with the humeral plate of the fore wings. The ventral arm is C-shaped and onto it is attached a sternal-pleural muscle. Close to the anterior or mesothoracic spiracle are two spiracular sclerites or peritremes. The mesopleural wall is divided by the pleural suture into the anterior episternum and the posterior epimeron. The pleural suture does not extend into the pleural arm. The precoxal suture is a deep furrow which divides the episternum into the anepisternum and the katepisternum. Dorsal to the precoxal suture is a small apodeme on the pleural arm. Basally the episternum is fused with the basisternum of the mesosternum. In the epimeron, the precoxal suture is short and delimits a narrow anepimeron and a wider katepimeron. Ventrally, the katepimeron fuses with the postcoxal bridge which in turn fuses with the furcasternum of the mesosternum. Posteriorly, the epimeron fuses with the postalar bridge. In the posterodorsal membranous area of the mesopleuron are the anterior and posterior subalar sclerites. The larger anterior subalar sclerite is rectangular in shape and is cut diagonally by a suture. At the posterodorsal end of this suture is the well developed posterior subalar apodeme onto which the sternal apophysis-anterior subalar and furcasternum-anterior subalar sclerite muscles are attached. The anterior margin of the anterior subalar sclerite is folded ventrally to form a smaller apodeme of which two muscles extend onto the coxal rim. The smaller posterior subalar sclerite is posterodorsal in position to the larger anterior subalar sclerite. When the fore wings extend horizontally the posterior subalar sclerite rests partly on the postalar bridge and partly on the anterior subalar sclerite.

*Metapleuron* (Figs 42 and 43). On each side the metapleural suture is well developed. Anterior to this suture is the episternum. The precoxal suture is distinct and extends from the episternal region into the epimeral region. In the episternal region the precoxal suture is a deep furrow. In the epimeral region, the entire ventral border of the precoxal suture is bound by a carina. Between the metathoracic spiracle and the precoxal suture is a narrow anepisternum. The greater part of the episternum is the katepisternum. Basally they fuse with the ventropleurite. The katepimeron is narrow and the greater part is membranous. The postcoxal bridge is absent in the metapleuron. The pleural wing process is short and supports the base of the hind wing. No observable basalar occurs in the metapleuron.

The subalare is a small triangular sclerite lying near to the posterior base of the hind wing. The anepimeron fuses with the antecosta of the postnotum.

### *The sternum*

*Prosternum* (Figs 49 and 50). The prosternum is represented by two areas, the anterior basisternum and the posterior furcasternum. The presternite is absent in the prosternum. Anteriorly, the lateral arms of the basisternum fuse with the anepisterna of the propleura. At the points of fusion the posterior ends of the cervical sclerites articulate. The basisternum is not a flat structure but medially bears a characteristic Y-shaped carina. Posteriorly, the basisternum fuses with the furcasternum. Two carinae occur on the anterolateral angles of the furcasternum. The two sternal apophyseal pits are located on the anterolateral margins of the furcasternum. In the membranous area between the coxae and the basisternum are the katepisterna. Matsuda (1956b) identified the sclerites in *Siphonurus columbianus* based on myological evidence. Similar muscles (notal-katepisternum muscles) have also been observed in the *Leptophlebia*. Compared with *S. columbianus*, the katepisterna are greatly reduced in *Leptophlebia*. In all *Leptophlebia* species we have observed, the prealar bridge of the mesothorax extends well into the prothorax. At the junctions of the prealar bridge and the presternite of the mesothorax, an arm from each side extends forward to hold the sternal apophysis of the prothorax. The entire lateral side of the sternal apophysis is fitted into a groove on this arm.

*Mesosternum* (Figs 49 and 50). The mesosternum is divided into the following regions: the presternite, the basisternum, and the furcasternum. The presternite is marked off from the basisternum by the presternal suture. Laterally the presternite fuses with the prealar bridge, the lateral apices form two small apodemes. On each apodeme a slender muscle extends obliquely backward to attach onto the basalar sclerite. The basisternum is U-shaped, and elevated medially, with the posterior half bisected by a median longitudinal carina. Posteriorly, the basisternum fuses with the furcasternum. Lateral to this junction are the two sternal apophyseal pits. On the rim of each pit there is a small finger-like projection near the coxal base forming a sternal articulation. Thus, together with the coxal process of the mesopleuron, the mesocoxal articulation is dicondylic in nature. The furcasternum is bilobed, with a median longitudinal invagination dividing the two lobes. This invagination widens a little anteriorly and to a much greater extent posteriorly. The lateral sides of the furcasternum fuse with the postcoxal bridges of the epimera. The furcasternum fuses with the metathorax. The two lines forming the boundary of the invagination extend posteriorly without reaching the posterior margin of the furcasternum.

*Metasternum* (Figs 49 and 50). The metasternum is a simple plate bisected medially by a longitudinal carina. Anterolaterally it fuses with the episterna of the metapleura. The posterior margin fuses with the first abdominal sternum. The two sternal apophyseal pits are located at the posterolateral margins. The structure of these pits is similar to those in the mesothorax, therefore the coxae also have a dicondylic articulation.

### *The cervical region*

#### *Nymphs*

*Cervical region* (Fig. 22). The cervical sclerite on each side is narrow and curved. Anteriorly they articulate with the occipital condyles of the head. Posteriorly they articulate with the anterolateral angles of the pronotum and the proepisterna.

### *The tergum*

*Protonotum* (Fig. 21). The pronotum is a simple plate bisected by the median notal suture or also the ecdysial suture. Anteriorly, the antecostal suture divides a narrow acrotergite from the pronotum. Fine setae are present on the acrotergite, and the anterolateral and lateral margins of the notum. The pronotum is separated posteriorly from the mesonotum by a membranous area.

*Mesonotum* (Fig. 21). The mesonotal plate is evaginated posterolaterally to form the fore wing buds. A median notal suture traverses the entire notum. In the fully mature nymphs, the notum bears the paired outer parapsidal sutures characteristic of the imago. Also the hind margin of the notum becomes more acute in later instars. The anterior phragmata are absent in the mesothorax.

*Metanotum* (Fig. 21). Internally, the postnotum of the mesothorax fuses with the anterior margin of the metanotum to form a small phragma at each of the anterolateral angles. The posterolateral sides of the metanotum are also evaginated to form the hind wing buds. Medially the metanotum is bisected by the median notal suture.

### *The pleuron*

*Propleuron* (Fig. 22). A distinct pleural suture extends from the coxal process obliquely upward; it divides the pleural plate into a smaller episternum and a larger epimeron. The area above the pleural suture extends to form an internal apodeme projecting into the prothoracic cavity. In the various instars examined, in no case was the pleuron fused with the prosternal element.

*Mesopleuron* (Fig. 22). The mesopleuron is a crescent-shaped plate. A distinct pleural suture divides the plate into the episternum and epimeron. In early nymphal instars, the precoxal suture is seen as a furrow bordering the dorsal submargin of the mesopleural plate. In later instars, the anapleural and katapleural regions of the episternum can be differentiated. Dorsally the pleural plate fuses with the posterolateral margin of the tergum, but ventrally it does not fuse with the mesosternum.

*Metapleuron* (Fig. 22). The metapleuron is also a curved plate divided into the episternum and epimeron by the pleural suture. The precoxal suture lies near the dorsal margin of the plate. Posterodorsally the mesopleuron fuses with the postnotum of the metanotum. The posterior margin of the metapleuron fuses with the first abdominal tergum.

### *The sternum*

*Prosternum* (Fig. 23). In both the early and late instars the structure of the prosternum is similar. The basisternum represents a membranous area anterior to the furcasternum. The furcasternum is sclerotized and triangular in shape. The two sternal furcal pits are situated at the posterior angles of the furcasternum. The sternal furcae are well developed and extend posteriorly into the mesothoracic cavity. In the membranous area between the basisternum and the coxae are the well developed katepisterna. Posteriorly, a membranous area separates the furcasternum from the mesothorax.

*Mesosternum* (Fig. 23). The mesosternum is a simple rectangular plate with the base expanded laterally. The sternal furcal pits are situated at the lateral margins where the

basisternum and furcasternum fuse together. In early instars the basisternum is more membranous. In later instars it becomes a little more convex medially, and the furcasternum becomes a little bilobed. A narrow membranous region divides the mesosternum from the metasternum.

*Metasternum* (Fig. 23). The metasternum is a simple plate which bears a few hairs on the lateral margins. The posterior margin fuses with the first abdominal segment. The third pair of sternal furcae are located at the anterolateral margins of the first abdominal sternum immediately behind the posterior margin of the metasternum.

#### *Thoracic muscles of the imagos*

The following is an account of the thoracic muscles in the imagos of *Leptophlebia pacifica* as seen from a sagittal view. It is necessary to study the muscles since it aids in the correct determination of the various thoracic sclerites. The thoracic muscles of the nymphs are not included since the thoracic sclerites of the nymph are relatively easy to determine. Each muscle is given a code and a name. In the code, pro-, meso- and metathoracic muscles are indicated by the Roman numerals I, II, and III respectively. Following the Roman numeral, each muscle within that particular segment is designated by an Arabic numeral. Each muscle is named by the skeletal parts to which it is attached. The two skeletal parts of attachment are hyphenated. The first listed is the origin and the second is the insertion.

The following two criteria are used in determining the origin and insertion of a muscle. First, the origin of a muscle is defined as its attachment to a stationary base, while the insertion is its attachment to a moveable part (Torre-Bueno, 1950). The second criterion to determine the origin and insertion of a muscle is that the origin is the broader area of attachment, whereas the insertion is the reduced area of attachment (Daly, 1964). When the distinction between the origin and insertion is uncertain, the sequence of the parts in the name is arbitrary and the muscle is marked with an asterisk.

#### *The prothorax*

##### *Muscles inserted on the cervical sclerites:*

- I-2     Sternal apophysis-cervical sclerite (Figs 1 and 19):  
This is a band of well developed muscle extending between the base of the prothoracic sternal apophysis to the middle region of the cervical sclerite. Contraction of this muscle retracts the head, since an angle is formed between the head and the cervical sclerite when this muscle contracts.
- I-7     Cervical membrane-cervical sclerite (Fig. 1):  
This is a relatively small muscle stretching between the dorsal cervical membrane and the anterior end of the cervical sclerite.
- I-8     Pronotum-cervical sclerite (Fig. 1):  
This muscle originates on the anterolateral part of the pronotum and inserts on the inner posterior end of the cervical sclerite. Function is similar to muscle I-2.
- I-10\*   Cervical sclerite-postoccipital ridge (Fig. 2):  
This muscle lies beneath muscle I-9 and joins the posterior end of the cervical sclerite with the laterodorsal portion of the postoccipital ridge. Function is similar to muscle I-2.



*Dorsal muscles:*

- I-3\* Pronotum-pronotum (Figs 1 and 2):  
This is a short muscle lying in the dorsal part of the notum extending between the mid and posterior portions of the pronotum.
- I-4 Anterior phragma-pronotum (Figs 1 and 2):  
This muscle arises from the anterior phragma and inserts anteriorly to the mid-lateral portion of the pronotum. It retracts the prothorax.
- I-5 Anterior phragma-pronotum (Figs 1 and 2):  
This muscle lies close to muscle I-4, originating on the anterior phragma and inserting on the anterolateral margin of the pronotum. Function is similar to muscle I-4.
- I-6 Pronotum-postoccipital ridge (Fig. 1):  
This is a short muscle connecting the anterodorsal margin of the pronotum with the laterodorsal portion of the postoccipital ridge. It raises or retracts the head.
- I-12 Anterior phragma-pronotum (Fig. 3):  
This is a thin muscle extending between the anterior phragma and the mid-lateral region of the pronotum. It lies laterad to muscles I-4 and I-5. Function is similar to muscle I-4.
- I-26\* Pronotum-pronotum (Fig. 8):  
This very small muscle stretches between the posterolateral and mid-lateral portions of the pronotum.

*Muscles attached on the postoccipital ridge:*

- I-9 Basisternum-postoccipital ridge (Fig. 2):  
This is a wide and thick muscle originating from the basisternum and inserting on the laterodorsal portion of the postoccipital ridge. It raises the head.
- I-1, I-1a, I-6 and I-10: These muscles, which attach on the postoccipital ridge, are classified and described in other portions of this section.

*Noto-pleural muscles:*

- I-11 Pronotum-katepisternum (Fig. 3):  
This is a thin muscle extending between the dorsal surface of the katepisternum and the mid-sublateral portion of the pronotum.
- I-14 Pronotum-pleuron (Fig. 5):  
This is an extremely delicate muscle extending between the apices of the pronotum and the pleural area near to the anterior part of the coxal rim.
- I-27 Pronotum-propleuron (Fig. 8):  
This muscle originates from the mid-lateral part of the pronotum and inserts on the pleuron close to the propleural apodeme.
- I-28 Pronotum-propleuron (Fig. 8):  
This muscle lies in front of muscle I-27 and has similar dorsal and ventral attachments as muscle I-27.

- I-29 **Pronotum-propleuron (Fig. 8):**  
This thin rectangular muscle lies beneath muscles I-27 and I-28. It holds the propleuron to the side of the pronotum.

*Noto-coxal muscles:*

- I-13 **Pronotum-basicoxite (Figs 3 and 4):**  
This muscle originates from the mid-pronotum and inserts on the anterior portion of the coxal rim. It functions as a protractor muscle of the fore leg.
- I-24 **Pronotum-basicoxite (Fig. 7):**  
This is a cylindrical muscle stretching between the mid-pronotum and the sub-anterior portion of the basicoxite. The position of this muscle is close to the coxal articulation, therefore it may function as an abductor muscle.
- I-25 **Pronotum-basicoxite (Fig. 7):**  
This muscle lies anterior to muscle I-24. It originates from the mid-pronotum and inserts on the anterior part of the coxal rim close to the coxal process. Function is similar to muscle I-24.

*Pleural-coxal muscles:*

- I-15 **Propleuron-basicoxite (Fig. 5):**  
This is a fine muscle stretching between the apodeme formed by the propleural plate and anterior portion of the basicoxite. This muscle probably functions as an abductor muscle of the coxa.

*Noto-trochanteral muscle:*

- I-19 **Pronotum-trochanter (Fig. 6):**  
This muscle is slender and originates on the mid-sublateral part of the pronotum and inserts on the trochanter. It functions as a depressor of the trochanter.

*Pleural-sternal muscle:*

- I-30 **Propleuron-sternal apophysis (Fig. 8):**  
This is a fine muscle running between the base of the sternal apophysis and the epimeron of the propleural wall. It compresses the pleuron.

*Sternal-coxal muscles:*

- I-21 **Sternal apophysis-basicoxite (Figs 7 and 19):**  
This is a very short muscle originating from the basal portion of the sternal apophysis and inserting on the posterior part of the coxal rim. It functions as a rotator of the coxa.
- I-22 **Sternal apophysis-basicoxite (Figs 7 and 19):**  
This cylindrical muscle connects the base of the sternal apophysis with the mid-basicoxite. It functions as an anterior rotator of the coxa.
- I-23 **Sternal apophysis-basicoxite (Figs 7 and 19):**  
This is a rather strong muscle joining the basal part of the sternal apophysis with the anterior part of the coxal rim. Function is similar to muscle I-22.

*Ventral longitudinal muscles:*

## I-1, I-1a Sternal apophysis-postoccipital ridge (Figs 1 and 19):

These two bands of muscles run between the sternal apophysis and the lower part of the postoccipital ridge. These muscles tilt the head downward.

*Coxal muscle:*

## I-17\* Coxa-coxa (Fig. 6):

This strong cylindrical muscle extends from the anterior coxal wall to the coxal condyle.

*Coxal-trochanter muscles:*

## I-16 Basicoxite-trochanter (Fig. 5):

This is a wide muscle running between the inner posterior coxal rim and the trochanter. It functions as a levator of the trochanter.

## I-18 Basicoxite-trochanter (Fig. 6):

This long cylindrical muscle connects the anterior portion of the basicoxite with the trochanter. Function is similar to muscle I-19.

## I-20 Basicoxite-trochanter (Fig. 7):

This is a wide and short band of muscle lying between the outer posterior coxal rim and the outer trochanteral rim. Function is similar to muscle I-16.

*The mesothorax**Dorsal muscle:*

## II-1 Anterior phragma-posterior phragma (Fig. 9):

This is the largest mesothoracic muscle that extends between the anterior phragmata and the posterior phragmata. The contraction of this muscle produces the downstroke of the fore wing. This muscle may also pronate the fore wing (Brodsky, 1970).

*Ventral muscles:*II-3\* Prothoracic sternal apophysis-mesothoracic sternal apophysis (Figs 9 and 19):  
This is the ventral longitudinal muscle connecting the prothoracic sternal apophysis with the mesothoracic apophysis.II-29\* Mesothoracic sternal apophysis-mesothoracic sternal apophysis (Fig. 19):  
It is a short transverse ventral muscle lying between the bases of the mesothoracic sternal apophysis.II-26 Mesothoracic sternal apophysis-coxa (Figs 14 and 19):  
This slender, ventral transverse muscle connects the posterior coxal margin with the outer margin of the mesothoracic sternal apophysis. The ventral transverse muscle that connects both middle legs, as described by Matsuda (1956b) in *Siphonurus columbianus*, is not found in *L. pacifica*.II-30 Mesothoracic sternal apophysis-coxa (Fig. 19):  
This is a fine muscle joining the basal portion of the sternal apophysis with the anterior meron of the coxa.

*Basalar muscles:*

All basalar muscles are attached on the posterior basalar sclerite; the anterior basalar sclerite does not have muscle attachments. These muscles serve as depressors of the costal margin of the wings during flight.

- II-8 Posterior basalar sclerite-prothoracic sternal apophysis (Fig. 11):  
This is an oblique muscle running between the base of the prothoracic sternal apophysis and the ventral arm of the basalar sclerite.
- II-9 Presternite-posterior basalar sclerite (Fig. 12):  
This is a fine muscle arising from the apodeme on the presternite of the mesothorax. It extends obliquely upward and backward, and inserts onto the ventral apex of the posterior basalar sclerite. As discussed by Matsuda (1956*b*), the ventral attachment of this muscle varies from species to species. Compared with the primitive condition in *Siphonurus columbianus*, the ventral attachment of this muscle in *L. pacifica* seems to have shifted backward from the prothoracic sternal apophysis to the sternum of the mesothorax.
- II-12a Posterior basalar sclerite-mesothoracic spiracle (Fig. 12): This muscle has a dorsal attachment near to muscle II-9 on the ventral apex of the posterior basalar sclerite and ventrally it attaches onto the atrial wall of the mesothoracic spiracle.
- II-10 Pleural wing process-posterior basalar sclerite (Figs 11 and 12): This muscle stretches between the anterodorsal arm of the posterior basalar sclerite and the pleural wing process.

*Subalar muscles:*

Subalar muscles serve as the depressor-extensor muscles of the wings, because of the close connection of the median plates with the anterior subalar sclerite (muscle II-22a).

- II-5 Furcasternum-anterior subalar sclerite (Figs 10, 11 and 12):  
This is a strong triangular muscle. It arises from and covers the entire area of the furcasternum. Dorsally it converges on the posterior apodeme of the anterior subalar sclerite. This muscle is known to occur only in the Ephemeroptera.
- II-20 Mesothoracic sternal apophysis-anterior subalar sclerite (Fig. 13):  
Ventrally, this slender muscle is attached on the posterior base of the mesothoracic sternal apophysis. It extends obliquely upward and backward and inserts onto the posterior apodeme of the anterior subalar sclerite.
- II-23 Anterior subalar sclerite-basicoxite (Fig. 14):  
Dorsally this muscle originates from the anterior apodeme of the anterior subalar sclerite and runs ventrally to attach onto the posterior portion of the coxal rim.
- II-22 Anterior subalar sclerite-basicoxite (Fig. 14):  
This fine muscle originates from the anterior apodeme of the subalar sclerite and ventrally has the same insertion as muscle II-21 on the posterior coxal margin.
- II-22a Anterior subalar sclerite-median plate:  
This is a small muscle joining the posterior part of the median plate with the anterodorsal angle of the subalar sclerite. On each side, this close connection between the median plate with the anterior subalar sclerite serves to transmit the "pull" exerted by other subalar muscles to depress the wing.

*Muscles of the axillary sclerites:*

- II-17 Mesothoracic sternal apophysis-second axillary sclerite (Fig. 13):  
This is a slender muscle lying between the sternal apophysis and the second axillary sclerite. Matsuda (1956*b*) reported two axillary muscles attached to the second axillary sclerite in *Siphonurus columbianus*. Of these two muscles, the one running between the second axillary sclerite and the precoxal suture is absent in *L. pacifica*. When at rest, the contraction of this muscle keeps the fore wing in a vertical position (Grandi, 1947*b*). This muscle possibly also controls the angle of incidence at flight (Brodsky, 1970).
- II-18 First axillary sclerite-basicoxite (Fig. 13):  
Dorsally, part of this muscle inserts on the anterior portion of the first axillary sclerite and the rest of the muscle on the anterodorsal arm of the posterior basalar sclerite. Ventrally, it is connected to the basicoxite. Compared with the results obtained by Knox (1935), Maki (1938), and Matsuda (1956*b*), the origin and insertion of this muscle seem to vary from species to species. Function of this muscle is similar to muscle II-17.

*Noto-pleural muscles:*

- II-4 Scutum-postalar bridge (Figs 10, 11 and 12):  
The dorsal end of this muscle is attached on the posterolateral hump of the scutum. Basally, the muscle is attached to the postalar bridge dorsal to the mesothoracic spiracle. Contraction of this muscle exerts a vertical pull instead of a horizontal one and therefore acts as a levator for the fore wing.
- II-6 Scutum-episternum (Fig. 10):  
Basally, this muscle attaches on the episternum. It widens dorsally and attaches to the anterior portion of the scutum. Contraction of this muscle produces the upstroke of the fore wing.
- II-7 Prescutum-anepisternum (Fig. 11):  
This is a wide but thin muscle arising from the anterior portion of the prescutum near to the anterior phragma. Posteriorly, it inserts on the anepisternum near to the precoxal suture.
- II-13 Scutum-anepisternum (Fig. 12):  
This short muscle originates on that part of the scutum that is immediately behind the posterior basalar sclerite and inserts on a small apodeme on the anepisternum near to the precoxal suture. Probably it functions as a wing abductor (Brodsky, 1970).

*Noto-coxal muscles:*

- II-11 Scutum-basicoxite (Fig. 11):  
Dorsally this muscle originates on the posterior portion of the outer parapsidal suture on the scutum. Ventrally it inserts on the anterior margin of the coxa. The contraction of this muscle produces the upstroke of the fore wing and at the same time it functions as a promotor muscle of the coxa.

II-19 Scutum-basicoxite (Fig. 13):

This muscle originates from the posterior portion of the outer parapsidal suture of the scutum and inserts on the posterior coxal rim. The contraction of this muscle also produces the upstroke of the fore wing and at the same time it functions as a remotor muscle of the coxa.

II-21 Scutellum-basicoxite (Fig. 14):

This is a very slender muscle running between the lateral margin of the scutellum and the posterior coxal margin. Function is similar to muscle II-19. By drawing the scutellum inward it may also be involved in pronation of the fore wing (Brodsky, 1970).

*Noto-trochanteral muscle:*

II-14 Scutum-trochanter (Fig. 12):

This muscle has a wide attachment on the scutum lateral to the anterior notal wing process. Ventrally it inserts on the apex of the trochanter. Contraction of this muscle produces the upstroke of the fore wing. It also functions as a depressor of the trochanter.

*Pleural-coxal muscle:*

II-15 Precoxal suture-basicoxite (Fig. 12):

This muscle originates from the precoxal suture and inserts on the anterior part of the basicoxite. It functions as an adductor of the coxa.

*Pleural-trochanteral muscle:*

II-16 Katepisternum-trochanter (Fig. 13):

This is a wide band of muscle that originates from the katepisternum and inserts on the apical region of the trochanter. It functions as a depressor of the trochanter.

*Pleural-sternal muscle:*

II-12b Presternite-mesothoracic spiracle (Fig. 12):

This is a very short muscle which originates on the apodeme of the presternite and inserts on the atrium leading from the mesothoracic spiracle. Muscles II-12a and II-12b both act as the dilators for the spiracle. An occulsor mechanism has not been observed. The closing of the atrium is likely due to the contraction of muscle II-9 which compresses and thus constricts the atrium wall.

*Coxal muscle:*

II-28\* Coxa-coxa (Fig. 14):

This is a major coxal muscle stretching between the upper and lower coxal margins.

*Trochanteral muscle:*

II-27 Trochanter-trochanter (Fig. 14):

This muscle extends from the anterior upper part of the trochanteral margin to the lower trochanteral margin.

*Coxal-trochanter muscles:*

- II-24 Coxa-trochanter (Fig. 14):  
This is a robust muscle extending between the anterior upper coxal margin and the apical part of the trochanter. It functions as a depressor of the trochanter.
- II-25 Coxa-trochanter (Fig. 14):  
This triangular muscle attaches with the wider dorsal end to the anterior coxal meron and ventrally inserts on the trochanter. Function is similar to muscle II-24.

*Intersegmental muscle:*

- II-2 Anterior phragma-prothoracic sternal apophysis (Fig. 9):  
This slender muscle runs between the anterior phragma and the dorsal apex of the prothoracic sternal apophysis.

*The metathorax*

- III-1\* Posterior phragma-antecosta (Fig. 15):  
This is a thick median dorsal longitudinal muscle running between the posterior phragma and the antecosta of the metathorax. It functions as the main depressor of the hind wing.

*Noto-pleural muscles:*

- III-2 Scutum-anepisternum (Fig. 16):  
Dorsally this muscle originates from the anterolateral portion of the scutum. Basally it inserts on the heavily sclerotized katepisternum. It functions as a levator of the hind wing.
- III-5 Precoxal suture-posterior phragma (Fig. 17):  
This is a very small and short muscle extending between the precoxal suture and the posterior phragma. Contraction of this muscle pulls the metathorax toward the mesothorax.
- III-6 Scutum-precoxal suture (Fig. 17):  
This slender muscle runs between the anterolateral margin of the scutum and the precoxal suture.
- III-20 Scutum-episternum (Fig. 18):  
This small muscle joins the anterior portion of the pleural wing process to the anterolateral margin of the scutum.

*Noto-coxal muscles:*

- III-3 Phragma-basicoxite (Fig. 16):  
This is a very fine muscle originating from the posterior phragma and inserting on the anterolateral portion of the coxal rim.
- III-4 Scutum-basicoxite (Fig. 16):  
This muscle originates close to muscle III-2 on the anterolateral part of the scutum. Ventrally it inserts on the anterior coxal rim. Contraction of this muscle produces the upstroke of the hind wing. It may also function as a promotor of the coxa.

- III-12 Scutum-basicoxite (Fig. 17):  
Dorsally this muscle arises on the scutum anterior to the anterior notal wing process and extends obliquely to attach to the posterior portion of the coxal margin near the coxal process. Contraction of this muscle produces the upstroke of the hind wing. It may also function as a remotor of the coxa.
- III-17 Scutellum-basicoxite (Fig. 18):  
This is a slender muscle; dorsally it attaches to the lateral part of the scutellum just behind the scuto-scutellar suture. Ventrally it attaches to the posterior coxal margin.

*Pleural-coxal muscles:*

- III-7 Precoxal suture-basicoxite (Fig. 17):  
This is a wide and flat muscle originating from the precoxal suture and inserting ventrally on the anterior portion of the coxal rim. Because of its rather anterior position on the coxal rim it probably functions as a promotor of the coxa.
- III-15 Pleural-basicoxite (Fig. 18):  
This is a cylindrical muscle with an attachment on the pleural plate near the pleural wing process; it converges ventrally on the posterior coxal margin. It functions as the abductor of the hind leg.
- III-16 Katepisternum-basicoxite (Fig. 18):  
Dorsally this muscle originates from the dorsal portion of the katepisternum below the precoxal suture and ventrally inserts on the posterior portion of the coxal rim. Its function is probably similar to muscle III-15.

*Pleural-sternal muscles:*

- III-9 Pleural wing process-sternal apophysis (Fig. 17):  
This slender muscle attaches to the metathoracic sternal apophysis and extends upward to attach to the pleural wing process.
- III-8 Epimeron-sternal apophysis (Fig. 17):  
This muscle has a similar attachment as muscle III-9 on the sternal apophysis and joins the ventral margin of the postnotum and epimeron. Contraction of this muscle compresses the thorax and therefore may be involved in the downstroke of the hind wing.

*Muscle on the axillary sclerite:*

- III-11 Sternal apophysis-second axillary sclerite (Fig. 17):  
This is the only observable muscle attached on the second axillary sclerite. It is a very fine muscle occurring between the axillary sclerite and the sternal apophysis. Contraction of this muscle keeps the hind wing in a vertical position when at rest.

*Coxal muscle:*

- III-19\* Coxa-coxa (Fig. 18):  
This coxal muscle extends between the upper and lower coxal margins.



*Trochanteral muscles:*

- III-13 Scutum-trochanter (Fig. 17):  
This muscle originates on the mid-lateral margin of the scutum and inserts on the trochanter. Contraction of this muscle produces the upstroke of the hind wing. It also functions as a depressor of the trochanter.
- III-18 Precoxal suture-trochanter (Fig. 18):  
This is a wide and flat muscle running obliquely between the precoxal suture and the trochanter. It functions as a depressor of the trochanter.

*Ventral muscles:*

- III-14 Sternal apophysis-coxa (Figs 18 and 19):  
This is a cylindrical muscle joining the metathoracic sternal apophysis with the coxal meron. It functions as a sternal remotor of the leg.
- III-25\* Sternal apophysis-sternal apophysis (Fig. 19):  
This is a slender, ventral, transverse muscle joining the bases of the sternal apophysis.
- III-26 Sternal apophysis-basicoxite (Fig. 19):  
This is a small ventral, transverse muscle joining the metathoracic sternal apophysis with the anterior part of the basicoxite. It functions as a sternal promotor of the leg.
- III-27, III-28 Sternal apophysis-second abdominal segment (Figs 15 and 19):  
These two ventral, longitudinal muscles originates from the posterior margin of the sternal apophysis and posteriorly attach to the anterior margin of the second abdominal segment.

*Intersegmental muscles:*

- \*III-21, III-22, III-23, III-24 Postnotum-epimeron-second abdominal segment (Fig. 15):  
These two pairs of muscles join the postnotum-epimeron with the anterior margin of the second abdominal segment.

### Comparative morphology of the imaginal thoracic exoskeleton of selected genera of *Leptophlebiidae*

The following is a comparative account of the thoracic exoskeleton of the imagos of selected genera of the *Leptophlebiidae*. This study is based on only some representative species of each genus. The method of selection of the genera is described in the section on the phylogeny and relationships of the genera.

#### *Genus Paraleptophlebia* Lestage, 1917

(Figs 26, 32, 38, 44 and 51)

In the present study *Paraleptophlebia bicornuta* McDunnough is chosen as a representative of the genus. *P. packi* Needham and *P. bradleyi* Needham were also studied, but only

the description of *P. bicarnuta* is given herein. *Paraleptophlebia* is represented in both the Palearctic and Nearctic regions; the three species examined in this study occur in North America.

### *The tergum*

*Pronotum* (Fig. 26). The pronotum is an H-shaped sclerite. A short median notal suture bisects the pronotum. Anteriorly, the antecostal suture sets off a narrow and distinct acrotergite. Along the antecostal suture the two anterosubmedian depressions develop into a pair of well formed apodemes. Laterally the notum extends downwardly to cover the greater portion of the pleura. The mid-posterior margin is more strongly excavated than the mid-anterior margin. Posteriorly, the pronotum is separated from the mesonotum by a membranous area.

*Mesonotum* (Fig. 26). The acrotergite extends lateroventrally to form the prealar bridge. Ventrally it fuses with the presternum to form a complete ring at the anterior end of the mesothorax. The antecostal suture separating the acrotergite and the scutum inflects to form the anterior phragmata for the attachment of the dorsolongitudinal muscles. The scutum occupies the largest area of the mesothorax in the form of a rounded protuberance. A median notal suture occupies the anterior two-thirds of the scutum. The posterior third of the scutum bears two humps marking the area where the scuto-phragma muscles are attached to the tergum. The scuto-scutellar suture has a truncated V-shape. On each side following the notal furrow, the submarginal area of the lateral portion of the scutal shield notches inwardly. The hind margins of the fore wings are attached to the posterior margin of the scutellum. The postnotum lies below the scutellum and fuses with the anterior portion of the metatergum to form the posterior phragmata. In each fore wing axillary region there are two distinct axillary sclerites (Fig. 32). The first sclerite is triangular with its inner lateral edge articulating with the anterior notal wing process of the mesonotum. Posteriorly, it articulates with the second axillary sclerite which is triangular-shaped, and articulates with the first axillary sclerite and the median plate. The posterior notal wing process occurs at the apex of the scutellum and articulates with the median plate. A narrow and elongated sclerite occurs at the posterior end of each fore wing base. It can be detected lying at the posterior end of the wing region close to the scutellum.

*Metanotum* (Fig. 26). The anterior part of the scutum inflects ventrally to fuse with the postnotum of the mesothorax to form the posterior phragmata. The scuto-scutellar suture is discontinuous in the middle portion. Margins of the hind wings are continuous with the posterior margin of the scutellum. The postnotum is similar to that in the mesonotum. A short median longitudinal suture divides the antecosta of the postnotum into right and left halves. Laterally the antecosta fuses with the metaepimera. In each axillary region are two axillary sclerites (Fig. 38). The first sclerite is very weakly sclerotized. The second axillary sclerite articulates between the median plate and the posterior notal wing process. The basalar and subalar sclerites are absent in the metanotum.

### *The pleuron*

*Propleuron* (Fig. 44). On each propleuron a pleural suture extends dorsally from the coxal process. Anterior to this is the episternum which extends ventrally to fuse with the

lateral arm of the basisternum. The katepisternum is present in the membranous area between the coxal base and the basisternum.

*Mesopleuron* (Fig. 44). A distinct pleural suture occurs on each mesopleuron and extends obliquely forward from the coxal process to meet with the precoxal suture. The apodeme that occurs in the area dorsal to the pleural suture is present. Anterior to this pleural suture is the episternum. It is divided by the precoxal suture into the anepisternum and the katepisternum. Ventrally, the episternum fuses with the basisternum of the mesothorax. Posterior to the pleural suture is the epimeron. The precoxal suture extends downward to the median region of the epimeron and divides it into the anepimeron and katepimeron. Ventrally, the epimeron fuses with the postcoxal bridge. Dorsal to the pleural suture is the pleural arm which supports the wing. A median suture appears on the pleural arm which possibly is a continuation of the pleural suture. Anterior to the pleural arm in the membranous area is the basalar sclerite. The basalar sclerite is irregular in shape. Posterior to the pleural arm are the anterior and posterior subalar sclerites.

*Metapleuron* (Fig. 44). The precoxal suture divides the metapleuron into the anapleural and katapleural areas. The carina bounding the ventral side of the precoxal suture in the epimeron is present. The pleural suture extends from the coxal process obliquely forward to meet with the precoxal suture. An approximate episternum and epimeron are thus present. The episternum is bounded anteriorly by the spiracle and posteriorly by the membranous area of the coxal base. Ventrally it fuses with a small triangular sclerite, the ventropleurite. The dorsal region of the anepimeron bears a short pleural arm. Posteriorly it fuses with the postnotum of the metatergum. The katepimeron is a narrow region and most of the ventral portion is highly membranous. There is no observable basalar or subalar sclerite in the metapleuron.

#### *The sternum*

*Prosternum* (Fig. 51). The anterior margin of the basisternum is concave, thus greatly reducing the area between the two arms of the Y-shaped carina. The anterolateral portions of the basisternum extend to fuse with the proepisterna. The basisternum fuses to the furcasternum without showing the line of fusion between them. The sternal apophyseal pits are situated at the posterolateral portions of the furcasternum. There are no carinae on the anterolateral portions of the furcasternum. The two sternal apophyses rest on the extensions from each side of the prealar bridge. The prosternum and mesosternum are separated by a membranous area. In the membranous area between the coxae and the basisternum are the katepisterna of the propleura.

*Mesosternum* (Fig. 51). The anterior portion of the mesosternum is the narrow presternite. It fuses with the prealar bridge of the mesotergum to form a complete ring. The presternal apodemes are not well developed. The basisternum is rectangular with a median longitudinal carina that occupies three-quarters of the length of the basisternum. The posterior suture of the basisternum is straight or a little rounded. The sides of the basisternum fuse with the episternum. The basisternum and furcasternum fuse, and the sternal apophyseal pits occur laterally at this junction. The rim of each apophyseal pit facing the coxa bears a finger-like projection that articulates with the coxa. Thus, the coxal articulation in the mesothorax is dicondylic. The furcasternum is bilobed with a median longitudinal

invagination. This invagination is narrow anteriorly but widens posteriorly. The two sutures forming the edges of the invagination are almost continuous with the posterior margin of the furcasternum. In *Paraleptophlebia* the posterior margin of the furcasternum is slightly concave.

*Metasternum* (Fig. 51). This is a simple plate bisected by a median longitudinal carina. The sides fuse to the ventropleurite. The sternal apophyseal pits are situated at the posterolateral angles of the metasternal plate.

### Genus *Habrophlebiodes* Ulmer, 1919

(Figs 27, 33, 39, 45 and 52)

For this genus, only the North American species *H. brunneipennis* Berner was studied. This genus is confined to the Oriental Region and Eastern North America.

#### *The tergum*

*Pronotum* (Fig. 27). The pronotum is a transverse plate bisected by a relatively long median notal suture. The acrotergite is present at the anterior margin. The pair of antero-submedian depressions is present but not formed into internal apodemes. The posterior margin is concave medially, and is separated from the mesonotum by a membranous area.

*Mesonotum* (Fig. 27). The antecostal suture sets off the acrotergite from the scutum at the anterior end. Internally this suture inflects to form the anterior phragmata. Laterally, the acrotergite fuses with the presternite to form the prealar bridge. On each side the prealar bridge extends anteriorly to support the prosternal apophyses. The prescutum on either side is separated from the scutum by a membranous prescutal suture. Anteriorly the prescutum fuses with the acrotergite and posteriorly it articulates with the basalar sclerite. The scutal shield is rounded, and each anterolateral margin is bound by the notal furrow. Posterior to the notal furrow is the anterior notal wing process which bears an internal apodeme. On the scutal surface are the median notal suture, and the two pairs of inner and outer parapsidal suture. The scutum is separated from the scutellum by the scuto-scutellar sutures, which fuse medially. In each fore wing axillary region (Fig. 33) are two axillary sclerites. A third piece of sclerite is found at the posterior part of the wing base lateral to the scutellum (Fig. 27). The scutellum is saddle-shaped with the anterolateral corners projecting forward to bear the posterior notal wing processes. The hind margins of the fore wings are in line with the posterior margin of the scutellum. On both sides, the posterior margin of the scutellum is notched inwardly. The postnotum consists of a precosta and an antecosta. The precosta is attached to the under surface of the scutellum. The antecosta forms part of the posterior phragmata and laterally fuses with the postalar bridges of the mesopleura.

*Metanotum* (Fig. 27). In this genus the hind wings are reduced to 11 % of the length of the fore wings. Associated with the reduction of hind wings are structural changes in the metanotum. In general, the metanotum is V-shaped. The scutum is unique as the posterior margin is V-shaped. The scutoscuteellar suture is wide. The scutellum is reduced to a narrow sclerite. In the hind wings (Fig. 39) only a single axillary sclerite is present. Apparently this is related to the reduction in the size of the hind wings. In the postnotum, the reduced

precosta attaches under the scutellum. The antecosta is bisected by a short median longitudinal suture, and laterally it fuses with the epimeron of the metapleura.

#### *The pleuron*

*Propleuron* (Fig. 45). Each propleuron is divided by the pleural suture into the anterior episternum and the posterior epimeron. The sclerotized area of the epimeron in *Habrophlebiodes* is greatly reduced.

*Mesopleuron* (Fig. 45). On either side in the anterior membranous area, there is only one basalar sclerite. The peritreme is weakly sclerotized. Each mesopleural wall is divided by the pleural suture into the anterior episternum and the posterior epimeron. The episternum is divided by the precoxal suture into the anepisternum and katepisternum. The apodeme in the area dorsal to the pleural suture is absent in *Habrophlebiodes*. The precoxal suture extends into the epimeron. The posterodorsal margin of the epimeron is notched inwardly. Ventrally, the epimeron fuses with the postcoxal bridge.

*Metapleuron* (Fig. 45). In each metapleuron a pleural suture extends dorsally from the coxal process to meet with the precoxal suture. The precoxal suture separates an anapleural area and a katapleural area in both the episternum and epimeron. The carina bordering the ventral side of the precoxal suture is thick and has a characteristic shape for the genus. Both the basalar and subalar sclerites are absent.

#### *The sternum*

*Prosternum* (Fig. 52). The basisternum is triangular with a Y-shaped carina. The furcasternum lacks a pair of anterolateral carinae. The pair of katepisterna lie in the membranous area between the coxae and the basisternum.

*Mesosternum* (Fig. 52). Anteriorly, the presternite is separated from the basisternum by the presternal suture. In *Habrophlebiodes* the basisternum is entire, smooth and oblong. In the furcasternum, the median longitudinal invagination does not extend to the posterior region. This invagination occupies the anterior two-thirds of the furcasternum only. Also, the furcasternum is a little expanded laterally.

*Metasternum* (Fig. 52). The metasternum is rectangular and is not bisected by a median longitudinal carina.

### *Genus Aprionyx Barnard, 1932*

(Figs 28, 34, 40, 46 and 53)

The thoraces of *Aprionyx tricuspидatus* Crass, and *A. natalicus* (Lestage) were examined. The following description is based on the thorax of *A. tricuspидatus*. This genus is confined to the extreme southern portion of Africa.

#### *The tergum*

*Pronotum* (Fig. 28). The pronotum is a simple transverse sclerite bisected medially by the median notal suture. The acrotergite is absent or weakly defined on the anterior margin. At the anterosubmedian area a pair of T-shaped depressions occur on the notum. The

posterior margin is excavated medially, and is separated from the mesothorax by a membranous area.

*Mesonotum* (Fig. 28). Anteriorly the acrotergite is separated from the scutum by the antecostal suture. The scutal shield is round. The scutum bears the median notal suture, and the inner and outer parapsidal sutures. The inner parapsidal sutures are peculiar in being as wide as the median notal suture. The scutum is incompletely separated from the scutellum by the scuto-scutellar suture, and fuse medially. Each fore wing has three axillary sclerites (Fig. 34). The postnotum consists of the precosta and antecosta. The precosta lies beneath the scutellum and the antecosta fuses laterally to the postalar bridges of the mesopleura.

*Metanotum* (Fig. 28). A pair of S-shaped transcutal ridges are found on the mid-scutal region. The scutum is separated from the scutellum by the scuto-scutellar suture. The hind wings have two axillary sclerites (Fig. 40). The antecosta of the postnotum is bisected by a short median suture.

### *The pleuron*

*Propleuron* (Fig. 46). On each propleuron the pleural suture divides the pleuron into the episternum and the epimeron, the apodeme formed by the pleural wall is well developed.

*Mesopleuron* (Fig. 46). In the anterior membranous area of each mesopleuron is a single basalar sclerite. The peritreme is weakly developed. Each mesopleuron is divided by the short pleural suture into the episternum and epimeron. Each of these areas is further subdivided by the precoxal suture into the anapleural area and the katapleural area. The apodeme in the area dorsal to the pleural suture is absent. The epimeron fuses with the postalar bridge posterodorsally and the postcoxal bridge ventrally. In the posterior membranous area are a larger anterior subalar sclerite and a smaller posterior subalar sclerite.

*Metapleuron* (Fig. 46). On each side, the pleural suture divides the metapleuron into the episternum and the epimeron. The episternum is further subdivided by the precoxal suture into the anepisternum and the katepisternum. Ventrally the episternum fuses to the ventropleurite. In the epimeron the precoxal suture is indistinct. Also, the epimeron is separated from the postscutellum of the metanotum by a suture.

### *The sternum*

*Prosternum* (Fig. 53). The basisternum is a narrow sclerite expanded anteriorly to fuse with the episternum and posteriorly to fuse with the furcasternum. The anterior and median areas bear a Y-shaped carina. Laterally, the basisternum is separated from the coxae by a membranous area. Although the katepisterna are seen in the nymphal stage, they are absent in the imago. The furcasternum is square and bounded by a furrow on each lateral margin. The sternal apophyseal pits lie on the two posterolateral angles of the furcasternum. Posteriorly, the prosternum is separated from the mesosternum by a membranous area. In this region the two sclerotized extensions of the prealar bridge extend to brace the two prothoracic sternal apophyses.

*Mesosternum* (Fig. 53). The presternal suture sets off a well developed anterior transverse sclerite, the presternite. On each side of the presternite where it fuses with the prealar

bridge, an internal apodeme forms. Posteriorly it fuses with the basisternum. The basisternum is a smoothly convex sclerite with the entire anterior margin slightly depressed. On each side, the anterior half of the lateral margin fuses to the episternum. The posterior margin is smoothly V-shaped with the two sternal apophyseal pits on each side. The basisternum of *Aprionyx* is characterized by lacking a median carina on the posterior half of the basisternum. The median longitudinal invagination of the furcasternum is also a distinguishing character. The margins of the invagination are parallel to each other except in the median region. The lateral margins of the furcasternum fuse on either side to the postcoxal bridges. Posteriorly, the furcasternum fuses with the metasternum.

*Metasternum* (Fig. 53). The metasternum is a rectangular plate expanded at the two anterolateral angles. The metasternum does not possess a median carina. Posteriorly, it fuses with the first abdominal segment and with the sternal apophyseal pit located on each of the posterolateral angles.

*Genus Traverella* Edmunds, 1948

(Figs 29, 35, 41, 47 and 54)

The species *T. albertana* was chosen for this study. This genus was a wide range, from the Nearctic Region to the southern portion of the Neotropical Region.

*The tergum*

*Pronotum* (Fig. 29). The pronotal plate is bisected by a median notal suture. At the anterior margin, the acrotergite is well differentiated. The notum is a little expanded at the posterolateral parts.

*Mesonotum* (Fig. 29). The prescutum is separated from the scutum by a narrow membranous prescutal suture. The scutum is rounded and has a characteristic blunt anterior end. The inner and outer parapsidal sutures are as broad as the median notal suture. The scutum and scutellum are incompletely separated by the scuto-scutellar suture, and fuse in the median region. In each fore wing are two axillary sclerites (Fig. 35). The postnotum consists of the precosta and the antecosta. The precosta lies beneath the scutellum, whereas the antecosta fuses with the postalar bridges of the mesopleura.

*Metanotum* (Fig. 29). The scutum possesses a pair of transcutal ridges. A wide, membranous scuto-scutellar suture separates the scutum from the scutellum. The scutellum is reduced. In each hind wing are two axillary sclerites (Fig. 41). The postnotum is similar to that of the mesothorax, except that the antecosta of the metapostnotum is bisected by a short median suture.

*The pleuron*

*Propleuron* (Fig. 47). Each propleura is divided by the pleural suture into the episternum and the epimeron. The propleural wall is not formed into an internal apodeme.

*Mesopleuron* (Fig. 47). In the membranous area of each mesopleuron is a single basalar sclerite. The peritreme is well developed. The mesopleural wall is divided by the pleural suture into the episternum and epimeron. These two areas are subdivided by the precoxal

suture into the anapleural region and the katapleural region. The epimeron has a membranous area separating it from the furcasternum of the mesosternum and the postalar bridge. The postcoxal bridge is absent. In the posterior membranous area are the anterior and posterior subalar sclerites.

*Metapleuron* (Fig. 47). Each metapleuron is divided by the pleural suture into the episternum and the epimeron. The episternum is further subdivided by the precoxal suture into the katepisternum and the anepisternum. The precoxal suture extends into the pleural wing process. The ventropleurite is absent. The precoxal suture is not found in the epimeron; instead a curved carina is present. Both the basalar sclerite and subalar sclerite are absent.

#### *The sternum*

*Prosternum* (Fig. 54). The arms of the basisternum extend forward to articulate with the posterior portion of the cervical sclerites. They do not fuse with the episterna of the propleura. A Y-shaped carina is present on the basisternum. The furcasternum, which is fused to the basisternum, has the shape of a truncated triangle.

*Mesosternum* (Fig. 54). The presternite fuses with the prealar bridge to form a ring at the anterior end of the mesothorax. At the points of fusion of the presternite and the prealar bridge, the internal apodemes are weakly developed. The basisternum is a flattened rectangular plate, and is depressed along the subanterior margin. Both mid-lateral margins are convex, but the posterior margin is smoothly concave. The two lateral margins of the median longitudinal invagination are wide apart. A membranous area occurs between the furcasternum, mesoepimeron and the metasternum.

*Metasternum* (Fig. 54). The metasternum is a simple rectangular plate, narrowly joined to the metapleuron at the two anterolateral angles. Posteriorly it fuses to the first abdominal segment. There is not median longitudinal carina on the metasternal plate.

#### *Genus Isca Gillies, 1951*

(Figs 30, 36, 48 and 55)

For this genus the species *Isca (Tanycola) serendiba* was studied. This genus is confined to the Oriental Region.

#### *The tergum*

*Pronotum* (Fig. 30). The pronotal plate possesses a well defined acrotergite at the anterior margin. The median notal suture bisects the notum. The median notal suture is relatively long.

*Mesonotum* (Fig. 30). The antecostal suture separates the acrotergite from the scutum. The narrow prescutum is separated from the scutum by a membranous prescutal suture. The rounded scutal shield bears the membranous median notal suture and a pair of membranous outer parapsidal sutures. The inner parapsidal sutures are not membranous and are very inconspicuous. In each fore wing are two axillary sclerites (Fig. 36). The second axillary sclerite forms a socket at the anterior end where it articulates with the posterior end of the first axillary sclerite. The posterior margin of the scutum-scutellum is



acutely V-shaped. The postnotum consists of the precosta and antecosta. The precosta is a transverse sclerite beneath the scutellum. The antecosta fuses laterally to the prealar bridges of the mesopleura.

*Metanotum* (Fig. 30). Due to the loss of the hind wings the scutum and scutellum are completely fused into a rectangular plate with no observable scuto-scutellar suture. Also correlated with the loss of the hind wings is the absence of any axillary sclerites. The precosta of the postnotum lies beneath the scutellum, and the antecosta fuses with the metapleura laterally.

#### *The pleuron*

*Propleuron* (Fig. 48). On each side, the propleuron is seen as a narrow crescent-shaped sclerite divided into the episternum and epimeron by the pleural suture. Anteriorly, the episternum articulates with the cervical sclerite and the lateral arm of the basisternum.

*Mesopleuron* (Fig. 48). On the anterior membranous area of each mesopleuron is a single basalar sclerite. The mesopleural wall is divided by a short pleural suture into the episternum and epimeron. These two regions are further subdivided by the precostal suture into the anapleural area and the katapleural area. The posterior margin of the epimeron is almost separated from the postalar bridge by a membranous cleft. The postcoxal bridge is absent; therefore, a membranous area separates the epimeron from the furcasternum. On the postalar bridge a membranous slit occurs. In the membranous area posterior to the pleural arm are the anterior and posterior subalar sclerites. The anterior subalar sclerite is greatly membranous. The posterior subalar sclerite is also greatly reduced.

*Metapleuron* (Fig. 48). Each of the metapleura is divided by the pleural suture into a greater episternum and a lesser epimeron. The precoxal suture is seen in both areas. Due to the loss of the hind wings there is a corresponding loss of the pleural wing processes. The dorsal margin of each metapleuron is smooth, and a ridge runs along the entire length of the margin.

#### *The sternum*

*Prosternum* (Fig. 48). The lateral arms of the basisternum extend forward to articulate with the cervical sclerites. The cervical sclerites of *Isca (Tanycola)* are acutely bent. The basisternum possesses a Y-shaped carina. The furcasternum is smooth and rectangular. The two sternal apophyses are well developed with an expanded basal part. The katepisterna are absent between the basisternum and the coxae.

*Mesosternum* (Fig. 48). The presternite fuses with the prealar bridge and an apodeme is well developed at each of the two points of fusion. The basisternum is a smooth square plate which is a little expanded basal-laterally. The lateral margins are not completely fused with the episterna. In *Isca (Tanycola)* there is a membranous cleft almost separating the entire lateral margin of the basisternum from the episternum. The posterior margin of the basisternum, and the two submedian longitudinal margins of the median invagination form an inverted U-shaped pattern. Both the posterior and lateral margins of the furcasternum are separated by a membranous area from the metasternum and the epimera respectively.

*Metasternum* (Fig. 55). The metasternum is a simple plate which fuses laterally with the first abdominal segment. At the anterolateral angles where it fuses with the episterna, two finger-like structures of pleural origin project into the membranous area.

### Discussion

#### *Comparison of homologous structures in the imaginal thoraces of the selected genera of Leptophlebiidae*

The section deals with the comparative aspect of certain structures in the imaginal thorax. Variations between homologous structures in selected genera (based on the representative species) are discussed. The information presented in this section, and other data, will form the basis for a phylogenetic analysis in a subsequent section.

#### *The tergum*

*Pronotum*. The six genera studied indicate that little variation occurs in the pronota. The observable variations among the six genera are the many degrees of differentiation of the acrotergite. In *Leptophlebia* and *Aprionyx* the acrotergites are weakly defined. In *Paraleptophlebia*, *Habrophlebiodes*, *Traverella*, and *Isca (Tanycola)* the acrotergites are well developed. In *Paraleptophlebia* the antecostal suture bears a pair of apodemes on the submedian area. Variations in the relative length of the median notal suture occur also in the genera studied. A shorter median notal suture occurs in *Leptophlebia* and *Paraleptophlebia*. An intermediate condition occurs in *Aprionyx* and *Traverella*, whereas this suture is elongated in *Habrophlebiodes* and *Isca (Tanycola)*.

*Mesonotum*. The mesonota of the six genera examined show variations in: the shape of the scutal shield, the structure of the median notal suture, the shape and structure of the inner and outer parapsidal sutures, the number of axillary sclerites, and the shape of the posterior margin of the scutum-scutellum area. Among the six genera observed, two types of scutal shields can be characterized. In *Leptophlebia* the scutal shield is elongated, whereas the scutal shield is rounded in the remaining genera. The most anterior hump of the scutal shield also has two kinds of variation: *Aprionyx*, *Leptophlebia*, *Paraleptophlebia*, and *Habrophlebiodes* have a rounded and a little pointed hump, whereas *Traverella* and *Isca (Tanycola)* have a broad and blunt anterior hump. Variations in the structure of the median notal suture and the inner and outer parapsidal sutures can be placed into three groups. In the first group the inner and outer parapsidal sutures are narrower than the median notal sutures; to this group belong *Leptophlebia*, *Paraleptophlebia*, and *Habrophlebiodes*. In the second group, the parapsidal sutures are as broad as the median notal suture; *Aprionyx* and *Traverella* belong to this group, but comparatively these sutures are broader in *Traverella* than in *Aprionyx*. In the third group, the median notal suture and the outer parapsidal sutures become membranous, and the inner parapsidal sutures are weakly defined; *Isca (Tanycola)* belong to this group. In the fore wing in *Aprionyx* there are three axillary sclerites, while in the other five genera there are two axillary sclerites. The second axillary sclerite of *Isca (Tanycola)* is peculiar in having a socket-like anterior end to articulate with the first axillary sclerite. The posterior margin of the scutum-scutellum varies. It is truncated in *Leptophlebia*, *Paraleptophlebia* and *Habrophlebiodes*, slightly rounded in *Aprionyx* and pointed in *Traverella* and *Isca (Tanycola)*.

*Metanotum.* This study has indicated that the structural pattern of the metanotum is different for each genus. In the six genera studied, the metanota of *Leptophlebia* and *Paraleptophlebia* are most similar to each other. They differ slightly in the length of the antecosta of the postnotum and both genera possess two axillary sclerites in each of the hind wings. In *Habrophlebiodes*, due to the reduction of the hind wings, only one axillary sclerite is found. Also correlated with the reduced hind wings are the greatly membranous scuto-scutellar suture and the reduced scutellum. *Aprionyx* and *Traverella* also possess two axillary sclerites in each hind wing. In *Isca (Tanycola)* due to the absence of the hind wings, the scutum and scutellum are fused, with the complete loss of the scuto-scutellar suture. There are no axillary sclerites in the metanotum of *Isca (Tanycola)*.

#### *The pleuron*

*Propleuron.* The structural pattern of the propleuron is relatively stable among the genera studied. Variations occur mainly in the degree of sclerotization and in the formation of a dorsal apodeme by the propleural wall. The propleura are well developed in *Leptophlebia*, *Paraleptophlebia*, and *Aprionyx*. *Habrophlebiodes*, *Traverella* and *Isca (Tanycola)* all possess various degrees of desclerotization of the propleura, especially *Isca (Tanycola)* where the propleura are greatly reduced. In *Leptophlebia*, *Paraleptophlebia*, *Habrophlebiodes*, and *Aprionyx*, each propleuron forms an apodeme on its mid-dorsal region. This apodeme is absent in *Traverella* and *Isca (Tanycola)*.

*Mesopleuron.* Of the six genera studied, the following morphological differences occur in the mesopleura: the number of basalar sclerites, the presence or absence of an apodeme on the pleural arm, the various degrees of membranization in the epimeron, the presence or absence of the postcoxal bridge, the structure of the anterior subalar sclerite, and the presence or absence of a membranous slit in the postalar bridge. Among the six genera studied, *Leptophlebia* possesses two basalar sclerites, and all of the other five genera possess only one basalar sclerite. The mesopleura of *Leptophlebia* and *Paraleptophlebia* are very similar, possessing an apodeme on the pleural arm obliquely dorsal in position to the pleural suture. This apodeme is absent in all other genera observed. The epimera of *Leptophlebia*, *Paraleptophlebia* and *Aprionyx* are entire and well sclerotized. In *Habrophlebiodes* a membranous notch occurs at the posterodorsal margin of the epimeron. In *Isca (Tanycola)* this is represented by a membranous elongated slit and in *Traverella* a membranous area separates the entire epimeron from the postalar bridge. The postcoxal bridge is present in *Leptophlebia*, *Paraleptophlebia*, *Habrophlebiodes*, and *Aprionyx*, but it is absent in *Traverella* and *Isca (Tanycola)*. The postalar bridge of *Isca (Tanycola)* is peculiar in having a transverse membranous slit. This feature is absent in all of the other five genera studied. Preliminary investigation shows that the anterior subalar sclerite and the pleural wing process vary in their shapes among the different genera. Due to the difficulty in staining and studying these regions, they are not discussed in this study.

*Metapleuron.* As in the metanota, the metapleura of the genera studied show many morphological differences, in the presence or absence of a subalar sclerite and structure of the pleural wing process, precoxal suture, epimeron, and the ventropleurite. *Leptophlebia*, *Paraleptophlebia*, and *Habrophlebiodes* are most similar to each other, all possess a carina in the epimeron immediately ventral to the precoxal suture. The shape of this carina is

narrow in *Leptophlebia* and *Paraleptophlebia*, but it is much wider in *Habrophlebiodes*. All three genera possess a ventropleurite. Among these three genera, *Leptophlebia* possesses a subalar sclerite, but *Paraleptophlebia* and *Habrophlebiodes* lack it. Also, the pleural wing processes are reduced in *Paraleptophlebia* and to a greater extent in *Habrophlebiodes*. *Aprionyx* is characterized by the absence of the precoxal suture in the epimeron. In addition the epimeron in *Aprionyx* is separated from the antecosta of the postnotum by the antecostal-epimeral suture. *Traverella* and *Isca* (*Tanycola*) are characterized by a greatly membranous ventropleurite. In *Isca* (*Tanycola*) the pleural wing processes are entirely lost due to the absence of hind wings.

### *The sternum*

*Prosternum.* In the six genera studied, the posternum is characteristic for each genus. The Y-shaped carina of the basisternum shows many minor variations among the six genera. The shape of the furcasternum is also variable. *Leptophlebia* has a square furcasternum, while that of *Traverella* is a truncated triangle. The remaining genera studied all have a rectangular furcasternum.

*Mesosternum.* From the standpoint of comparative morphology, the mesosterna of the different genera of Leptophlebiidae are most interesting as they offer very clear and distinct differences that readily allow comparison. In the six genera of Leptophlebiidae observed, the mesosterna can be grouped into three different types. In the first type, the median longitudinal invagination of the furcasternum is narrow and widens slightly at both the anterior and posterior ends. To this group belong *Leptophlebia*, *Paraleptophlebia*, and *Habrophlebiodes*. *Leptophlebia* can be distinguished by the narrower and more acute posterior margin of the basisternum, while the basisternum of *Paraleptophlebia* has a broader and rounder posterior margin. Also, in *Leptophlebia* the lateral margins of the median longitudinal invagination do not reach the posterior margin of the furcasternum. In *Paraleptophlebia* the lateral margins of the median longitudinal invagination extend to the posterior margin of the furcasternum. The mesosternum of *Habrophlebiodes* can be distinguished from those of *Leptophlebia* and *Paraleptophlebia* in both the basisternum and the furcasternum. The basisterna of *Leptophlebia* and *Paraleptophlebia* possess a carina which is absent in *Habrophlebiodes*. In addition, the median longitudinal invagination is less than half the length of the furcasternum in *Habrophlebiodes*, and in *Leptophlebia* and *Paraleptophlebia* the median longitudinal invagination is much longer. The second type of mesosternum is represented by *Aprionyx* which has a smooth basisternum similar to that of *Habrophlebiodes*. However, the median longitudinal invagination is wider than the first type. The two lateral margins of the invagination are almost parallel. The third type of mesosternum is found in *Traverella* and *Isca* (*Tanycola*) in which the width of the median longitudinal invagination in the furcasternum is greater than in the first and second types. Further, the lateral margins of the furcasternum are not fused to the epimera due to the loss of the postcoxal bridges. The posterior margin of the furcasternum is also separated from the metasternum by a membranous region. The mesosterna of *Traverella* and *Isca* (*Tanycola*) differ in the way that the basisternum is fused with the furcasternum. In *Traverella* the lateral margins of the basisternum are continuous with the lateral margins of the median longitudinal invagination of the furcasternum. In *Isca* (*Tanycola*) the lateral margins of these two regions are not fused.

*Metasternum*. The structure of the metasternum is nearly constant in the *Leptophlebiidae*. It is a simple rectangular sclerite. Only two types of metasterna are found in the six genera of *Leptophlebiidae* observed. In the first type the metasternum possesses a median longitudinal carina. This group includes *Leptophlebia* and *Paraleptophlebia*. In the second group, *Habrophlebiodes*, *Aprionyx*, *Traverella*, and *Isca* (*Tanycola*) this median longitudinal carina is absent.

*Sexual dimorphism in the thorax of the imagos*

One of the objectives of this study was to investigate whether sexual dimorphism occurs in the thorax of the *Leptophlebiidae*. Unless otherwise stated all data pertain to *Leptophlebia pacifica*.

Most female specimens observed were weakly sclerotized and had to be stained in acid fuchsin to recognize the various sclerites. On the other hand, the male specimens were usually very well sclerotized. It is not known whether this phenomenon is genetic or whether the male and female exoskeletons react differently to the preservatives. Further investigation is required to determine the nature of this differential sclerotization.

TABLE I  
*Species of Leptophlebiidae examined*

Genus	Species	Form	Sex	Distribution of genus
<i>Leptophlebia</i> Westwood	<i>L. pacifica</i> (McDonnough)	Imagos	♂♀	Holarctic
		Nymphs	♂♀	
	<i>L. cupida</i> (Say)	Imagos	♂♀	
	<i>L. intermedia</i> (Traver)	Imagos	♂	
<i>Paraleptophlebia</i> Lestage	<i>P. bicornuta</i> McDunnough	Imagos	♂♀	Holarctic
	<i>P. packi</i> Needham	Imagos	♂♀	
<i>Habrophlebiodes</i> Ulmer	<i>H. brunneipennis</i> Berner	Imagos	♂	Oriental & Eastern Nearctic
<i>Aprionyx</i> Barnard	<i>A. tricuspидatus</i> Crass	Imagos	♂♀	Ethiopian (extreme southern portion of Africa)
	<i>A. natalicus</i> (Lestage)	Imagos	♂♀	
<i>Traverella</i> Edmunds	<i>T. albertana</i> Edmunds	Imagos	♂♀	Nearctic & Neotropical
<i>Isca</i> Gillies				
Subgenus <i>Tanycola</i> Peters & Edmunds				
	<i>I. (T.) serendiba</i> Peters & Edmunds	Imagos	♂	Oriental

Most often females of various species of *Leptophlebiidae* are larger than the corresponding males. Some metric comparisons were made on specimens of several species by measuring the length of the notum (a straight line in dorsal aspect from the anterior margin of the pronotum to the hind margin of the metanotum) and the width of the mesonotum (between the two anterior notal wing processes). The difference in the measurements between the males and females were tested statistically by the one-tailed *t* test with the level of significance set at 95 %. The results are given in Tables II and III. The length of the mesothorax in the females is significantly longer than the males in *Habrophlebia vibrans* (Needham), *Leptophlebia cupida*, and *Ulmeritus uruguayensis* Traver. For *Atalonella* sp. although

$P < 0.10$ , but with a  $t$  value of 2.07, the result is very close to the 95% level. *Habrophlebiodes americana* (Banks) is the only species in which the length of the mesothorax in the female is not significantly longer than that of the male (90%). The difference in the size of the male and female thorax is more evident when comparing the widths of the mesothorax. From Table III it can be seen that in all the species studied, the width of the mesothorax in the female is significantly greater than the male.

TABLE II

Comparison of the length of the thorax in the male and female imagos of some Leptophlebiidae, using the one-tailed  $t$  test

Species	Range (mm)		Mean (mm)		$t$	$N$	Level of significance
	♂	♀	♂	♀			
<i>Atalonella</i> sp.	2.00-2.20	2.00-2.50	2.09	2.21	2.07	13	$P < 0.10$
<i>Habrophlebia vibrans</i>	1.30-1.50	1.50-1.90	1.41	1.68	9.00	28	$P < 0.001$
<i>Habrophlebiodes americana</i>	1.30-1.50	1.40-1.60	1.42	1.49	1.72	22	$P = 0.10$
<i>Leptophlebia cupida</i>	3.00-3.50	3.10-3.70	3.19	3.46	4.28	38	$P < 0.001$
* <i>Ulmeritus uruguayensis</i>	1.80-2.40	2.30-2.80	2.15	2.54	8.67	38	$P < 0.001$

\* Measurements made from subimagos only.

TABLE III

Comparison of the width of the mesothorax in the male and female imagos of some Leptophlebiidae, using the one-tailed  $t$  test

Species	Range (mm)		Mean (mm)		$t$	$N$	Level of significance
	♂	♀	♂	♀			
<i>Atalonella</i> sp.	0.60-0.65	0.70-0.90	0.62	0.74	4.00	13	$P < 0.01$
<i>Habrophlebia vibrans</i>	0.40-0.50	0.50-0.70	0.44	0.60	6.96	28	$P < 0.001$
<i>Habrophlebiodes americana</i>	0.40	0.40-0.50	0.40	0.48	6.15	22	$P < 0.001$
<i>Leptophlebia cupida</i>	1.00-1.30	1.10-1.40	1.13	1.27	5.00	38	$P < 0.001$
* <i>Ulmeritus uruguayensis</i>	0.80-1.05	1.00-1.20	0.88	1.07	8.64	38	$P < 0.001$

\* Measurements made from subimagos only.

The male and female thoracic sclerites show no differences in shape and form. Therefore, the thorax morphology is useful in correctly associating conspecific male and female imagos. This fact is of particular importance in mayfly taxonomy since satisfactory methods for correctly associating males and females of a given species are limited. Most characters now used in diagnosing species are either sexually dimorphic, or are secondary sex characters. Previously, the only available method to correctly associate the sexes was to rear both sexes from the immature stage.

#### *Nymphal thoracic morphology*

The nymphal thorax of *L. pacifica* was studied with the intention of finding some external morphological characters that could correctly associate the nymphs and imagos of

a given species. Thoracic exoskeletons of a series of nymphs from early instars to late instars were examined. No attempt was made to determine the exact instar of each nymph, but all specimens possessed well developed abdominal gills. The size of these nymphal thoraces ranged from 1.50 to 5.00 mm.

This study indicated that the thoracic sclerites change very little from the early to late nymphal instars. The more obvious changes observed in the notum were the lengthening of the wing buds and the appearance of the outer parapsidal sutures in the later instars. In the pleuron, the anapleural and katapleural areas become more distinct in late instars. In a late instar nymph the basisternum of the mesothorax becomes more sclerotized and slightly convex medially. The mesofurcasternum becomes slightly bilobed in form.

No morphological correlations exist between the thoraces of the nymphs and the imagos. Therefore, the possibility of associating the nymph and the imagos of a given species on the basis of their external thoracic morphology is eliminated. However, it was found in this study that in the last nymphal instar the sternum of the imago can be seen through the thin cuticle of the nymph. Therefore, by knowing the sternum of the imago one can correctly associate the nymphs and imagos of a given species. This finding is of particular importance in mayfly taxonomy since at present the association of conspecific nymphs and imagos depends on rearing the nymphs to the imagos.

The comparative morphology of the nymphal thorax has not been thoroughly studied in this research. However, based on preliminary data, the thoracic exoskeletons of the nymphs display generic specificity. Because the nymphs and imagos of the Ephemeroptera have different rates of evolution, two independent sets of thoracic characters are available for phylogenetic studies. In future studies we plan to include descriptions and discussions of the nymphal thorax of various genera.

#### *Thoracic musculature of the Leptophlebiidae*

The thoracic muscles of the imagos of *L. pacifica* were studied in detail to learn the identity of various sclerites of the exoskeleton. A detailed description of the muscles of *L. pacifica* has been given in an earlier section of this study. However, further discussion of the observations and a comparison with the thoracic muscles of other mayflies is given here.

The thoracic musculature of the Ephemeroptera is characterized by the presence of a furcasternum-subalar sclerite muscle (II-5), a mesothoracic sternal apophysis-second axillary sclerite muscle (II-17), and the absence of the ventral longitudinal muscle between the meso- and metathoracic sternal apophysis. Matsuda (1956a) postulated that the musculature of insects is a "plastic system" in that the insertion and origin can shift within certain limits. This was demonstrated by comparing the data from this study and those obtained by Matsuda (1956b) for *Siphonurus columbianus*. For example, in the mesothorax of *L. pacifica*, muscle II-18 originates on the basicoxite and inserts partially on the first axillary sclerite. The homologous muscle in *S. columbianus* runs between the first axillary sclerite and the coxal process. The mesothoracic muscle II-9 of *L. pacifica*, when compared with the homologous muscle in *S. columbianus*, indicates a shifting of the origin from the prothoracic sternal apophysis to the presternite of the mesothorax. Matsuda described three axillary muscles in the metathorax of *S. columbianus*. In *L. pacifica*, only one axillary muscle was recorded. But muscle 78 (first axillary sclerite-coxa) as described by Matsuda

for *S. columbianus* can be homologized with muscle III-12 in *L. pacifica* postulating a dorsal shift from the first axillary sclerite to the anterior notal wing process. This dorsal shift is probably due to the weakly developed first axillary sclerite in the metathorax of *L. pacifica*. These findings support Matsuda's contention that innervation can be a basis for the homology of muscles but does not represent direct evidence for the homology of sclerites.

The organization of the thoracic muscles of *Leptophlebia* is further characterized by the absence of the basalar-coxal muscle which was reported by Maki (1938) to be present in *Ecdyonurus hyalinus*. Also the transverse muscle connecting the two mesothoracic coxae of *S. columbianus* is absent in *L. pacifica*. In the mesothorax of *L. pacifica* only one muscle is attached to the second axillary sclerite, while in *S. columbianus* two muscles are attached to the second axillary sclerite.

In the mesothorax of *L. pacifica* muscle II-22a, which runs between the subalar sclerite and the median plate, is of particular interest. This is the first time that such a muscle has been reported in the Ephemeroptera. The function of this muscle is very similar to those muscles occurring between the second axillary sclerite and the subalar sclerite in *Dissosteria* (Acridinae: Orthoptera) as described by Snodgrass (1935). It serves to transmit the pull exerted by the subalar muscles in depressing the wings. The similar function of this muscle between the Ephemeroptera and other pterygotes is considered by Matsuda (pers. comm.) as convergent evolution.

The fact that no muscles are attached to the basisternum of the pterothorax seems to support the view that the basisternum is secondary in development. Börner (1908) pointed out that the notopleural position is primitive for the dorsoventral muscle, and this condition is found in *L. pacifica*. The basisternum-postoccipital ridge muscle (I-9) in the prothorax of *L. pacifica* offers some difficulty in explanation. It may be postulated that this is a secondarily developed muscle, since the basisternum is not developed in the nymphal stage. This view can only be confirmed by further study of the musculature of the nymphs.

#### *Use of thoracic characters in taxonomy and phylogeny*

In order to determine which characters of the thorax of the imagoes are congeneric among the species a study was completed on the thoraces of three species of *Leptophlebia*, *L. pacifica*, *L. cupida* and *L. intermedia*. *Leptophlebia pacifica* is the largest among the three species studied, and its distribution is restricted to the northwestern portion of North America. *Leptophlebia cupida* is a little smaller than *L. pacifica*, and its range includes the northern and eastern United States. *Leptophlebia intermedia* is the smallest of these three species and occurs in the southeastern United States.

Examination of the notum, pleuron and sternum showed that no significant differences in shape and structure occur in these parts among the three species. The notum and pleuron display remarkable constancy within the genus. However, in the mesosternum the proportion of the length and width of the mesobasisternum and mesofurcasternum vary among the three species. This observation was further subjected to statistical analysis. Three characters, length of the mesosternum, width of the basisternum, and width of the furcasternum were plotted against each other. Their differences in proportion were visually illustrated by a triangular scatter diagram (Fig. 20). In this diagram the relative proportions and not the absolute sizes are compared. The percentage contributions to the sum of the



characters are plotted and not the actual value of a given character. Due to the scarcity of adult specimens, five specimens of *L. cupida* and *L. intermedia* were measured, and six specimens of *L. pacifica* measured were used. In this study only male imagos were used, and the specimens of each species were collected from the same locality and at the same period of time.

In Fig. 20, each species occupies a definite area, although an overlap occurs between *L. cupida* and *L. intermedia*. Each field is defined by a set of points and is more or less elongated, but differently orientated. Whether the close proximity of *L. cupida* and *L. intermedia* indicates a close phyletic relationship is difficult to determine without additional data. While the sample size is small, the diagram does show an allometric difference among the mesosterna of the three species.

Based on this study of three species of *Leptophlebia*, it appears that the diagnostic characters studied in the thorax are congeneric although some minor differences especially in size do occur between different species within a genus. The uniformity of species within other genera of Leptophlebiidae has been further substantiated by casual observation of other genera of the Leptophlebiidae. Therefore, we believe that detailed examination of the thorax of only one species per genus is normally sufficient for studies on the evolution of the leptophlebiid thorax, and the relationships of such studies to the phylogeny of the genera.

In this study an attempt was made to interpret the pleuro-sternal region of the Leptophlebiidae by the existing and conflicting evolutionary theories presented by Ferris (1940), Matsuda (1956*a, b*, 1960, 1963), and Du Porte (1965). Many insect groups were examined by these authors, however; except for Matsuda (1956*b*), none of these authors studied the Ephemeroptera. Since we have considered only one family of the Ephemeroptera in this study, and as our data appear to support the concept advanced by Matsuda (1956*b*), we have accepted his interpretation of the pleuro-sternal region. The basis of this concept stems from the work of Snodgrass (1927) and Weber (1928).

In Matsuda's revised hypothetical ancestral plan of the pleural wall, he considered the subcoxal ring, which was primitively complete, subsequently divided into the outer anapleural ring and the inner katapleural ring by the precoxal suture. In the course of evolution, the precoxal suture was reduced to various degrees in different groups of insects. He considered the primitive anapleural ring of the subcoxae to be composed of the anepimeron, anepisternum, pre-episternum, ventropleurite, and with two membranous clefts in the episternal region, namely the anapleural cleft and the basalar cleft. The subalare is considered to be tergal in origin and the basalare is pleural in origin. This concept and nomenclature was applied consistently in this study to interpret the pleural region and especially the pterothorax. In regard to the interpretation of the origin and evolution of the sternum we agree with Snodgrass's view (1927, 1935) that the primitive sternum consisted of an uninvginated open sternum.

Within the family Leptophlebiidae, *Leptophlebia* and *Paraleptophlebia* are considered to be the most plesiomorphic genera by Peters & Edmunds (1970). The species *Leptophlebia pacifica* was studied in detail as the genus *Leptophlebia* represents a primitive member of the Leptophlebiidae according to Peters & Edmunds (1970). The basic morphology of the imagos and nymphs was described for this species. Species of five other genera of various degree of specialization were also studied in the imaginal stage. While those genera selected and included for this study are from widely differing phyletic lines, detailed

studies of some closely related genera have also been made but not included herein. Further several genera of the other two related families within the superfamily Leptophlebioidea, the Ephemerellidae and Tricorythidae, were also examined. Finally, species of genera from the most primitive living family, Siphonuridae, were observed, e.g. *Siphonurus* and *Isonychia*. This method was most helpful in determining the plesiomorphic pattern of the leptophlebiid thorax and tracing the evolution of character traits among the various genera of Leptophlebiidae.

During the completion of this study it was often asked to what extent flight mechanics, and reduction of wing surface and venation influenced the morphology of the mayfly thorax. Reduction of the fore and hind wings has occurred to various extents in many phyletic lines of the Leptophlebiidae and the hind wings are independently lost in several lines. Therefore, it has been suggested verbally by several mayfly workers that the external thoracic morphology is of no importance in understanding the phylogeny and relationships of the leptophlebiid genera. This study has indicated that some morphological traits are influenced by flight mechanics and wing reduction. The reduction in the number of axillary sclerites and the desclerotization or loss of the scuto-scutellar suture in the metanotum is certainly correlated with the reduction to loss of hind wings. Those characters influenced by wing reduction are described below. However, the majority of the thoracic structures studied in this project appear to have little or no correlation with the flight mechanics and reduction of the wings. As discussed below many thoracic characters are similar in *Leptophlebia*, *Paraleptophlebia*, and *Habrophlebiodes*, even though the fore and hind wings of *Paraleptophlebia* are reduced compared to those of *Leptophlebia*, and even more reduced in *Habrophlebiodes*. Certainly the reduction of the wings of *Paraleptophlebia* and *Habrophlebiodes* indicates changes in the flight mechanics. Further, many of these same characters are modified in other phyletic lines irrespective of wing reduction.

While the evolution of the thorax within the Leptophlebiidae will be better understood when all genera of the Leptophlebiidae and more genera in more primitive families can be studied, some preliminary conclusions can now be given. Further, these conclusions appear to be important in understanding the phylogeny and relationships of the Leptophlebiidae. Only the imagos will be discussed herein, but preliminary investigation indicates that the thoraces of the nymphs will be important in further interpreting the phylogeny of the genera.

The leptophlebiid pronotum is a fairly constant feature. Essentially, it is a plate bisected by a median notal suture, and possesses an acrotergite at the anterior margin. Variations in the relative length of the median notal suture occur in the different genera studied. Prolongation of this suture appears to be an apomorphic character and appears in at least two apomorphic lines of descent as seen in *Habrophlebiodes* and *Isca* (*Tanycola*). This corresponds to daughter lines IB and IIB5a respectively in the phylogeny proposed by Peters & Edmunds (1970). A shorter median notal suture occurs in the plesiomorphic genera *Leptophlebia* and *Paraleptophlebia* [in daughter line IAI of Peters & Edmunds (1970)]. Some of the most primitive existing genera of mayflies, *Siphonurus* and *Isonychia*, still retain a relatively short median notal suture. The lengths of the median notal suture in *Aprionyx* and *Traverella* are of an intermediate condition. Their phylogenetic significance will be better understood when more comparative data are available.

Several differences of phylogenetic significance occur in the mesonotum. The scutal shield or hump can be characterized as rounded to elongate. The elongated shield is

apparently the plesiomorphic condition in the Leptophlebiidae, as it is also found in genera of other more primitive families of mayflies. Among the leptophlebiids this situation is retained only in *Leptophlebia*. All other genera of Leptophlebiidae observed have an intermediate condition or a rounded shield.

The median notal suture and the inner and outer parapsidal sutures of the mesonotum are also of phylogenetic significance. Based upon the six genera of leptophlebiids studied, these scutal sutures can be divided into threetypes. In the first type, the parapsidal sutures are much finer than the median notal suture; this arrangement occurs in *Leptophlebia*, *Paraleptophlebia*, and *Habrophlebiodes*. The first type of scutal sutures is probably characteristic of daughter line I in the phylogeny proposed by Peters & Edmunds (1970). In the second type, the median notal suture and the parapsidal sutures have a similar width; this condition occurs in *Aprionyx* and *Traverella*. The width of these scutal sutures in *Traverella* is larger than that in *Aprionyx*. In the third type, the median notal suture and outer parapsidal sutures are membranous and the inner parapsidal sutures are represented by two fine lines on the scutal surface; this is an apomorphic trait and is found in *Isca* (*Tanycola*). This third type has occurred independently in other genera of mayflies such as *Homeonueria* and *Oligoneuriella*.

In the genera of Leptophlebiidae observed, two axillary sclerites occur in the fore wing, except in *Aprionyx* which has three axillary sclerites. This condition in *Aprionyx* appears to be a plesiomorphic feature since three axillary sclerites are found in the fore wings of the primitive genera *Siphonurus* and *Isonychia*. It is highly probable that the three-sclerite condition occurred in the leptophlebiid ancestors, and in the course of evolution it was retained only in the phyletic line that gave rise to *Aprionyx* [daughter line IIA in the phylogeny proposed by Peters & Edmunds (1970)]. *Isca* (*Tanycola*) has the most specialized axillary sclerites of the genera studied, since a socket-like anterior articulating edge occurs in the second axillary sclerite.

The posterior area of the mesonotum known as the scutum-scutellum is truncated to pointed posteriorly. *Leptophlebia*, *Paraleptophlebia*, and *Habrophlebiodes* possess the truncated type. *Aprionyx* is intermediate and *Traverella* and *Isca* (*Tanycola*) possess a pointed type.

The configuration of the metanotum is specific for each genus, and is very useful in generic differentiation. A major trend of evolution of the metanotum has been the reduction to loss of the hind wings, a feature which has occurred several times in the Leptophlebiidae. Sometimes, correlated with the reduction of the hind wings, is the reduction in the number of axillary sclerites, and the membranization or loss of the scuto-scutellar suture. Reduction or absences of the hind wings is considered herein to be a specialized feature. *Leptophlebia*, *Paraleptophlebia*, *Aprionyx* and *Traverella* all possess two axillary sclerites in the hind wings. Although, the hind wings of *Paraleptophlebia* are relatively reduced, they are not accompanied by a reduction in the number of axillary sclerites. In the specialized genus *Habrophlebiodes* the lengths of the hind wings is one-ninth that of the fore wings. Only one axillary sclerite occurs in each wing, and a highly membranized V-shaped scuto-scutellar suture separates the scutum from the scutellum.

In *Isca* (*Tanycola*) the hind wings, along with their axillary sclerites, are absent. Also, the scutum and scutellum are inseparably fused.

In the propleuron, desclerotization has occurred several times in the phylogeny of the Leptophlebiidae. Although this phenomenon needs further study, desclerotization of the

propleuron is undoubtedly related to the structure and function of the prothoracic legs. Desclerotization of the propleuron is an apomorphic condition in leptophlebiids and occurs in *Habrophlebiodes*, *Traverella*, and *Isca* (*Tanycola*). The propleura are well developed in the primitive genera *Leptophlebia*, *Paraleptophlebia* and *Aprionyx*.

The basic structural pattern is fairly constant in all the genera observed. Therefore, leptophlebiid mesopleuron is conservative in evolution. The close affinity of *Leptophlebia* and *Paraleptophlebia* is well shown in that both genera possess an internal apodeme on the pleural arm obliquely dorsal in position to the pleural suture. This apodeme is absent in all other genera observed. This close affinity is in agreement with the phylogeny proposed by Peters & Edmunds (1970). *Leptophlebia* is the only genus that possesses an anterior basalar sclerite as well as a posterior basalar sclerite. The nature of the anterior basalar sclerite is difficult to determine. It is probably secondarily derived since no muscles are attached to it.

In the evolution of the mesopleuron, membranization has occurred in several of the lines of descent studied. Membranization is considered here to be an apomorphic condition. In such primitive genera as *Leptophlebia*, *Paraleptophlebia*, and *Aprionyx* the epimera are entire and well sclerotized. In the specialized genus *Habrophlebiodes* a membranized notch occurs in the posterodorsal margin of the epimeron. In *Isca* (*Tanycola*) this condition is represented by a membranized slit; in *Traverella* a membranous area separates the entire epimeron from the postalar bridge. The secondary membranization of the postcoxal bridge is of phylogenetic significance, because it is unique to the daughter lines IIB4 and IIB5 in the phylogeny proposed by Peters & Edmunds (1970). In the genera studied, the postcoxal bridge is present in *Leptophlebia*, *Paraleptophlebia*, *Habrophlebiodes*, and *Aprionyx*, but is membranous in *Traverella* and *Isca* (*Tanycola*).

The configuration of the metapleuron is specific for each of the genera of Leptophlebiidae studied. Morphologically, the metapleura of *Leptophlebia*, *Paraleptophlebia*, and *Habrophlebiodes* are similar as the relation of the precoxal suture to the pleural suture is similar in all three genera. Furthermore, they all have a carina ventral to the precoxal suture in the epimeron. This feature is not shared by the other genera studied and probably is characteristic of daughter line I as given by Peters & Edmunds (1970). A gradual reduction of the pleural wing processes occurs in *Paraleptophlebia* and *Habrophlebiodes*. This reduction can be correlated with the gradual reduction of the hind wings in these two genera and is considered to be an apomorphic character. Of all the genera studied, only *Leptophlebia* possesses a subalar sclerite in the metapleuron. This is probably a plesiomorphic condition since the subalar sclerite also occurs in the primitive genus *Siphonurus*.

Phylogenetically, the metapleura of *Aprionyx*, *Traverella*, and *Isca* (*Tanycola*) represent three distinct lines of evolution. The precoxal suture in *Aprionyx* does not extend into the epimeron, and the ventropleurite is not membranized. In *Traverella*, the precoxal suture extends into the epimeron, but the ventropleurite is highly membranous. In *Isca* (*Tanycola*) the precoxal suture extends into the epimeron but the pleural wing processes are lost, and replacing them is a smooth and straight dorsal margin for the metapleuron. The ventropleurite is highly membranous. It appears that the character states described above in these lines of evolution represent various degrees of specialization.

The configuration of the prosternum is specific for each genus. Further research on other genera is needed to interpret the evolution of the prosternum within the Leptophlebiidae.

The mesosternum includes some of the most useful characters with which to trace

evolutionary lines within the Leptophlebiidae. As discussed earlier in the section comparing the homologous structures of these six selected genera, three basic structural patterns were discovered.

In the first type the median longitudinal invagination of the furcasternum is narrow and widens slightly at both the anterior and posterior ends. *Leptophlebia*, *Paraleptophlebia*, and *Habrophlebiodes* possess this type. Further research may reveal that this type of mesosternum occurs in all genera included in the daughter line I as proposed by Peters & Edmunds (1970). Daughter line I represents an ancient Northern Hemisphere dispersal.

In the second type of mesosternum the median longitudinal invagination of the furcasternum is wider than the first type. The two lateral margins of the invagination are almost parallel to each other. This type is represented in the genus *Aprionyx* and some other Southern Hemisphere leptophlebiid genera. This second type corresponds to daughter line IIA of the phylogeny proposed by Peters & Edmunds (1970). Daughter line IIA includes a group of genera that exhibits a Paleantarctic dispersal.

The third type of mesosternum is represented in *Traverella* and *Isca* (*Tanycola*). In this type, the width of the median longitudinal invagination in the furcasternum is greater than in the first and second types. Also, the lateral margins of the furcasternum are not fused to the epimera and the metasternum. This is considered to be a specialized type and characteristic of daughter line IIB4 and IIB5 in the phylogeny proposed by Peters & Edmunds (1970); however preliminary data suggest that this type is not found in daughter line IIB1, IIB2, and IIB3.

The ancestral leptophlebiid mesosternum was probably composed of a narrow, flat basisternum and a furcasternum with a narrow, straight median longitudinal invagination. This pattern resembles that in the primitive existing members of the Ephemeroidea and Siphonuridae and Edmunds (1962) pointed out the Leptophlebiidae probably arose from a primitive stock that lead to the existing Ephemeroidea. From this hypothetical ancestor, evolution to the first type of mesosternum involved the development of a median carina in the basisternum and a widening of the median longitudinal invagination at the anterior and posterior ends of the furcasternum, as in *Leptophlebia* and *Paraleptophlebia*. The smooth and shield-like basisternum is secondarily derived in *Habrophlebiodes*. The shortening and widening of the median longitudinal invagination of the furcasternum is also secondarily derived.

The second type of mesosternum was probably derived by developing a smooth and shield-like basisternum and a further widening of the median longitudinal invagination, as seen in *Aprionyx*.

Evolution of the third type of mesosternum resulted in an extremely wide, median, longitudinal invagination, and at the same time it fused anteriorly with the posterior margin of the basisternum. The postcoxal bridge and the area between the mesosternum and metasternum became membranous as seen in *Traverella* and *Isca* (*Tanycola*).

The evolution of these mesosternal structures and their significance in interpreting the phylogeny of the genera will be better understood when all genera of the Leptophlebiidae have been studied. However, the present data appear to support the phylogeny of the genera as proposed by Peters & Edmunds (1970).

The metasternum varies little among the leptophlebiid genera. *Leptophlebia* and *Paraleptophlebia* are the only two genera that possess the median longitudinal carina. The fused mesosternum and metasternum are considered here as a plesiomorphic character found in

*Leptophlebia*, *Paraleptophlebia*, *Habrophlebiodes*, and *Aprionyx*. The separation of the mesosternum and metasternum by a membranous area, as shown by *Traverella* and *Isca* (*Tanycola*), is considered here to be apomorphic.

### Summary

Among the Ephemeroptera, the family Leptophlebiidae is one of the most diversified and widely distributed groups. Peters & Edmunds (1964, 1970) have conducted extensive studies on the generic classification and phylogeny of this family. Based on preliminary examination, Peters (1966) suggested the probable use of the thoracic exoskeleton for further phylogenetic studies. This study was undertaken to determine the basic morphology of the leptophlebiid thorax, and based on the study of selected genera of Leptophlebiidae to discover whether such data could be used to better understand the phylogeny and relationship of the leptophlebiid genera.

Because of its plesiomorphic nature and its relatively large size, *Leptophlebia pacifica* was studied in detail. The study of this species included the thoracic exoskeleton and internal musculature of the imagos and the thoracic exoskeleton of the nymphs. Because the structure of the nymphal thorax is relatively simple, a detailed study of the internal musculature was not made.

The imagos of six genera of various degrees of specialization were chosen for comparative study. They are *Leptophlebia*, *Paraleptophlebia*, *Habrophlebiodes*, *Aprionyx*, *Traverella* and *Isca* (*Tanycola*).

Sexual dimorphism in the thoraces of the imagos is expressed in two ways. The thorax of the males is usually more sclerotized than that of the females. Also, the thorax of the females is usually larger than that of the males. Beside these two points, the male and female thoraces are morphologically similar. Thus, the two sexes of a species can be correctly associated in cases where specific differences do exist.

The thoracic exoskeleton of the nymphs of *L. pacifica* was studied in detail and compared with the adult thorax, in the hope of finding morphological characters that could correctly associate conspecific nymphs and imagos. This was found to be impossible at the gross anatomical level because the nymphal thorax displays no resemblance to that of the imago. However, it was found that in the last nymphal instar the sternum of the imago can be seen through the thin sternal cutical of the nymph. Therefore, by knowing the sternal character of the imago one can correctly associate the old nymphs with imagos.

Three muscles are unique to the Leptophlebiidae and other mayflies. These are the furcasternum-subalar sclerite muscle, the mesothoracic sternal apophysis-subalar sclerite muscle, and the mesothoracic sternal apophysis-second axillary sclerite muscle. A study also confirmed the view of Matsuda (1956a) that the musculature is a "plastic system". The origin and insertion of a muscle can shift within certain limits. Also, for the first time, a median plate-subalar sclerite muscle was found in the Ephemeroptera. This muscle helps to depress the wings during flight. Since the dorsoventral muscles of the mesothorax are attached ventrally on the pleuron instead of the basisternum, the view is supported that the basisternum is secondarily developed.

Three species of *Leptophlebia* were examined to determine which thoracic characters of the imagos were congeneric. The species studied were *L. pacifica*, *L. cupida* and *L. intermedia*. Only similar sexes of the three species were compared. The thoracic characters of

the imagos remained constant among the three different species of the genus. However, allometric differences were detected in the mesosternum and were studied statistically. It appears that the diagnostic characters found in the thorax are congeneric, although some minor differences especially in size do occur between species of the same genus. This is further substantiated by examination of other genera of the Leptophlebiidae. Therefore we believe that detailed examination of the thorax of only one species per genus is normally sufficient for studies on the evolution of the leptophlebiid thorax, and the relationships of such studies to the phylogeny of the genera.

Evolution of homologous thoracic structures in the six genera was studied. An attempt was made to determine the plesiomorphic and various apomorphic natures of the thoracic structures. It was found that the pronotum is conservative in evolution. The mesonotum provided some characters of phylogenetic significance, namely, the median notal suture, the parapsidal sutures, the axillary sclerites, and the scutum. Three types of parapsidal and median notal sutures were discovered. The first type is shared by *Leptophlebia*, *Paraleptophlebia*, and *Habrophlebiodes*; the second type occurs in *Aprionyx* and *Traverella*, and the third type is represented in *Isca* (*Tanycola*). The metanotum was found to show generic specificity and is of taxonomic value. Based on Matsuda's (1963) concept of the ancestral insect pleuron, the evolution of the pleura of the pterothorax in the six genera of Leptophlebiidae was considered. The evolutionary trend of the pleuron is towards desclerotization which occurred to various extents in the several phyletic lines of the leptophlebiids studied. The metapleuron was found to be specific for each genus. The prosternum, with its many morphological variations, also proved to be of taxonomic value. The mesosternum was particularly significant in studying the relationships of the leptophlebiid genera. Three types of mesosterna were discovered, with *Leptophlebia*, *Paraleptophlebia*, and *Habrophlebiodes* possessing the first type, *Aprionyx* the second type *Traverella* and *Isca* (*Tanycola*) the third type.

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#### REFERENCES

- Börner, C. (1908). Die Tracheenkiem der Ephemeren. *Zool. Anz.* **33**: 806-823.  
Brodsky, A. K. (1970). Organization of the flight system of the mayfly *Ephemera vulgata* L. (Ephemeroptera). *Ent. Obozr.* **49**: 307-315.  
Daly, H. V. (1964). Skeleto-muscular morphogenesis of the thorax and wings of the honey bee *Apis mellifera* (Hymenoptera: Apidae). *Univ. Calif. Publ. Ent.* **39**: 1-77.  
Du Porte, E. M. (1965). The lateral and ventral sclerites of the insect thorax. *Can. J. Zool.* **43**: 141-154.

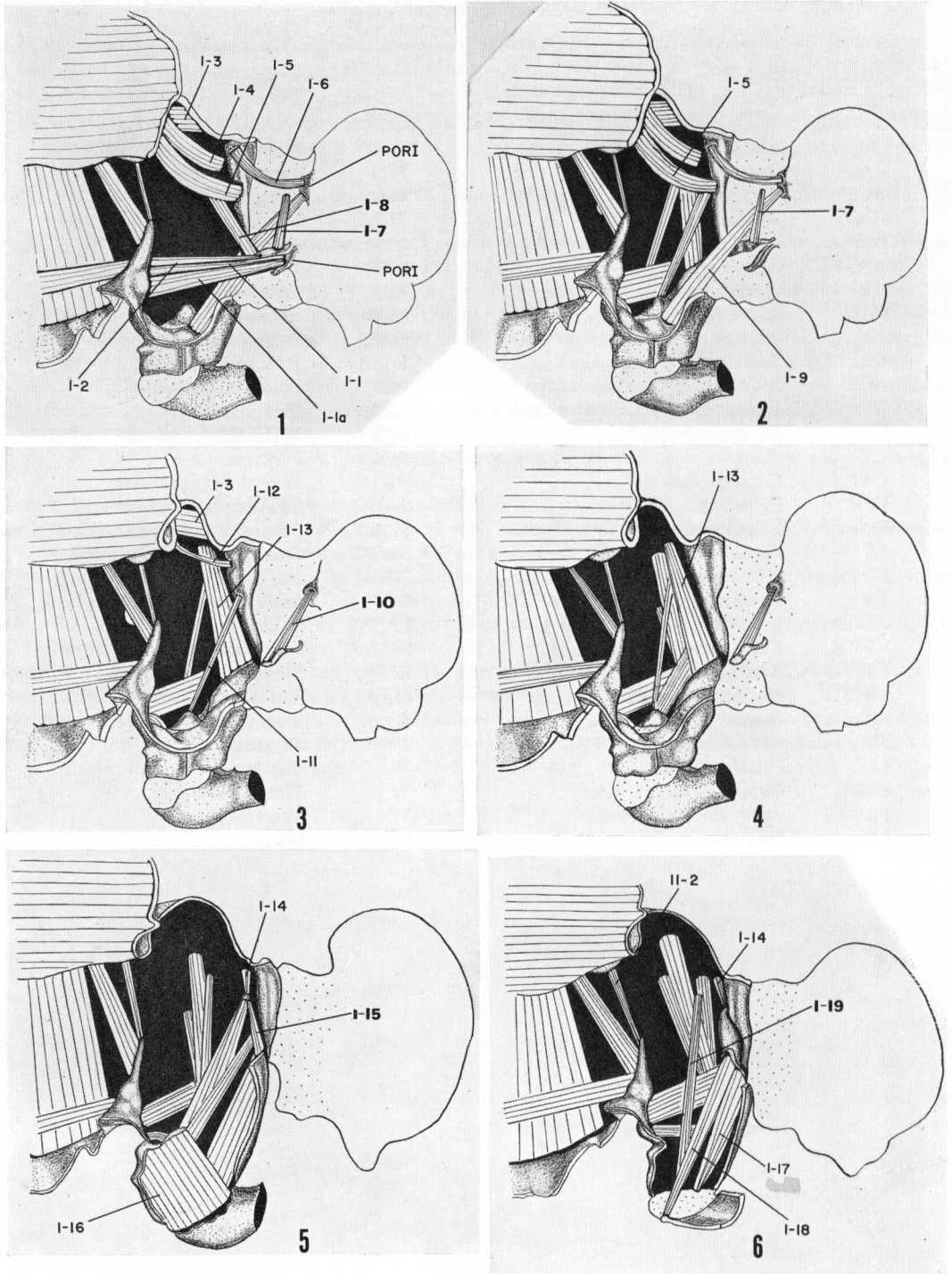
- Edmunds, Jr., G. F. (1962). The principles applied in determining the hierarchic level of the higher categories of Ephemeroptera. *Syst. Zool.* **11**: 22–31.
- Ferris, G. (1940). The myth of the thoracic sternites of insects. *Microentomology* **13**: 49–56.
- Grandi, M. (1947). Contributi allo studio delgi "Efemeroidei" Italiani VIII. Gli scleriti ascellari (pseudopteralia) delgi Efemeroidei, loro morfologia e miologia comparate. *Boll. Ist. Ent. Univ. Bologna* **16**: 85–114.
- Knox, V. (1935). The body wall and musculature of the thorax. In *The biology of mayflies with a systematic account of North American species*: 135–178. Needham, J. G., Traver, J. R. & Hsu, Yin-Chi (eds). Ithaca: Comstock Pubs.
- Landa, V. (1948). Contributions to the anatomy of Ephemerids larvae 1. Topography and anatomy of tracheal system. *Věsn. čsl. zool. Spol.* **12**: 25–82.
- Landa, V. (1959). Problems of internal anatomy of Ephemeroptera and their relation to the phylogeny and systematics of their order. *Int. Congr. Zool.* **15** (Pap. 54): 1–2.
- Landa, V. (1969). Comparative anatomy of mayfly larvae (Ephemeroptera). *Acta ent. bohemoslovaca* **66**: 289–316.
- Maki, T. (1938). Studies on the thoracic musculature of insects. *Mem. Fac. Sci. Agric. Taihoku imp. Univ.* **24**: 1–343.
- Matsuda, R. (1956a). The comparative morphology of the thorax of two species of insects. *Microentomology* **21**: 1–65.
- Matsuda, R. (1956b). Morphology of the thoracic exoskeleton and musculature of a mayfly *Siphonurus columbianus* (McDunn.) (Siphonuridae, Ephemeroptera). A contribution to the subcoxal theory of the insect thorax. *J. Kans. ent. Soc.* **29**: 92–113.
- Matsuda, R. (1960). Morphology of the pleurosternal region of the pterothorax in insects. *Ann. ent. Soc. Am.* **53**: 721–731.
- Matsuda, R. (1963). Some evolutionary aspects of the insect thorax. *A. Rev. Ent.* **8**: 59–76.
- Peters, W. L. (1966). *A revision of the generic classification of the Eastern Hemisphere Leptophlebiidae (Ephemeroptera)*. Doctoral Thesis. University of Utah, Salt Lake City.
- Peters, W. L. & Edmunds, Jr., G. F. (1964). A revision of the generic classification of the Ethiopian Leptophlebiidae (Ephemeroptera). *Trans. R. ent. Soc. Lond.* **116**: 225–253.
- Peters, W. L. & Edmunds, Jr., G. F. (1970). A revision of the generic classification of the Eastern Hemisphere Leptophlebiidae (Ephemeroptera). *Pacif. Insects* **12**: 157–240.
- Snodgrass, R. E. (1927). Morphology and mechanism of the insect thorax. *Smithson. misc. Collns* **80**: 1–108.
- Snodgrass, R. E. (1935). *Principles of insect morphology*. New York.
- Torre-Bueno, J. R. de la, (1950). *A glossary of entomology*. New York: Brooklyn Entomological Society.
- Weber, H. (1928). Die Gliederung der Sternopleuralregion des Lepidopteren-Thorax. Eine vergleichende Morphologische Studie zur Subcoxaltheorie. *Z. wiss. Zool.* **131**: 181–254.



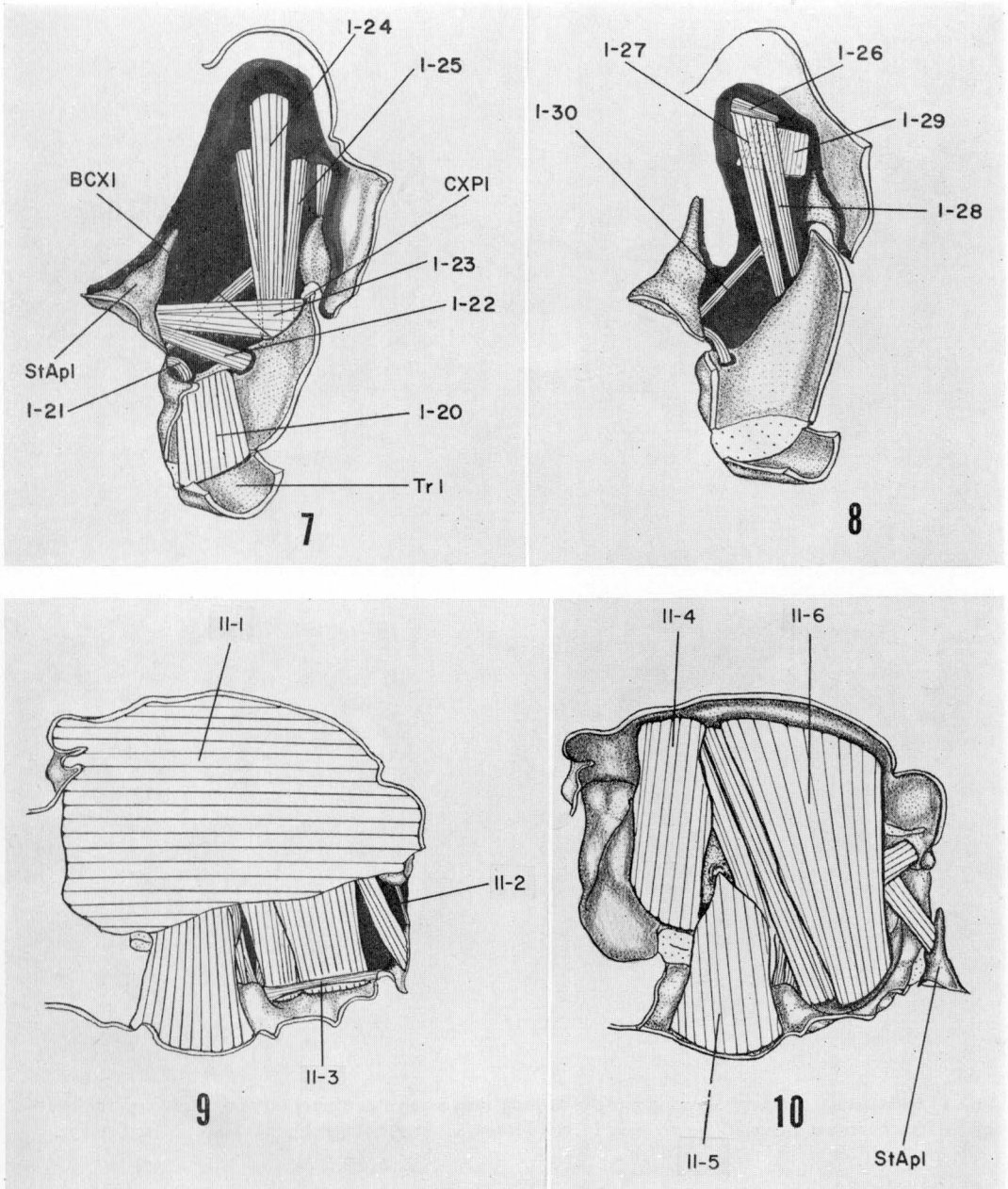
*Abbreviations used in figures*

In this study the terminology for the thoracic exoskeleton was mainly adapted from those of Know (1935) and Matsuda (1956*b*) and is as given below. New terms are given to those morphological structures which were not previously named by Knox (1935) or Matsuda (1956*b*). Pro-, meso- and metathoracic structures are distinguished from each other by Arabic numerals 1, 2 and 3 after the abbreviations.

AB	Abdominal segment	PCB	Postcoxal bridge
AC	Antecosta	PCS	Precostal suture
ACS	Antecostal suture	PH	Phragma
ANEP	Anepimeron	PLS	Pleural suture
ANP	Anterior notal wing process	PN	Postnotum
ANST	Anepisternum	PNP	Posterior notal wing process
AP	Apodeme	POR	Postoccipital ridge
ATG	Acrotergite	PrAl	Prealar bridge
AX	Axillary sclerite	PrScS	Prescutal suture
BA	Basalar sclerite (Basalare)	PrStAp	Presternal apodeme
BCX	Basicoxite	PrStS	Presternal suture
BS	Basisternum	PSC	Prescutum
CV	Cervical sclerite	PST	Presternite
CX	Coxa	PTR	Peritreme
CXP	Coxal process	PWP	Pleural wing process
EPM	Epimeron	SA	Subalar sclerite (Subalare)
EPS	Episternum	SaApl'	Subalar apodeme (Anterior)
FS	Furcasternum	SaAp2'	Subalar apodeme (Posterior)
FWP	Fore wing pad	SC	Scutum
HP	Humeral plate	SCT	Scutellum
HWP	Hind wing pad	SP	Spiracle
KEPM	Katepimeron	SSS	Scuto-scutellar suture
KEPS	Katepisternum	ST	Sternum
MNS	Median notal suture	StAp	Sternal apophysis
MP	Median plate	StApP	Sternal apophyseal pit
NF	Notal furrow	T	Tergum
PAL	Postalar bridge	TG	Tegula
PAR1	Parapsidal suture, inner	Tr	Trochanter
PAR2	Parapsidal suture, outer	VP	Ventropleurite
PC	Precosta	W	Wing

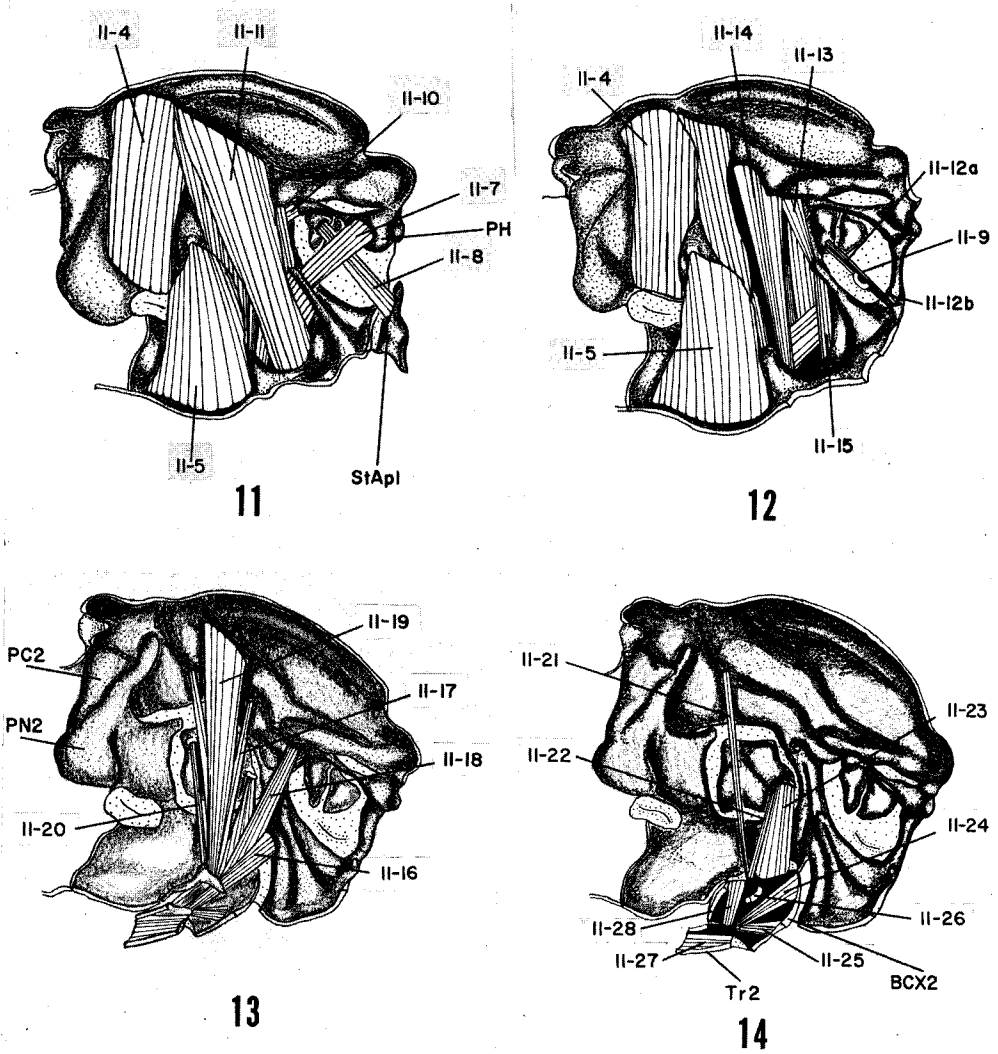


FIGS 1 to 6. Serial drawings showing muscles at progressive stages of dissection of the right sagittal half of the imaginal prothorax of *Leptophlebia pacifica*: 1, first stage; 2, second stage; 3, third stage; 4, fourth stage; 5, fifth stage; 6, sixth stage.

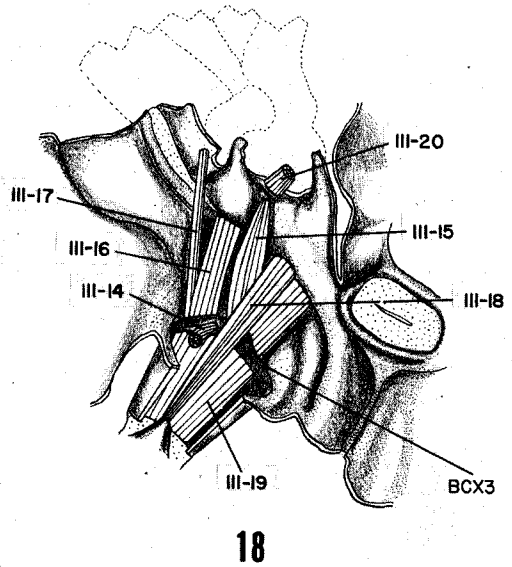
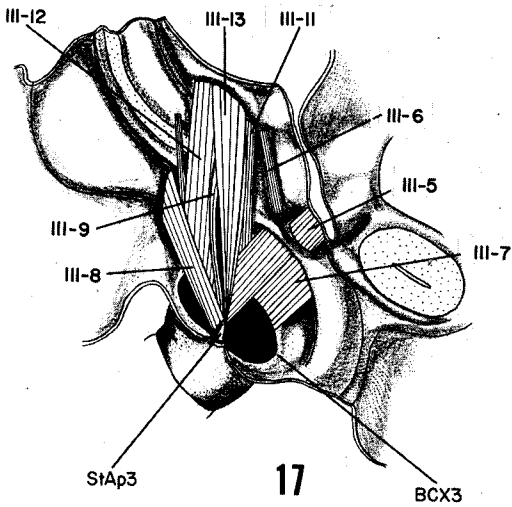
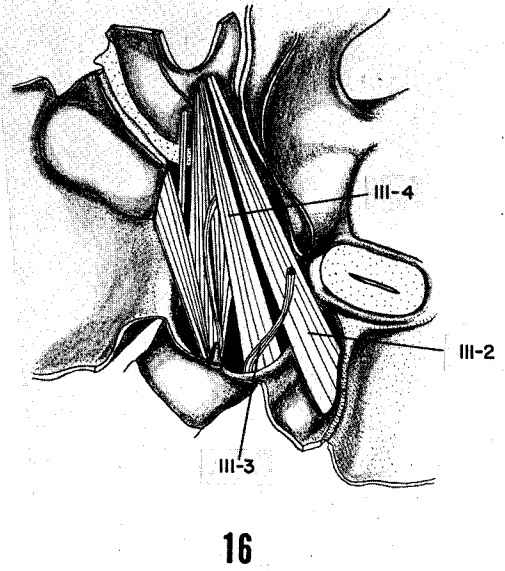
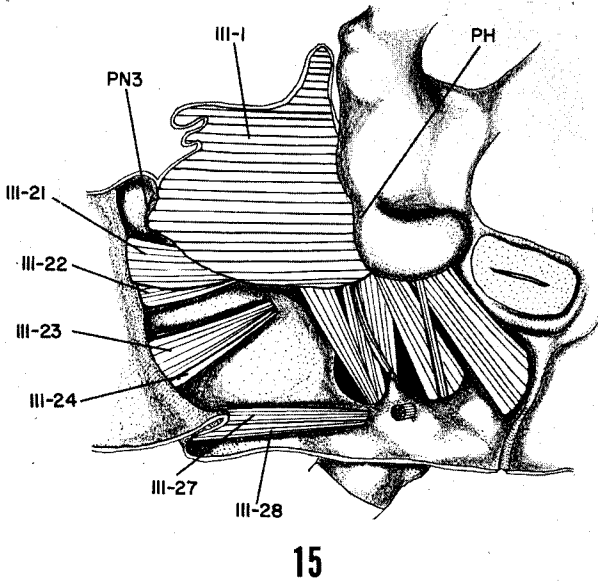


FIGS 7 and 8. Serial drawings showing muscles at progressive stages of dissection of the right sagittal half of the imaginal prothorax of *Leptophlebia pacifica*: 7, seventh stage; 8, eighth stage.

FIGS 9 and 10. Serial drawings showing muscles at progressive stages of dissection of the right sagittal half of the imaginal mesothorax of *Leptophlebia pacifica*: 9, first stage; 10, second stage.



FIGS 11 to 14. Serial drawings showing muscles at progressive stages of dissection of the right sagittal half of the imaginal mesothorax of *Leptophlebia pacifica*: 11, third stage; 12, fourth stage; 13, fifth stage; 14, sixth stage.



FIGS 15 to 18. Serial drawings showing muscles at progressive stages of dissection of the right sagittal half of the imaginal metathorax of *Leptophlebia pacifica*: 15, first stage; 16, second stage; 17, third stage; 18, fourth stage.

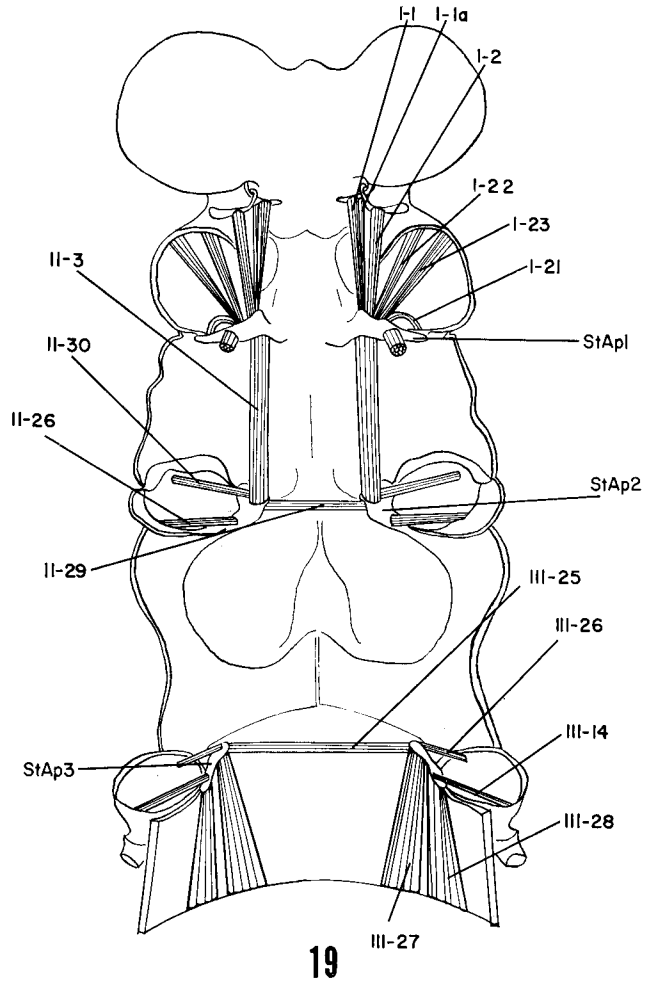


FIG. 19. Dorsal view of the ventral muscles of the imago of *Leptophlebia pacifica*.

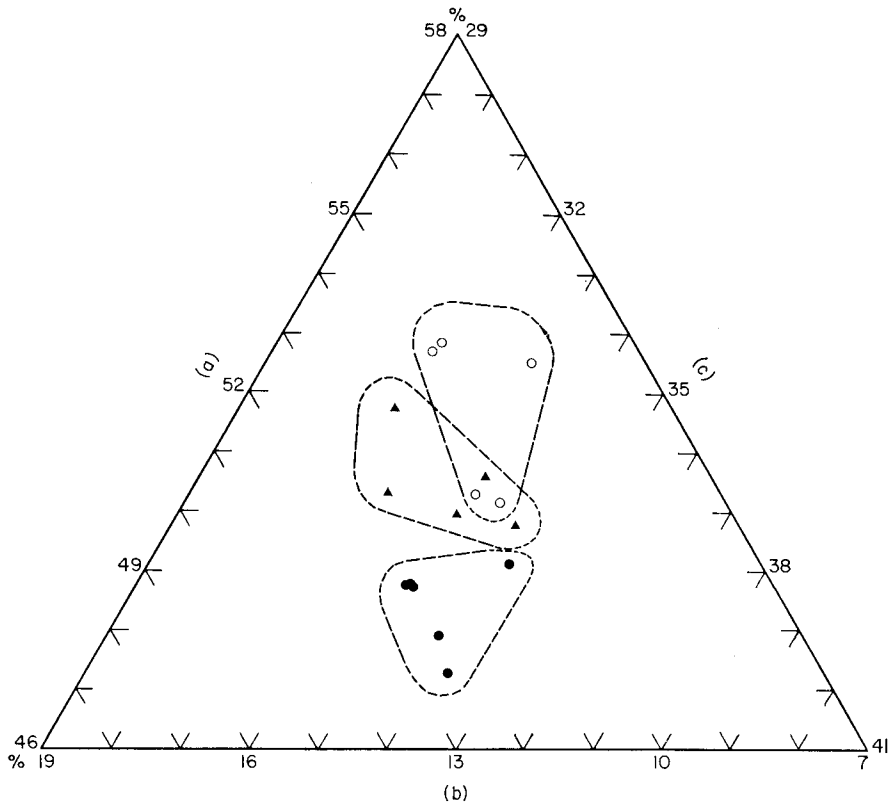
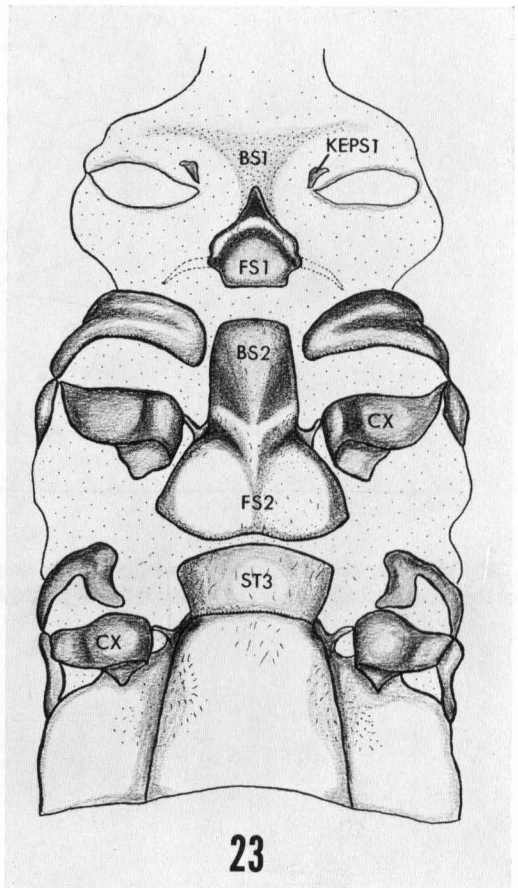
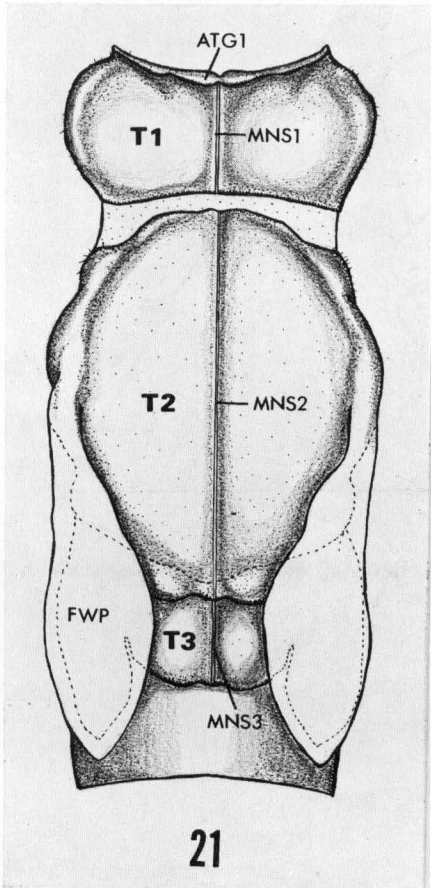
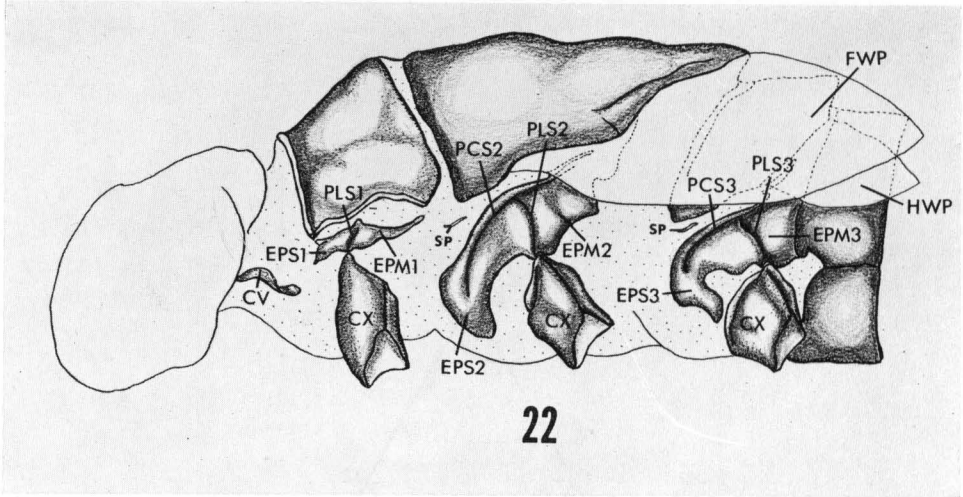
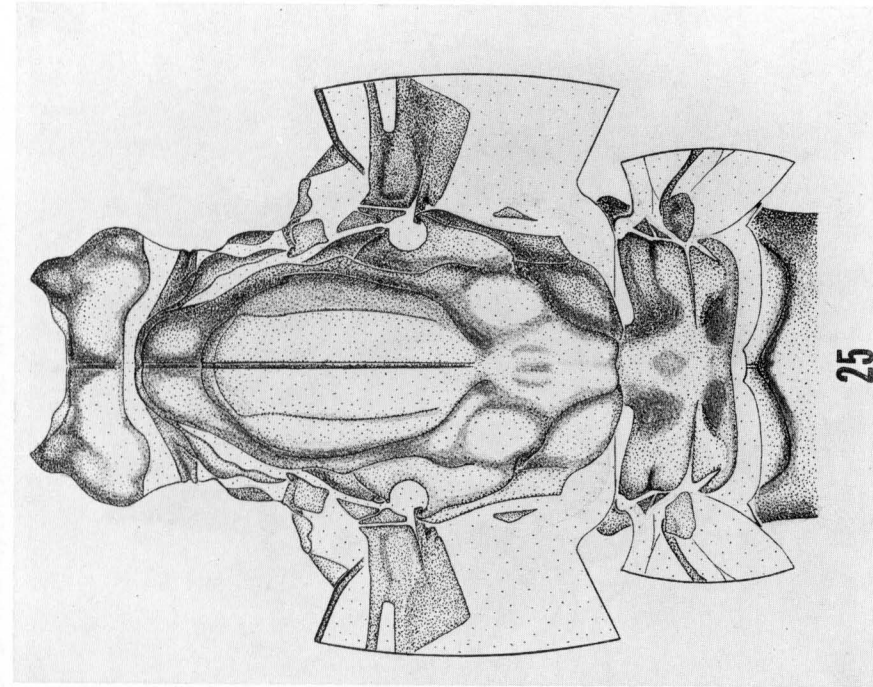


FIG. 20. Triangular graph indicating the length of the mesosternum (a), width of the mesobasisternum (b), and width of the mesofurcasternum (c) of three species of *Leptophlebia*.

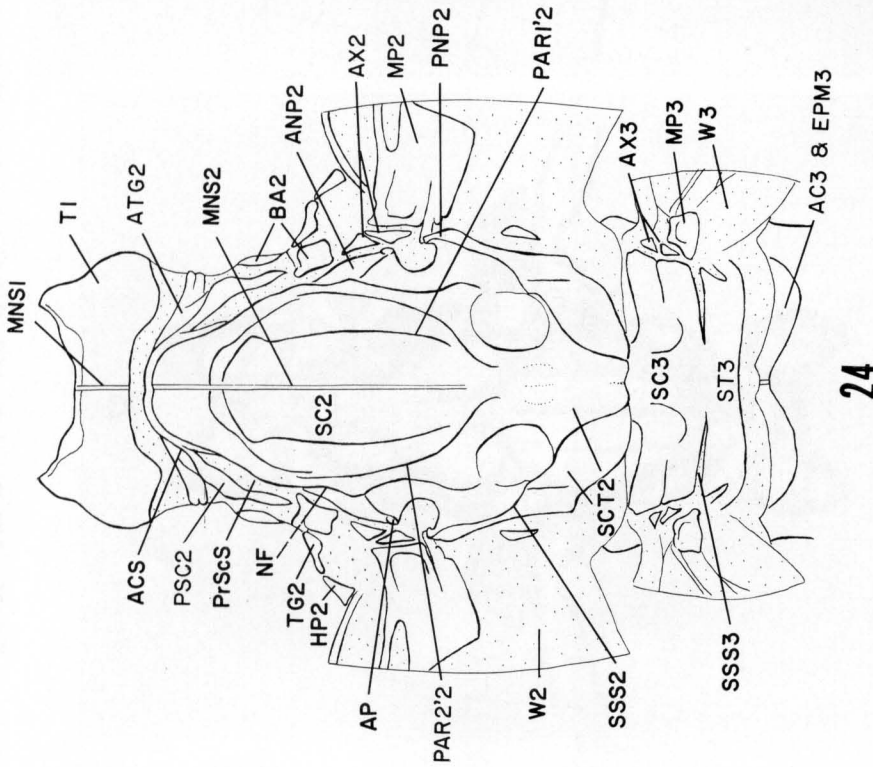


FIGS 21 to 23. Nymph of *Leptophlebia pacifica*: 21, dorsal view of the thoracic terga; 22, lateral view of the thoracic pleura; 23, ventral view of the thoracic sterna.



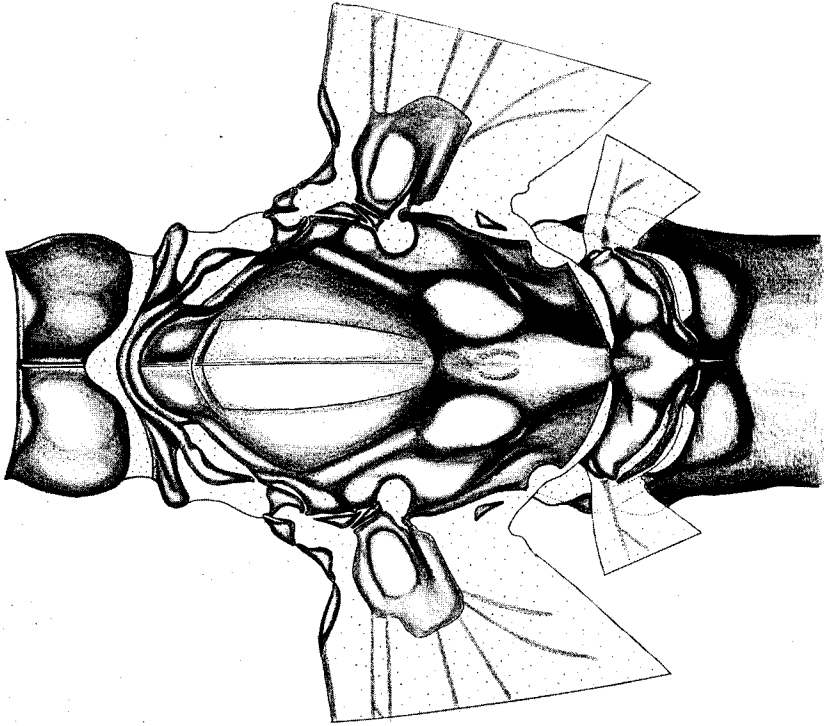


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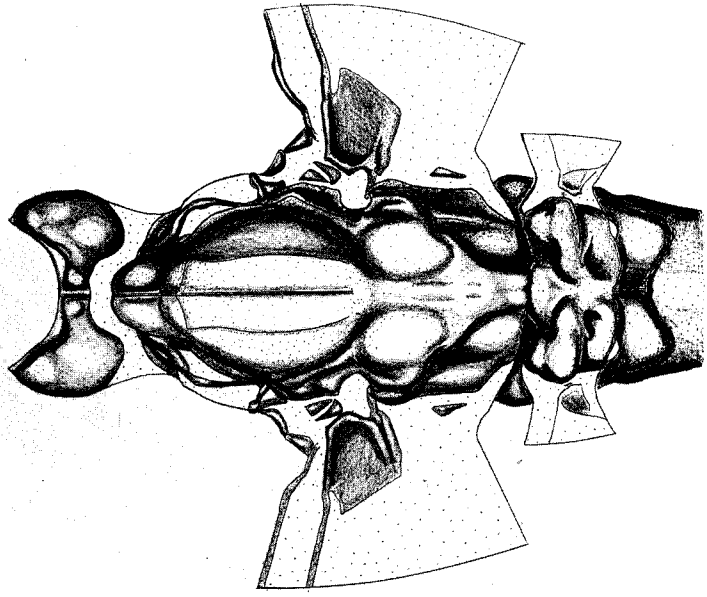


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Figs 24 and 25. Dorsal view of the thoracic terga of the male imago: 24, showing abbreviations of terminology used in paper; 25, *Leptophlebia pacifica*.

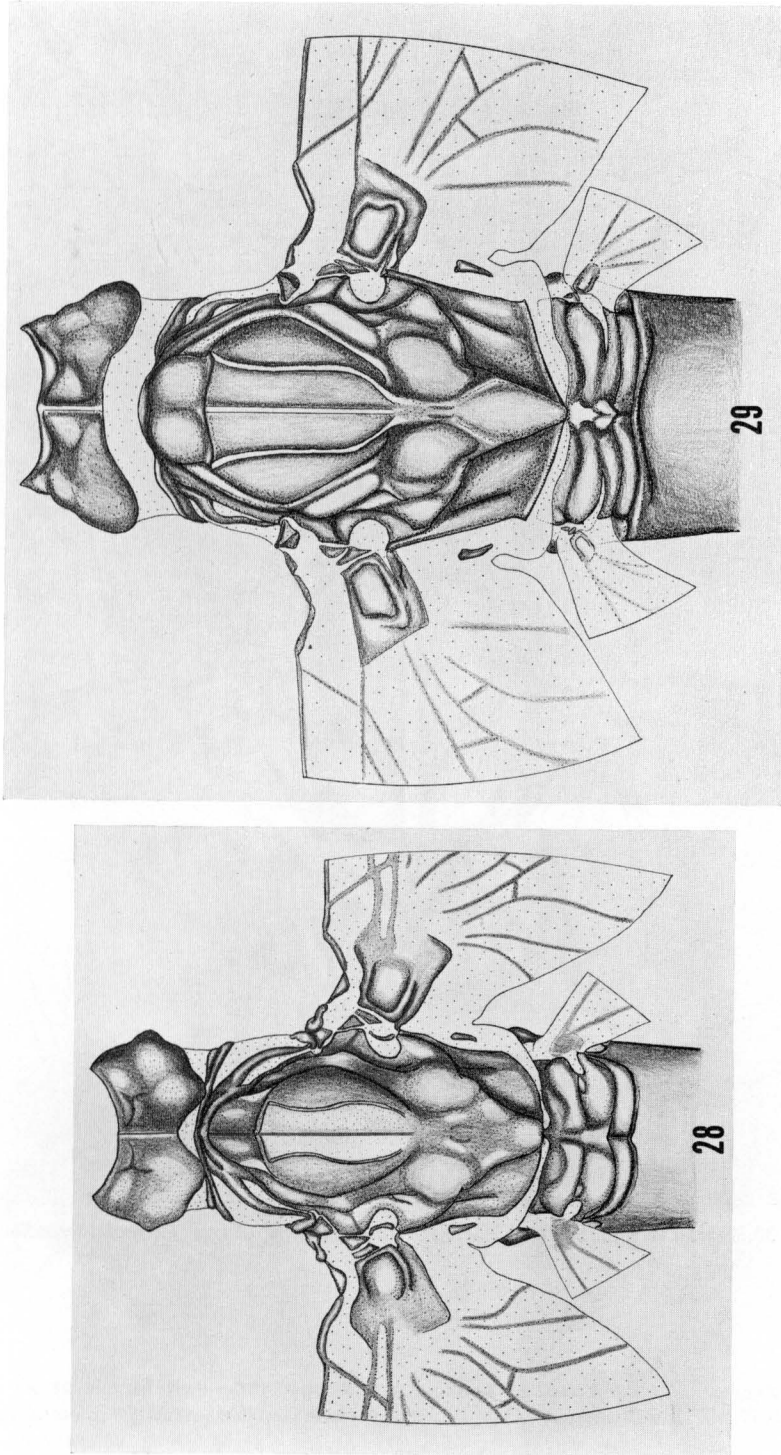


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FIGS 26 AND 27. Dorsal view of the thoracic terga of the male imago: 26, *Paraleptophlebia bicornuta*; 27, *Habrophlebiodes brunneipennis*.



FIGS 28 and 29. Dorsal view of the thoracic terga of the male imago: 28, *Aprionyx tricuspis*; 29, *Traverella albertana*.

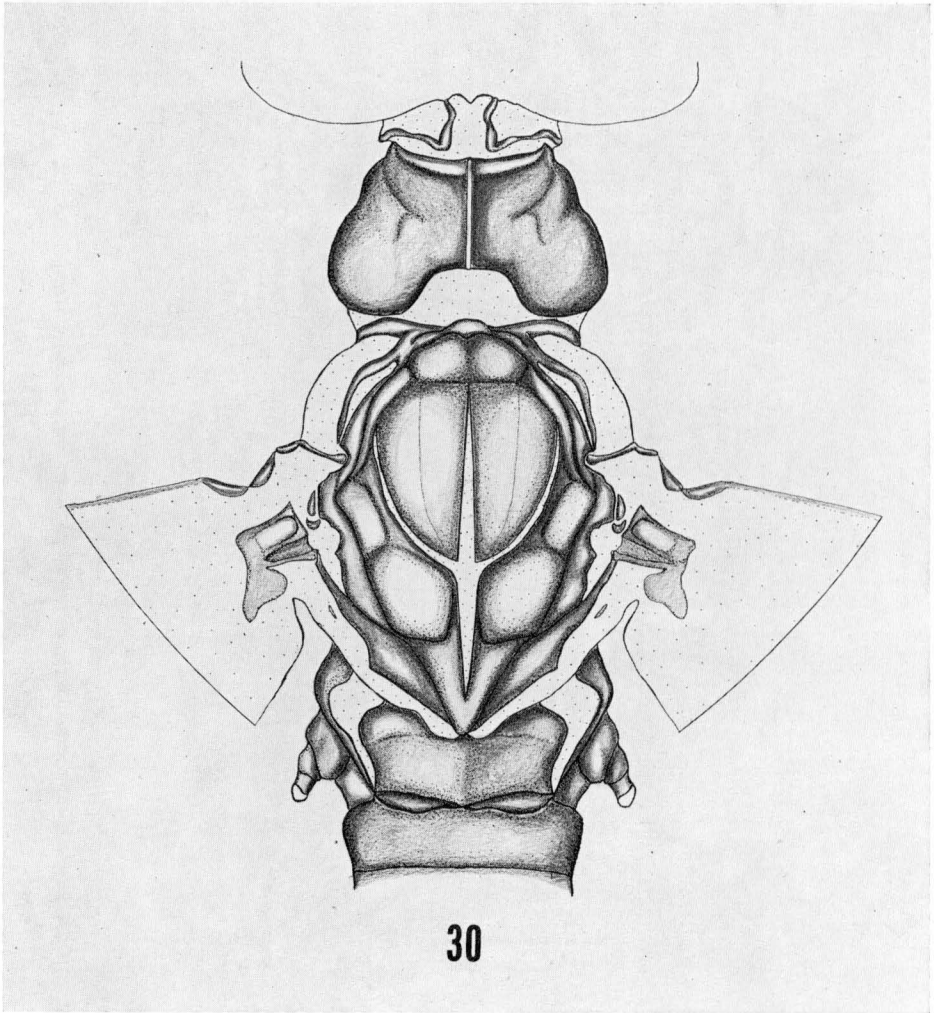
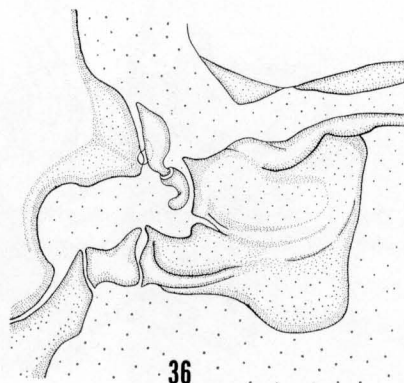
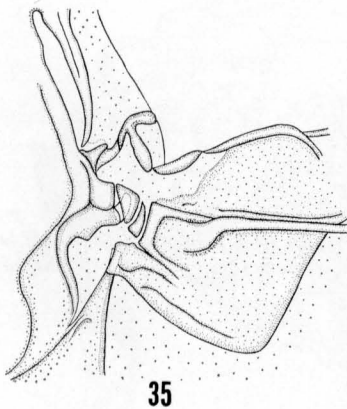
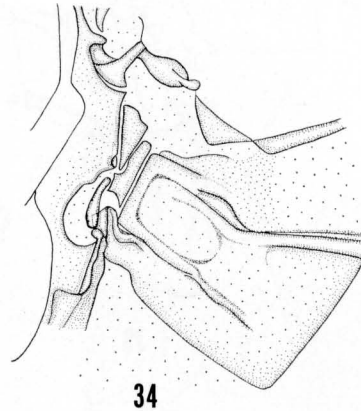
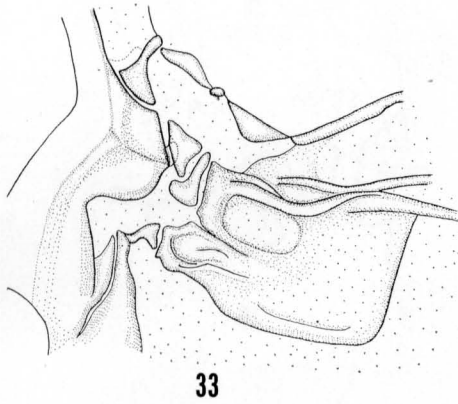
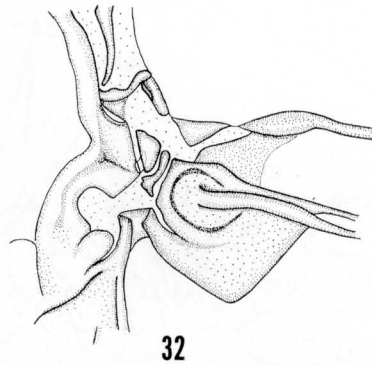
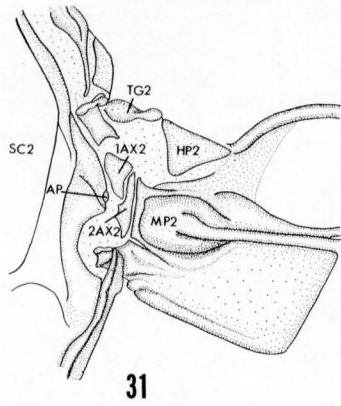
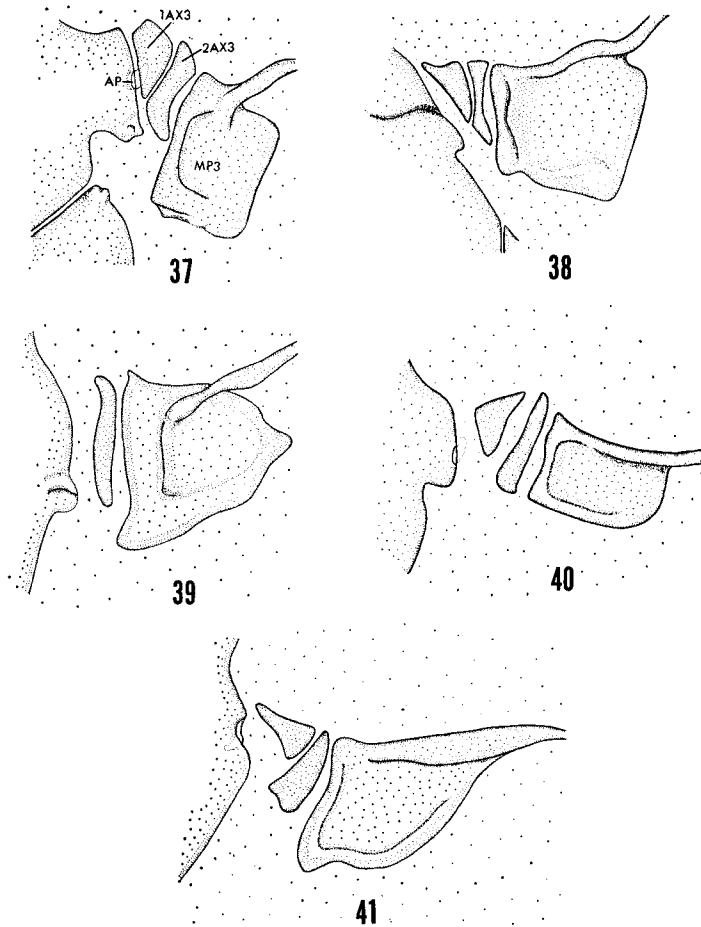


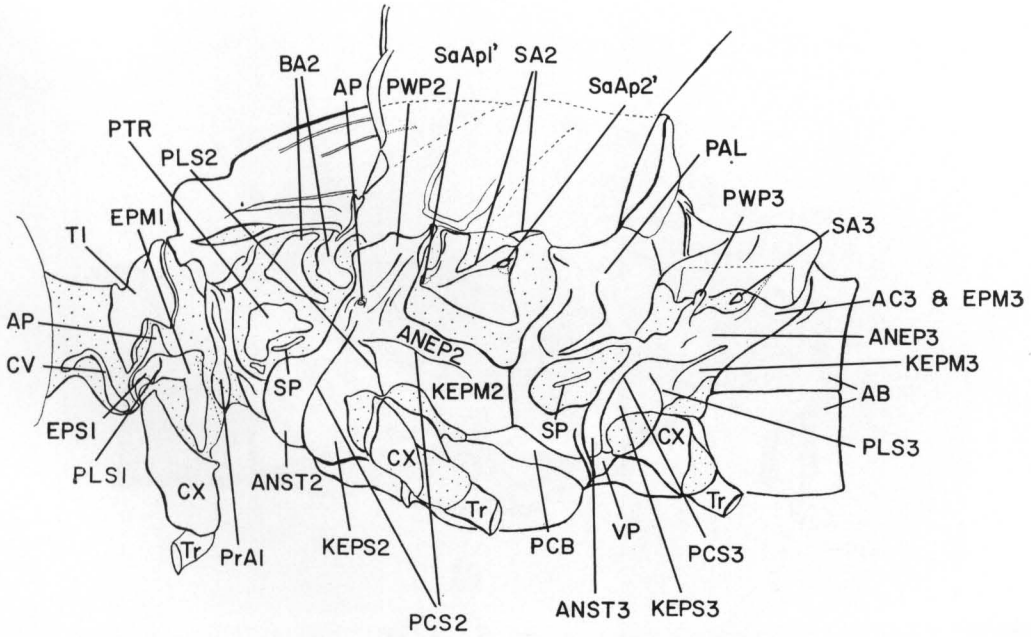
FIG. 30. Dorsal view of the thoracic terga of the male imago of *Isca (Tanycola) serendiba*.



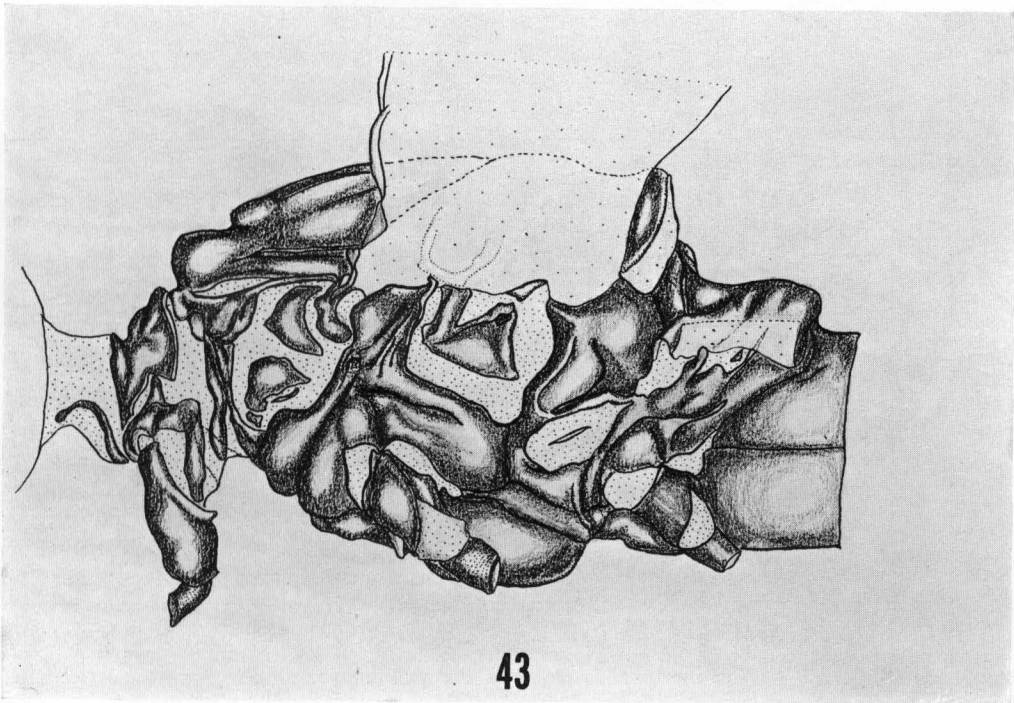
FIGS 31 to 36. Dorsal view of the mesothoracic axillary region of the male imago: 31, *Leptophlebia pacifica*; 32, *Paraleptophlebia bicornuta*; 33, *Habrophlebiodes brunneipennis*; 34, *Aprionyx tricuspoidatus*; 35, *Traverella albertana*; 36, *Isca (Tanycola) serendiba*.



FIGS 37 to 41. Dorsal view of the metathoracic axillary region of the male imago: 37, *Leptophlebia pacifica*; 38, *Paraleptophlebia bicornuta*; 39, *Habrophlebiodes brunneipennis*; 40, *Aprionyx tricuspидatus*; 41, *Traverella albertana*.

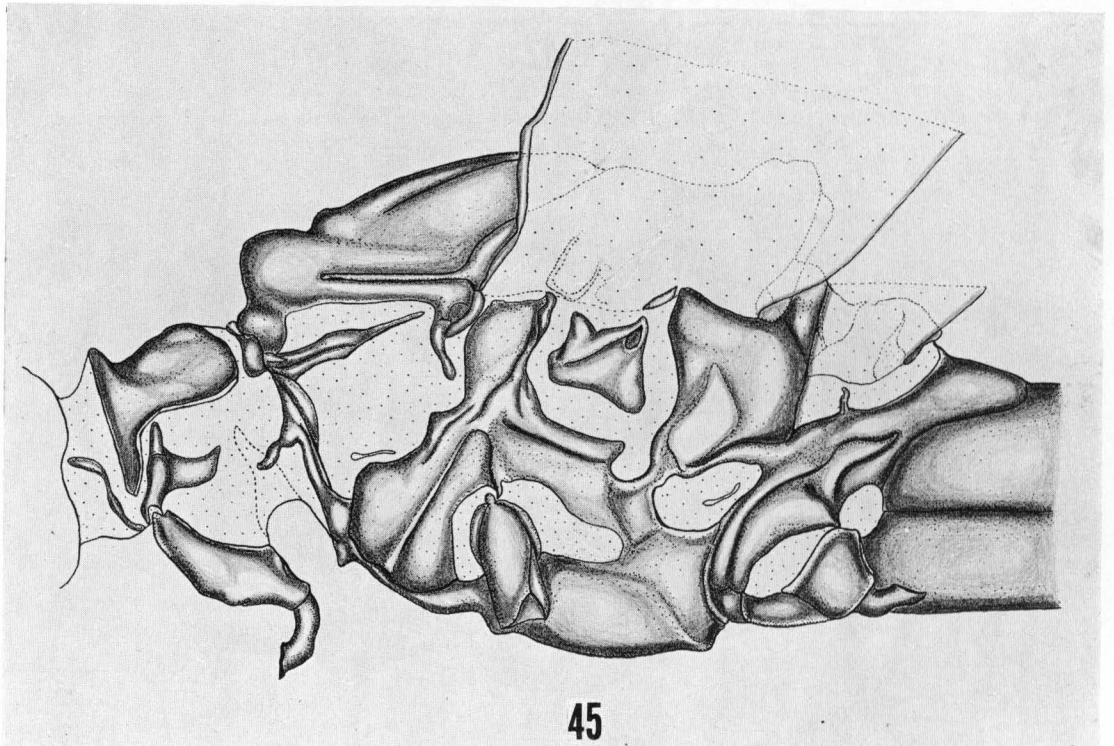
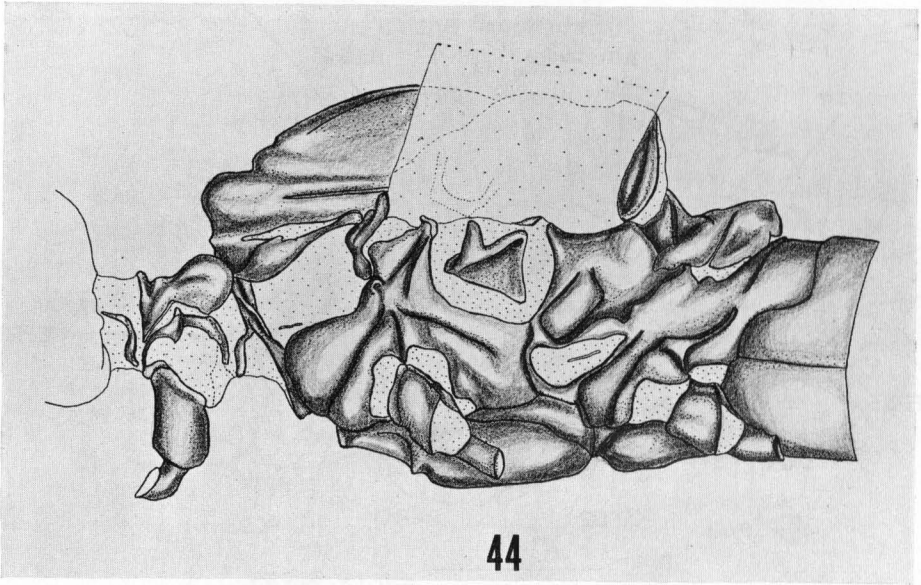


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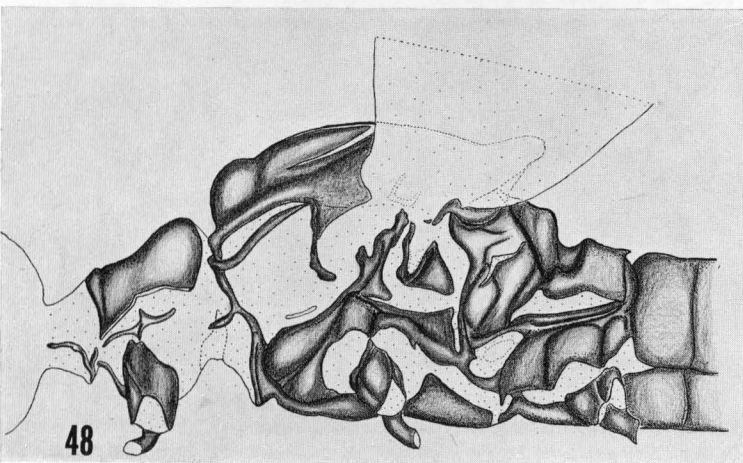
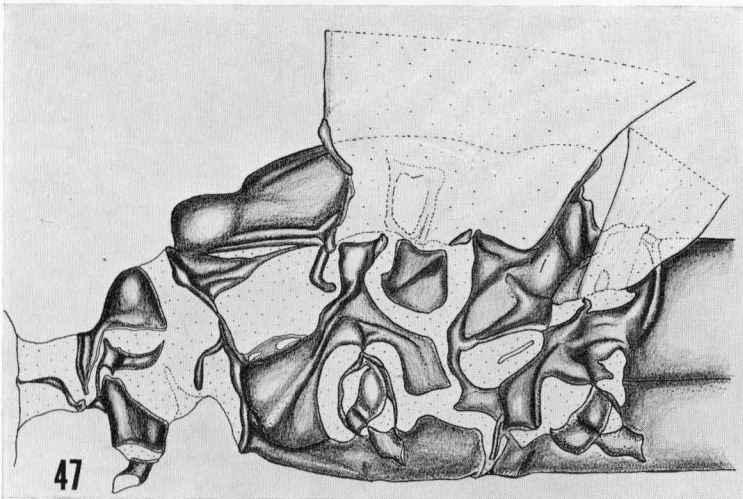
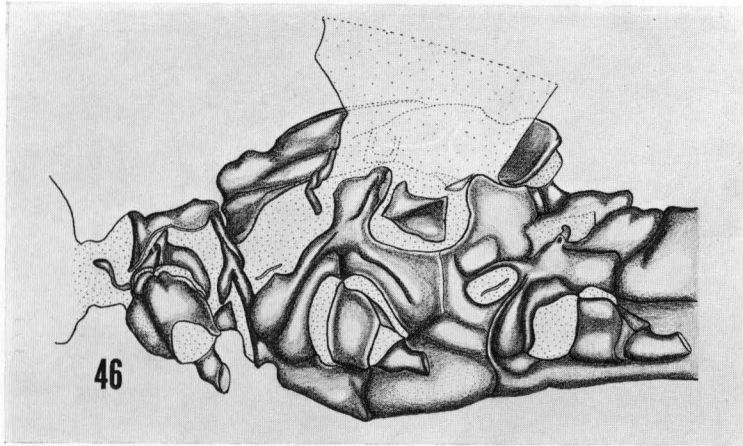
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FIGS 42 and 43. Lateral view of the thoracic pleura of the male imago: 42, showing abbreviations of terminology used in paper; 43, *Leptophlebia pacifica*.

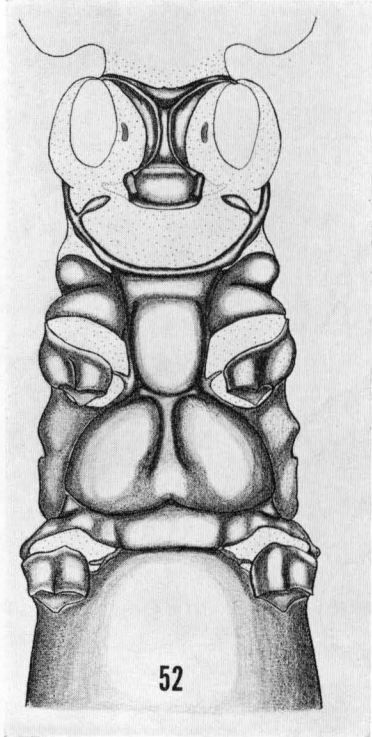
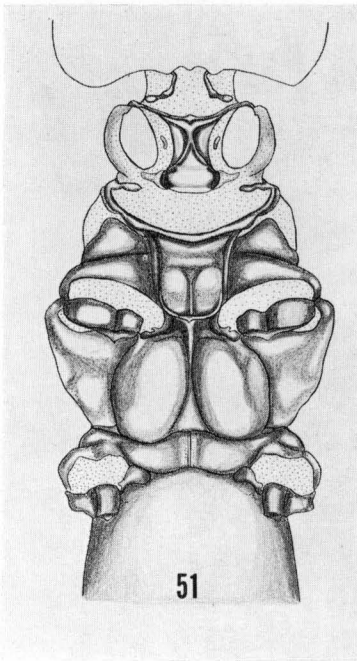
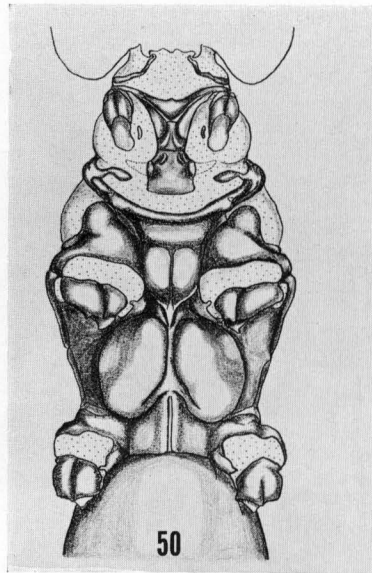
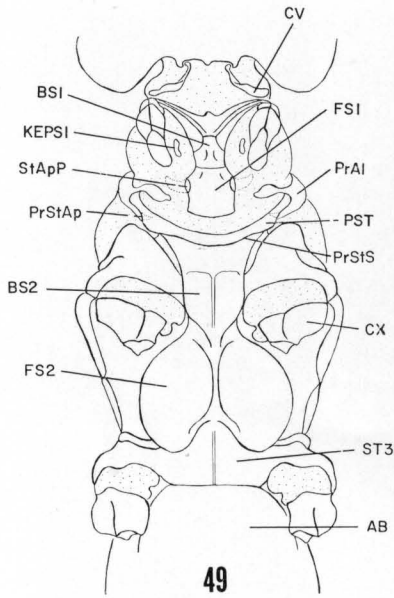


FIGS 44 and 45. Lateral view of the thoracic pleura of the male imago: 44, *Paraleptophlebia bicornuta*; 45, *Habrophlebiodes brunneipennis*.

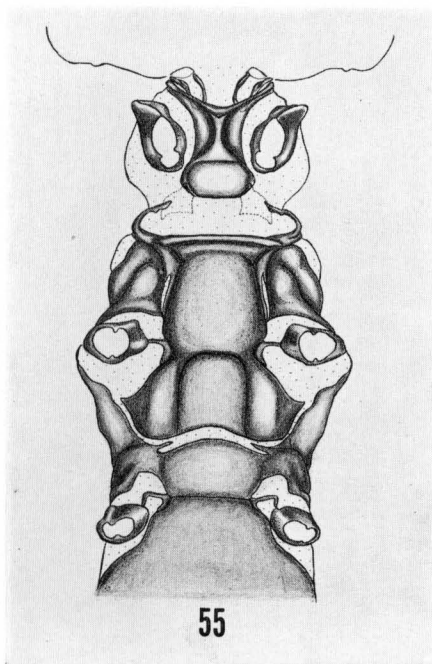
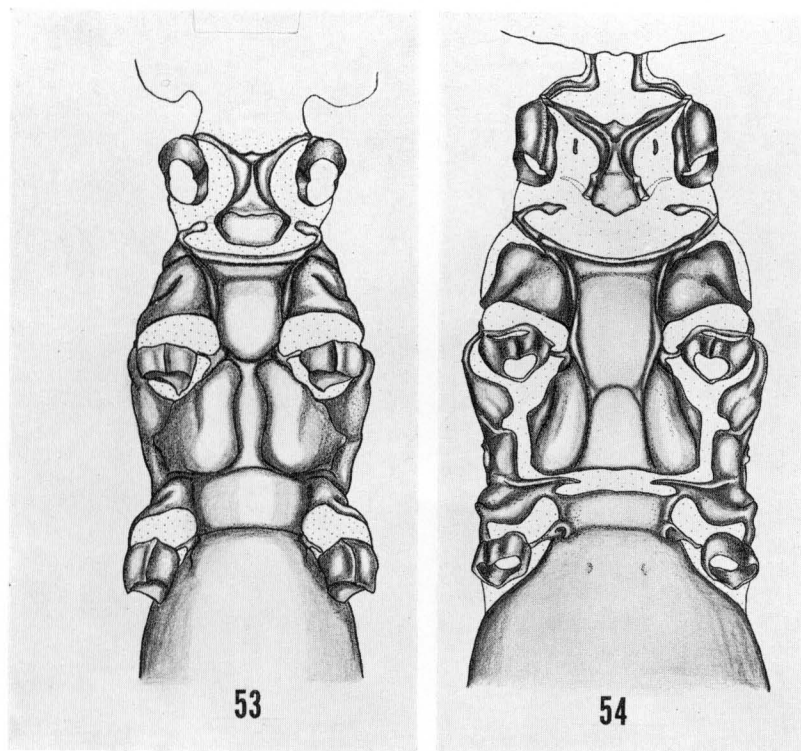




FIGS 46 to 48. Lateral view of the thoracic pleura of the male imago: 46, *Aprionyx tricuspидatus*; 47, *Traverella albertana*; 48, *Isca (Tanycola) serendiba*.



FIGS 49 to 52. Ventral view of the thoracic sternite of the male imago: 49, showing abbreviations of terminology used in paper; 50, *Leptophlebia pacifica*; 51, *Paraleptophlebia bicornuta*; 52, *Habrophlebiodes brunneipennis*.



FIGS 53 to 55. Ventral view of the thoracic sterna of the male imago: 53, *Aprionyx tricuspидatus*; 54, *Traverella albertana*; 55, *Isca (Tanycola) serendiba*.