Comparative Morphological Assessment of the Psyllid Pleuron (Insecta, Hemiptera, Sternorrhyncha)

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ABSTRACT A unique set of morphological characters based on the hemipteran (sensu lato) thorax are used to define the pleuron of Psylloidea. New external and internal topographical descriptions of pleurites of all three thoracic segments are provided based on observations of specimens from various genera representing the current taxonomic arrangement of Psylloidea. Variations in propleurite morphology and the anteroventral angle of the episternum among taxa are clarified. The mesothoracic pleural sulcus is found to be a distinct groove formed by the deep fossa of the pleural apophysis and is not a secondary structure, as assigned by previous authors. A newly discovered internal apodeme of the metathoracic trochantin and a serially homologous structure in the mesothorax isolate the trochantinal territory of the second segment. The metathoracic pleural sulcus appears to be pressed against the ventral edge of the metepimeron, as previously described for the mesothorax of certain species of other insects having a strongly developed meron. Use of morphological interpretations and newly discovered apodemes to assess primary homology of structures for phylogenetic and taxonomic studies is discussed. A glossary of standardized morphological terms for thoracic structures of non-heteropteran Hemiptera based on this study and other recent and former dissertations on the insect thorax is provided. J. Morphol. 252:276–290, 2002.
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KEY WORDS: thorax; pleural sulcus; trochantin; insect; morphology; serial homology; evolution

To date, a thorough morphological assessment of the thorax of Psylloidea has not been performed. The absence of such a study is probably owing to the minute size of psyllids (0.5–6 mm in length) and confusion over development of internal metathoracic furcae and the meron of the coxa. These developments appear to be adaptations for the combined abilities to fly and jump and obfuscate interpretation of certain structures, such as the pleural sulcus, trochantin, and wing process, essential for assessing homology of constitutive pleurites and sternites among representatives of the group. To date, psyllid systematists have mainly focused on defining head, wing, and genital characters for taxonomic descriptions, or only prothoracic pleurites if the thorax is applied.

REVIEW OF PREVIOUS STUDIES

The first comparative morphological study on the thorax of arthropods was published by Audouin (1824). Based on the simple 'philosophical' approach of global unity among living organisms, Audouin proposed nomenclature for thoracic components of every order of insect. Most of the modern appellations to thoracic nomenclature come from this fundamental work, in which each sclerite receives a topological definition (see glossary in Appendix).

Stough (1910) studied the general morphology of the hackberry psylla, *Pachypsylla celtidismamma*, and was the first to use modern morphological terms to describe the psyllid thorax. Crawford (1914) made the first attempt at a comparative morphological assessment to infer homology of certain structures of psyllids by examining several distant genera. He studied the psyllid thorax and had difficulty making certain morphological interpretations of the prothoracic trochantin, partial mesothoracic pleural sulcus and metapleuræ. Taylor (1918), studying the psyllids *Apsylla cistellata* and *Euglyptoneura robusta*, provided a number of reinterpretations of Crawford's (1914) illustrations to define the psyllid thorax. Subsequent morphological studies by Brittain (1922) and Minkiewicz (1924), on *Psylla mali*, and Boselli (1928), on *Homotoma ficus*, provided no new insights on interpreting structures of the psyllid thorax. However, Weber (1929) examined the internal apodemes and musculature of the psyllid thorax. His study provided clear illustrations and interpre-

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tations of origins and insertions of muscles on apodemes in the pro- and mesothorax of *P. mali*. However, he was not able to clarify the skeletomuscular features in the metathorax, the most modified thoracic segment of psyllids.

Heslop-Harrison (1951) sought taxonomically useful characters in the thorax of psyllids and concluded they were only present in the prothorax and provided no new insights concerning the metathorax. Noteworthy progress on the nomenclature of thoracic sclerites of psyllids was made by Tremblay (1965) using *Bactericera tremblayi*. Tremblay adopted Italian translations of the general terms for insects defined by Snodgrass (1908, 1909, 1927, 1935). Journet and Vickery (1978) made a similar effort on defining the sclerites of Nearctic species of *Craspedolepta*, adopting the nomenclature of Matsuda (1970) for the generalized insect thorax. But a number of misinterpretations made by Matsuda were repeated by Journet and Vickery. Several other studies dealing with the taxonomy of psyllids (Pflugfelder, 1941; Ramírez-Gómez, 1955; Dobreanu and Manolache, 1962; Hodkinson and White, 1979; Brown and Hodkinson, 1988; Ossiannilsson, 1992) included general morphological assessments, but none offered new interpretations of the psyllid thorax than provided by Crawford (1914) earlier. No new insights on defining components of the psyllid thorax resulted from these latter studies. This created a presumption that characters associated with the psyllid thorax were not taxonomically significant and the psyllid thorax has been largely ignored since.

Generalized Pleuron of Insects

Weber's 1933 theory, the "subcoxal constitution of the lateral parts of the thoracic metamera" theory, proposed that the pleural sclerites were derived from "subcoxae," basal elements of the appendages situated between the primitive tergum and sternum. This theory also suggested ventral portions of the subcoxae were fused with the sternum. Bitsch (1994), noting this theory was originally proposed by Heymons (1899), made a counterproposal that the bases of the appendages were established by the coxae. However, prior to Heymons, Hansen (1893) suggested the basal part of the leg was established by a reduced sclerite, the trochantin, not the coxae. Crampton (1909) later separated the trochantin into an anterior, antecoxal region and a posterior, coxal region demarcated by the trochantinal sulcus. He argued that the trochantin originally articulated with the coxa by dorsal and anterior condyles.

Snodgrass (1927) illustrated numerous examples of close associations between pleural sclerites and the base of appendages. A "new subcoxal theory" proposed by Weber (1952) invoked that subcoxae were divided into two arches; a dorsal, or anapleural, and a ventral, or catapleural arch. He further stated a catapleural ring connected the ventral and lateral condyles of the coxae. Carpentier and Barlet (1959) maintained the pleurae of apterygotes were actually defined by three arches, the third arch being the trochantin. Barlet (1950) asserted the catapleura and the subcoxa, as defined by previous authors, were homologous structures. Barlet further proposed the anapleura was actually a secondary sclerotization of the pleural membrane and suggested the trochantin was separated from the anterior margin of the coxa. According to Gouin (1959), the thoracic pleura of insects was formed by a precoxopodial appendiculary segment, called the podopleura, and by non-appendiculary elements forming the troncopleura.

Typical sclerites forming the pleuron of a winged insect, as defined by Snodgrass (1935), are as follows (Fig. 1A): 1) An episternum (*eps*) anterior to the pleural sulcus (*pls*), joining the tergum (*nt*) dorsally by a prealar bridge (*pbr*), and the sternum (*st*) ventrally by a precoxal bridge (*prcx*). 2) An epimeron (*epm*) posterior to the pleural sulcus, connected to the tergum dorsally by a postalar bridge (*pobr*), and to the sternum ventrally by a postcoxal bridge (*pocx*). 3) A trochantin (*trn*), that tends to be vestigial or vanishes in higher orders of insects (Snodgrass, 1927), anterior to the coxa (*cx*) that articulates with the precoxal bridge (*prcx*) by a condyle anteriorly. The pleural sulcus separates the eupleuron into two parts. This sulcus can be traced as a groove from a ventral condyle, where the pleuron and coxa articulate, in almost a straight line dorsally to the pleural wing process (*pwp*). A portion of the wing articulates with this process, which acts as a fulcrum for mechanical advantage in wing movement.

Over 30 years after Snodgrass, Matsuda (1970) reinterpreted the generalized insect thorax of winged insects. His reinterpretation was strongly influenced by the 1950s interpretations of Carpentier and Barlet. As such, Matsuda named the relatively simpler structures present in the thorax of winged insects based on the more complex model of apterygotes, in which sulci, clefts, and sclerites are much more numerous (Fig. 1B). Unfortunately, the Matsuda model is impractical for inferring homology or identifying the many reduced sclerites and sulci in the psyllid pleuron.

According to Crampton (1909), the episternum and epimeron of winged insects evolved from a common sclerite that divided as infolding developed in order to create internal insertion points for thoracic muscles, especially for pterygotes. A major infold, the pleural sulcus, is a key structure in the pleuron of adult pterygotes. Two key elements of this sulcus are the pleural apophysis (pleural arm sensu Snodgrass, 1927), which extends inward and ventrally in juxtaposition to the sternal apodeme, and

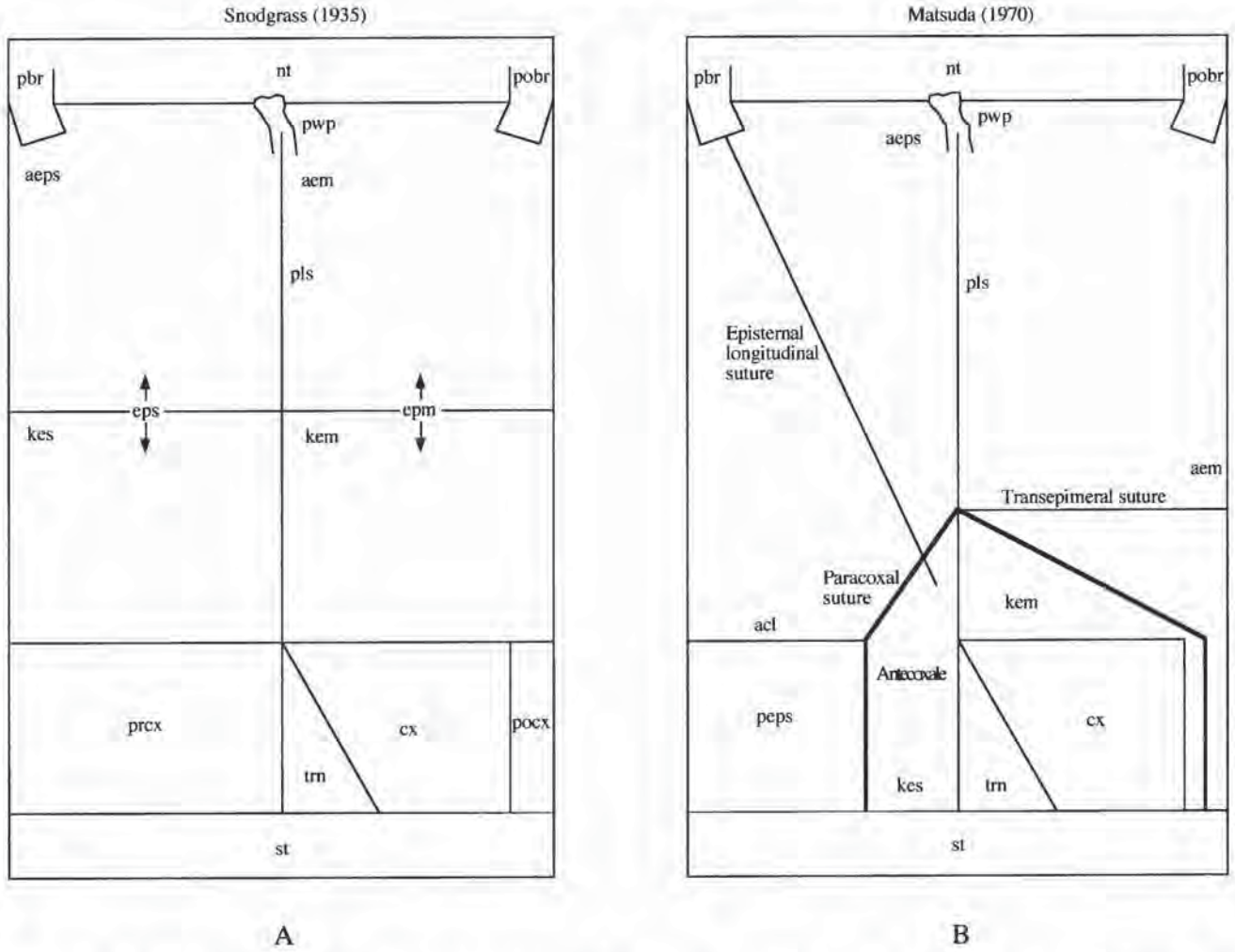


Fig. 1. **A:** Schematic diagram illustrating the principal sclerites and features of a generalized ptero-pleuron of insects, after Snodgrass (1935). *aem*, anepimeron; *aeps*, anepisternum; *cx*, coxa; *epm*, epimeron; *eps*, episternum; *kem*, katepimeron; *kes*, katepisternum; *nt*, notum; *pbr*, prealar bridge; *pls*, pleural sulcus; *pobr*, postalar bridge; *pocx*, postcoxal bridge; *prcx*, precoxal bridge; *pwp*, pleural wing process; *st*, sternum; *trn*, trochantin. **B:** Schematic diagram illustrating the principal sclerites and features of a generalized ptero-pleuron of insects, after Matsuda (1970). *acl*, anapleural cleft; *peps*, preepisternum.

the ventral articulation condyle (pleural coxal process sensu Snodgrass, 1927), the point of articulation of the coxa with the thorax. Secondary grooves eventually divided the episternum into a dorsal anepisternum (*aeps*) and a ventral katepisternum (*kes*), and the epimeron into a dorsal anepimeron (*aem*) and a ventral katepimeron (*kem*) (Fig. 1A) (Snodgrass, 1935).

In the studies on general morphology of the insect pleuron cited above, few details were provided with regard to skeletomusculature or other internal features of the pleuron. Moreover, the thorax of non-heteropteran Hemiptera (sensu lato) was largely ignored. Only two structures were described, the internal pleural ridge, which is the inner part of the pleural sulcus, and the pleural apophysis (Snodgrass, 1935)

Review of the Pleuron of Non-Heteropteran Hemiptera (sensu lato)

Taylor (1918) was first to publish a detailed morphological description focusing on the pleuron of non-heteropteran Hemiptera (sensu lato) (viz., "Homoptera," Sternorrhyncha + Clypeorrhyncha + Archaeorrhyncha). A more generalized description of the "homopterous" thorax was more recently provided by Matsuda (1979).

Collar region. According to Taylor (1918), there are three pairs of cervical sclerites in the generalized "homopterous" thorax. However, Matsuda (1970, 1979) insisted that the lateral cervical sclerite was only present in Cicadidae and reports of this sclerite in other "homopterans" were misinterpretations.

Prothorax. The episternum and epimeron are always present, but the trochantin can be vestigial or absent. The episternum is sometimes divided into an anepisternum and a preepisternum (Matsuda, 1979), and is connected to the sternum by a precoxal bridge (Taylor, 1918). These pleurites do not necessarily fuse with the pronotum dorsally, although their margins appear to meet in most families (Taylor, 1918).

Mesothorax. The episternum can be divided by the anapleural cleft (*acl*) into a dorsal anepisternum (*aeps*) and a ventral preepisternum (*peps*) (Fig. 1B) (Matsuda, 1979). A transepimeral sulcus sometimes divides the epimeron into separate dorsal and ventral sections. The trochantin can either be present or absent. A secondary sulcus, at times, divides the episternum. The pleural sulcus can be incomplete, being visible only in the dorsal or ventral portion of the ptero-pleuron. There are no clear distinctions between the sclerites lying ventral to the anapleural cleft (Taylor, 1918). This region is referred to as either the pre-episterno-katepisternum + basisternum or the katepisternal complex by Matsuda (1970, 1979). The epimeron appears to fuse with the postscutellum, leaving no visible sulcus (Taylor, 1918). The mesothoracic spiracle lies just in front of the episternum and is surrounded by a peritreme.

Metathorax. Unlike the other thoracic segments, the pleuron in this segment can be undivided (viz., the pleural sulcus is absent). The metathoracic spiracle is located in the episternum and is surrounded by a peritreme. The trochantin is always present.

MATERIALS AND METHODS

Insects

Species and relevant collecting information of psyllids examined for this study are as follows: *Psylla buxi* (Linné, 1767) Grignon, France, June 1950 by J. Balazuc (MNHN), in 70% ethanol; *Diaphorina citri* Kuwayama, 1907, Guadeloupe, Great Antilles, November 1999 by J. Etienne (MNHN), in 95% ethanol; *Apsylla cistellata* (Buckton, 1896), India (date not recorded), by C. Thakur (BMNH), dry; *Gyropsylla clypeata* Brown and Hodkinson, 1988, Costa Rica, February 1994 by Paul Hanson (BMNH), dry; *Euphyllura phyllireae* Förster, 1848, Vauvenargues, June 1976 (collector unknown) (MNHN), dry; *Rhodochlanis suaedae* Hodkinson and Hollis, 1981, Spain, May 1979 by I. Hodkinson (BMNH), dry; *Craspedolepta bulgarica* Klimaszewski, 1961, Iran, September 1966 by Georges Remaudière (MNHN), dry.

Dissections and Light Microscopy

Specimens were first softened by boiling in saturated potassium hydroxide, rinsed, and then dissected in distilled water. The cuticle of *Diaphorina citri* was stained with chlorazol black according to the methods of Carayon (1969) and examined and photographed under glycerin.

Scanning Electron Microscopy

Specimens of *Psylla buxi* were progressively dehydrated in a graded series of increasing concentrations of ethanol in water to a final concentration of 95% and then air-dried. Specimens were affixed to standard SEM studs using double-sided tape, sputter-coated with gold-palladium, and examined using a JEOL JSM-840 scanning electron microscope.

RESULTS: THORAX OF PSYLLOIDEA

Exopleuron (Figs. 2, 3)

Collar region. In Psylloidea, as in most Hemiptera, the laterocervical sclerites are absent. If Taylor's (1918) description of the generalized "homopterous" thorax having three small sclerites in this region is correct, then the disappearance of these sclerites in psyllids must be a secondary event. But, Weber (1929) describes a "*Kehlplatte*" (viz., plates from the neck) in *Psylla mali* consisting of two pairs of very reduced sclerites. This *Kehlplatte* might represent vestigial sclerites belonging to the collar region. In the Weber (1929) study, one of these "plates" resembles a reduced sclerite, but the other "plate" is the anteroventral extension of the proepisternum. Weber expresses confusion in his article, labeling a plate as "Kehlplatte" in one drawing (*KPl*, p. 73) then labeling it "Trochantinus" in a subsequent drawing (*Tt1*, p. 116). We were unable to resolutely identify this sclerite in our examinations.

Prothorax. The prothoracic pleurites are readily visible in most genera we examined. The episternum and epimeron are generally unequal in size. Although the episternum may be quite slender or membranous in some species (e.g., *Euphyllura phyllireae*), the epimeron is easily visible. A barely distinguishable trochantin, as defined in *Bactericera tremblayi* (Tremblay, 1965), appears as a long, narrow sclerite in *E. phyllireae* and *Rhodochlanis suaedae* articulating with the katepisternum.

In general, a pleural sulcus (*pls1*) can be traced from its ventral articulation with the condyle of the coxa (*ccx1*) to the pronotum, dorsally. However, this sulcus follows varying paths, from a straight dorsoventral path (*Craspedolepta bulgarica*), to an anteroventral path in cases where its dorsal origin is posterior to the pronoto-pleural limit instead of the medial portion of the pronotum (*Gyropsylla clypeata*). The external feature marking location of the pleural apophysis is the fossa of the pleural apophysis (Emeljanov, 1981) (*fpa1*) adjacent to the condyle of the coxa (*ccx1*) in the ventral part of the pleural sulcus (*pls1*) (Fig. 2).

Sclerites anterior to the mesothorax. Three sclerites, of possible epipleural origin, are visible

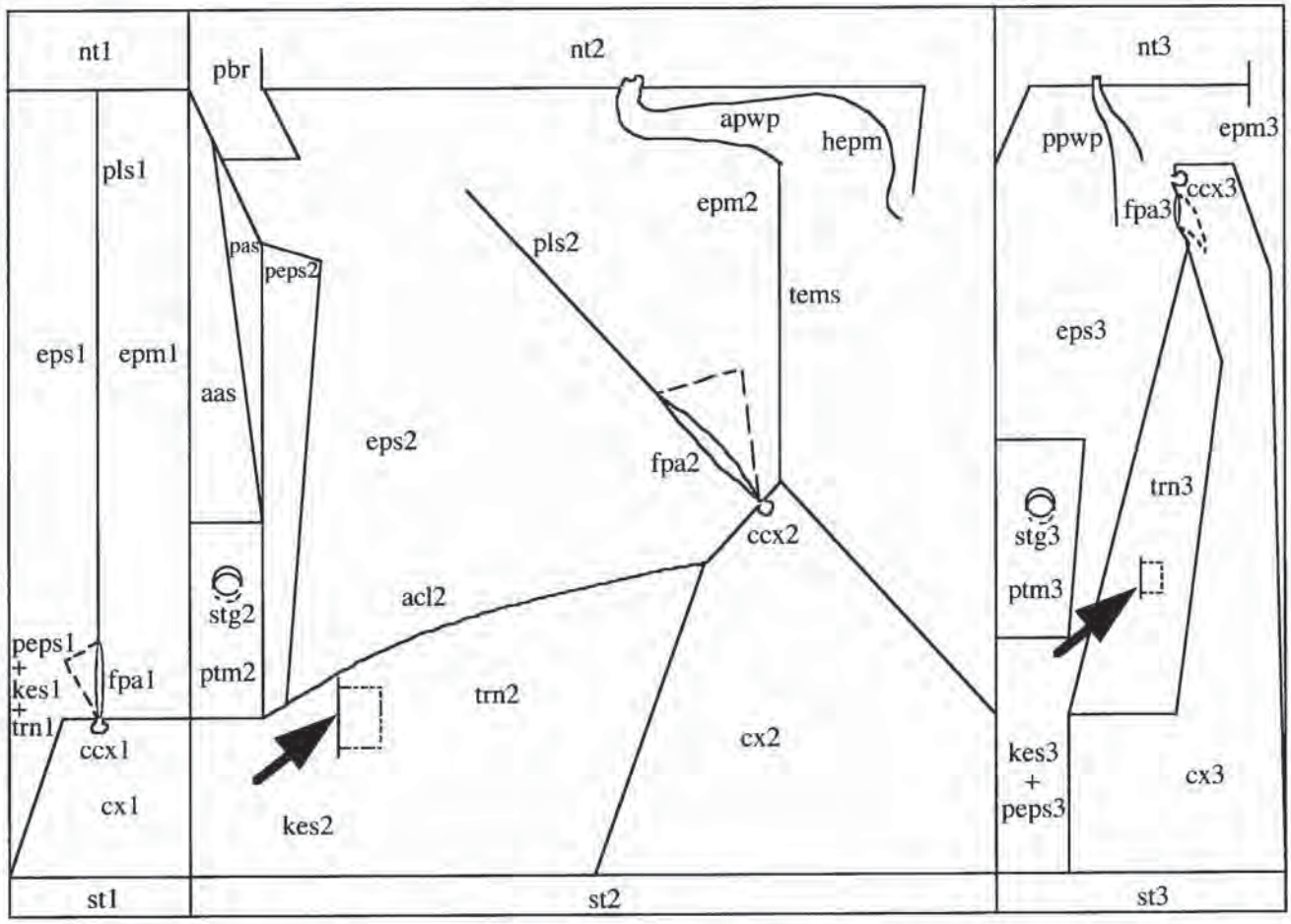
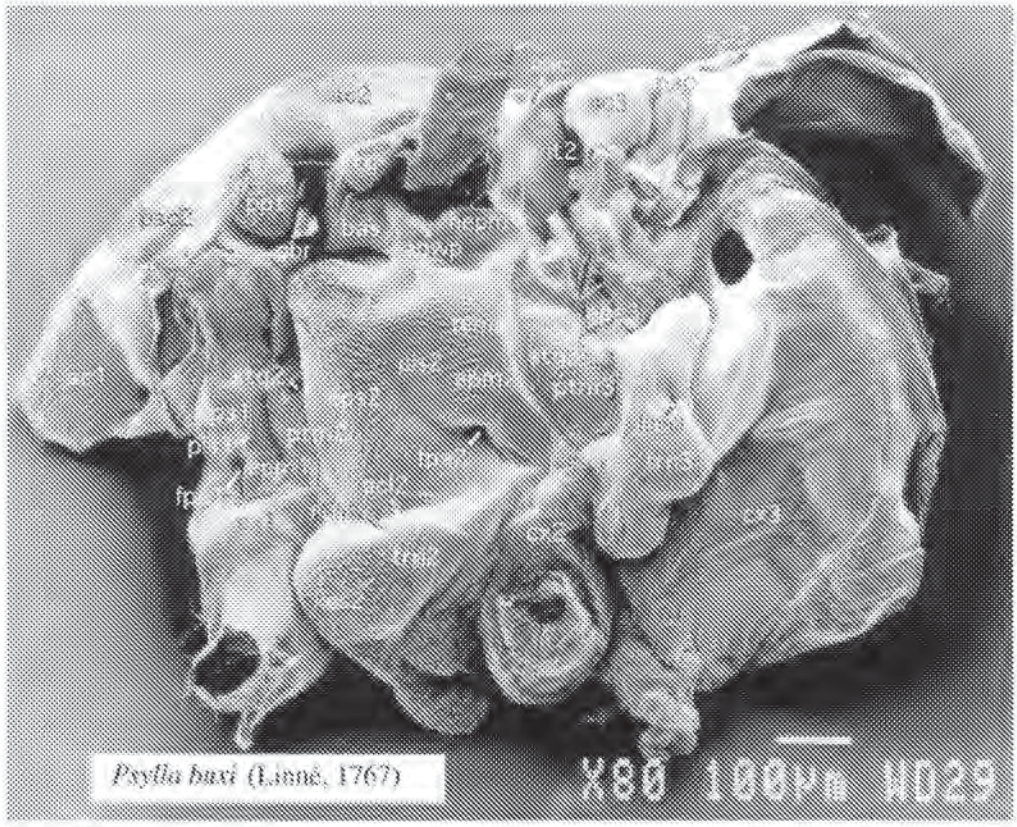


Fig. 2. Schematic diagram illustrating the principal features of the typical psyllid thorax. Arrows indicate the position of the meso- and metathoracic fossae of the trochantinal apodemes. *aas*, anterior accessory sclerite; *apwp*, anterior pleural wing process; *ccx*, condyle of the coxa; *fpa*, fossa of the pleural apophysis; *ftna*, fossa of the trochantinal apodeme; *hepm*, heel of the epimeron; *pas*, posterior accessory sclerite; *ppwp*, posterior pleural wing process; *ptm*, peritreme; *stg*, spiracle; *tems*, transepimeral sulcus.

between the proepimeron (*epm1*), and the prealar bridge (*pbr*). These sclerites are the anterior and posterior accessory sclerites (*aas* and *pas*), and the peritreme (*ptm2*) surrounding the mesothoracic spiracle (*stg2*). Crawford (1914) suggested the anterior accessory sclerite was a fragment that separated from the dorsal part of the peritreme. Further studies on muscle attachments are needed to clarify the origin of these sclerites.

Mesothorax. The mesopleurites are the largest pleural sclerites in the thorax of psyllids. The individual pleurites, however, are not always discernibly separated. The episternum (*eps2*) exhibits a great deal of variation in shape, depending on the position and path of the pleural sulcus (*pls2*) and anapleural cleft (*acl2*). The anterodorsal orientation of the episternum is dependent on the manner in how it is connected with the prealar bridge (*pbr*). The episternum has a hemispherical prominence at this interface, separated from the prealar bridge by the prescuto-episternal sulcus. The anapleural cleft may have an oblique, as in *Psylla buxi*, or almost horizontal orientation, as in *Homotoma ficus*. This cleft can exist as either a deep groove or a membranous area or can be absent altogether, as in *Diaphorina citri*. The ventral katepisternal complex (*kes2*) sometimes possesses a particular, but prominent apodeme (Ouvrard, 2000), termed here the trochantinal apodeme, that is only visible internally (*tna2*, Fig. 4). The location of this apodeme is generally marked externally by the fossa of the trochantinal process (*ftna2*, Fig. 3) that usually lies in the anteroventral margin, but can also appear in the central portion of this complex, as in *P. buxi*. This fossa has been described as the mesothoracic spiracle by Heslop-Harrison (1952) and later by Journet and Vickery (1978). However, no tracheal apparatus is visible on the internal aspect of this fossa. The Heslop-Harrison (1952) study presents an additional error by describing the most anterior spiracle of the thorax as belonging to the prothorax instead of the mesothorax. The valid position of the mesothoracic spiracle is similar to the position of the metathoracic spiracle, anterior to the pleurites of



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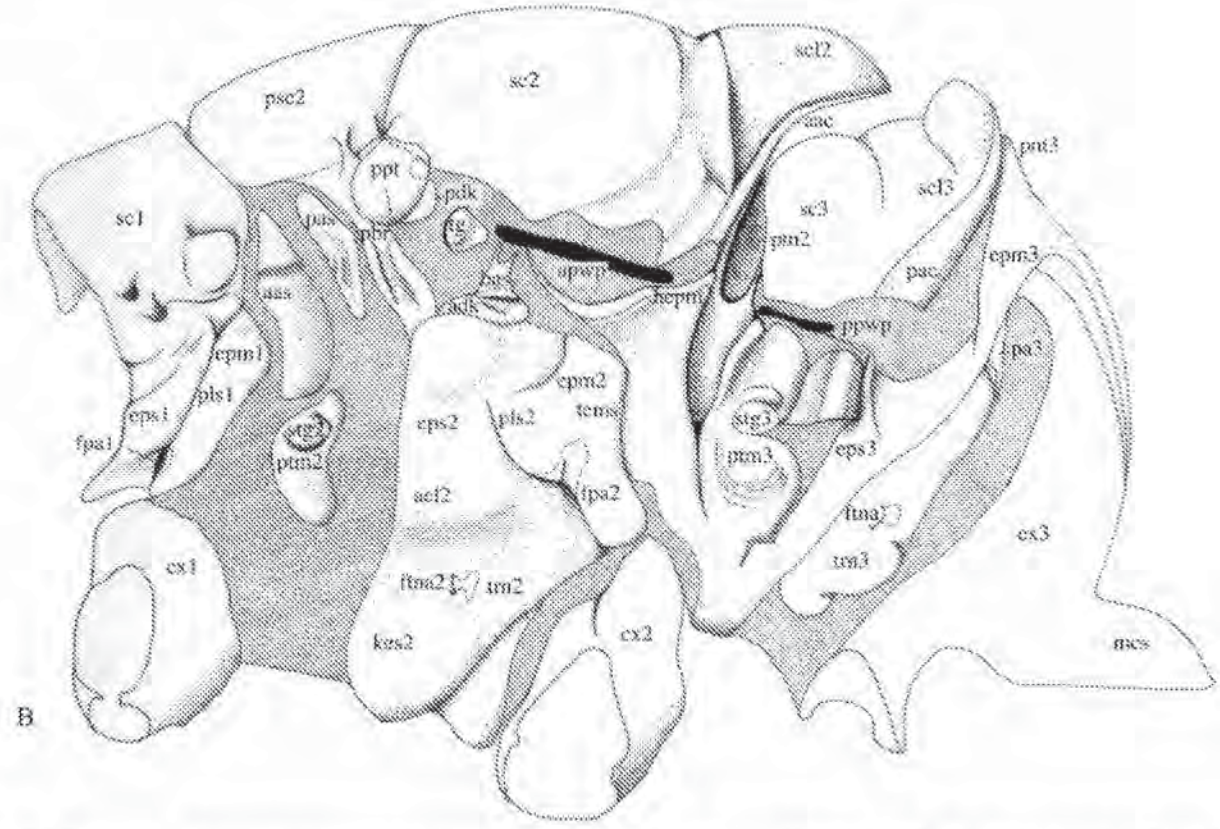

B

Fig. 3. **A:** Scanning electron micrograph showing external lateral view of thorax of *Psylla buxi*. *bas*, basalare; *pa*, pleural apophysis; *pnt*, pseudonotum; *psc*, prescutum; *sc*, scutum; *scl*, scutellum; *tg*, tegula. **B:** Diagram of external lateral view of thorax of *Psylla buxi*. *aac*, anterior axillary cord; *adk*, anepisternal disc; *mcs*, meracanthus; *pac*, posterior axillary cord; *pdk*, pronator disk; *ppt*, parapterum.

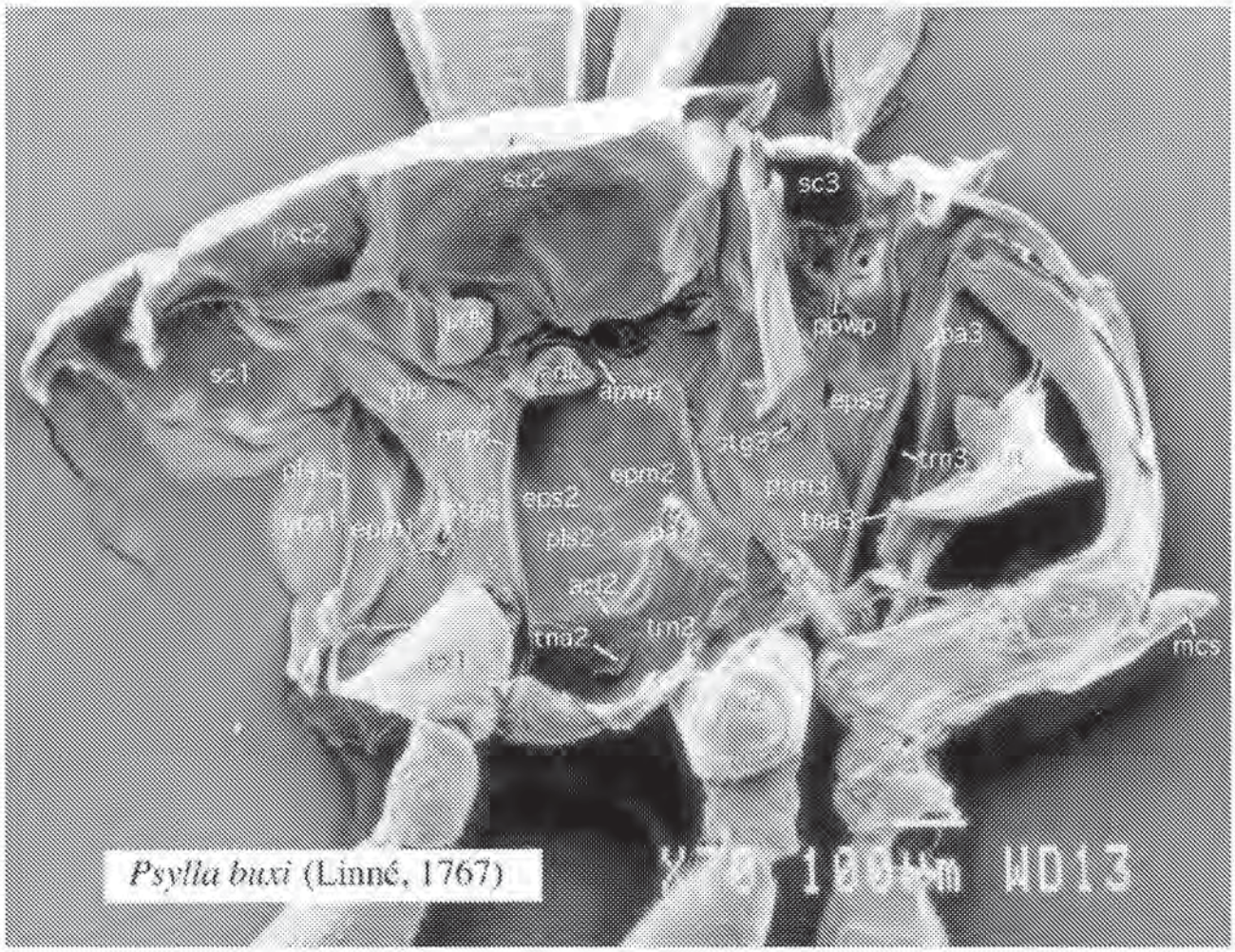

Fig. 4. Scanning electron micrograph of internal sagittal section of thorax of *P. buxi*, lateral view. *trt*, trochanter tendon; *tna2*, trochantinal apodeme.

their respective segments. If this positioning of the spiracles is the general rule, then it is inconsistent to establish the position of the prothoracic spiracle (sensu Heslop-Harrison, 1952) as being posterior to the pleurites of the first segment. Actually, the ventral portion of the mesopleurites has often been misinterpreted with regard to their positional relation with the sternum. The position of the anapleural cleft indicates the pleuro-sternal limit is more ventral than previously presumed by Matsuda (1970), the original describer of the anapleural cleft. The presence of an apodeme also in the metathoracic trochantin near the anapleural cleft (cf. "Metathorax" of this section and "Endopleuron" of Results) provides a demarcation for the putative mesothoracic trochantin territory (*trn2*) through serial homology. We have thus termed this apodeme the trochantinal apodeme (*tna2*: Fig. 4).

The epimeron in the mesothorax is more complex than the episternum because of a vertical secondary sulcus named here the transepimeral sulcus (*tems*, Fig 3). This sulcus might be homologous to the sternepimeral carena in "Auchenorrhyncha" described by Emeljanov (1981). Some authors have interpreted this sulcus as the pleural sulcus (Matsuda, 1970, 1979; Journet and Vickery, 1978), but the transepimeral sulcus does not have an internal pleural apophysis and should be considered a secondary sulcus. The posterior limit of the mesopleuron is not clearly defined. This limit can be traced vertically and dorsally as a separation between the mesopostphragma and the median part of the apical edge of the mesepimeron (*epm2*). However, these areas are not separated ventrally where the mesepimeron is partially fused to the metepisternum (*eps3*). The widest portion of the mesepimeron lies anterior to the transepimeral sulcus. The dorsal posterior edge of the sclerite (anterior to the third peritreme and posterior to the transepimeral sulcus) supports the base of the pleural wing process (*apwp*). This process curves horizontally in order to connect the anterior portion of the wing base upon

the median dorsal edge of the mesopleuron. In the Cicadomorpha + Archaeorrhyncha (sensu Sorensen et al., 1995) ("Homoptera"), this curved process is termed the heel of the epimeron (*hepm*) or astragalus by Emeljanov (1981). It is a significant and an easily distinguishable feature connected posteriorly to the mesopostnotum, separating the posterodorsal angle of the mesopleuron from the lateral part of the mesopostnotum. The pleural wing process is thin and flexible and can be depressed distally to the dorsal edge of the mesopleuron. It is separated from this edge by a somewhat narrow membranous area. Orientation of the distal, or supportive, part of the pleural wing process can vary in either an anterior or dorsal direction.

Frequently, the pleural sulcus in the mesothorax follows a circuitous path as it extends from the condyle of articulation of the coxa (*ccx2*: Fig. 2) to approximately the midway point of the pleuron, but never meets the wing base. Based on observations of orthopteran nymphs, Snodgrass (1909) found the pleural sulcus was incomplete prior to wing development, but was complete (viz., extended to the wing base) in adults. The incomplete pleural sulcus observed in adult psyllids may explain the relative weakness of their flight (Clark, 1962). Crawford (1914) claimed the pleural sulcus could be traced to the base of the wing process in *Apsylla*. However, our findings do not concur. We found the dorsal end of the pleural sulcus is close to the wing base in this genus but does not contact it (Fig. 6B). The fossa of the pleural apophysis (*fpa2*) is greatly enlarged at the anterior end of the sulcus. Orientation of the pleural sulcus in psyllids is highly variable, from relatively straight and vertical (as in most Pterygota) to serpentine and/or nearly horizontal. When horizontal, the sulcus sometimes merges with the anapleural cleft.

The katepisternal complex, so-named in relation to the katepimeral complex of Crampton (1909), is formed by the katepisternum (*kes2*) and the trochantin (*trn2*) and is separated from the anepisternum by the anapleural cleft. The katepisternal complex is rounded and striated, with each groove roughly isolating elements of the katepisternal complex.

Metathorax. The metathorax of psyllids is highly derived and reflects their unique ability to jump compared with other sternorrhynchans. As such, it is difficult to interpret the homology of many components of the psyllid metathorax to those of other thoracic segments of psyllids or other insects. There is extensive development of large attachment areas for muscles, especially on the internal furcae, in the metathorax of psyllids. Moreover, the metapleuron is greatly modified by vertical extension of the coxal meron. This extension results in dorsal displacement of other sclerites towards the metanotum and particularly the condyle of articulation of the coxa with the pleuron (*ccx3*: Fig. 2). This extension of the coxal meron has forced the epimeron and the episternum to develop into a long thickened arch extending over the metacoxa. Unlike the mesothorax, the delimiting point between the postnotum and the epimeron is not visible.

Anteriorly, the metathoracic spiracle (*stg3*) is surrounded by a variably sclerotized peritreme (*ptm3*). The sclerite dorsal to this peritreme can be interpreted as either being a secondarily sclerotized area or as corresponding to the anterodorsal angle of the metepisternum. A narrow wing process (*pwp*: Fig. 3B) is situated just posterior to this area and is an articulating point for the wing. Unlike the mesothorax, no sulcus visibly separates the dorsal part of the metepimeron from the metapostnotum. Posteriorly, the metepimeron is highly constricted and extends posteriorly to the middle of the coxa.

The trochantin (*trn3*) is well developed and extends along the posterior edge of the metapleuron anterior to the coxa. The trochantin does not serve as a ventral articulation for the coxa. An external fossa (*ftna3*) of the metathoracic trochantinal apodeme is visible on the surface of the relatively tuberculated metathoracic trochantin (Ouvrard, 2000). A second apodeme is visible anterior to the coxo-pleural condyle and posterior to the dorsal apex of the trochantin: it appears as a small anterodorsally elongated triangle with one angle orienting inwards. We suggest this apodeme is homologous to the pleural apophysis (*pa3*: Fig. 3B), in view of lack of other interpretable apodemes near the condyle. A pleural sulcus is barely visible, if at all, on the metathorax of psyllids as a result of major displacement of the pleural sclerites. Dorsally directed enlargement of both the coxa and trochantin forced a counterclockwise rotation of the epimeron onto the episternum. The movement of these sclerites is accompanied by a dorsal migration of the pleural apophysis (cf. Discussion, Fig. 7).

Endopleuron (Figs. 4 and 5)

Prothorax. Examination of the prothoracic pleuron from an internal aspect reveals two readily visible structures, the pleural sulcus and the pleural apophysis. The pleural apophysis is a relatively reduced "finger-like" structure located at the base of the pleural sulcus. The ventral portion of the anterior of the episternum may include an extension that projects to the probasisternum. This extension corresponds to the katepisternal complex and forms the precoxal bridge in cases where there is no visible separation between these regions. In *Psylla buxi*, the anapleural cleft is quite visible internally and separates this katepisternal complex from the dorsal section of the episternum (Fig. 5B).

The dorsal end of the pleural sulcus diverges into a V-shaped pronoto-pleural sulcus that is difficult to discern (*snp* - Fig. 5A); the anterior arm of this sulcus is termed the pronoto-proepisternal sulcus and the posterior termed the pronoto-proepimeral

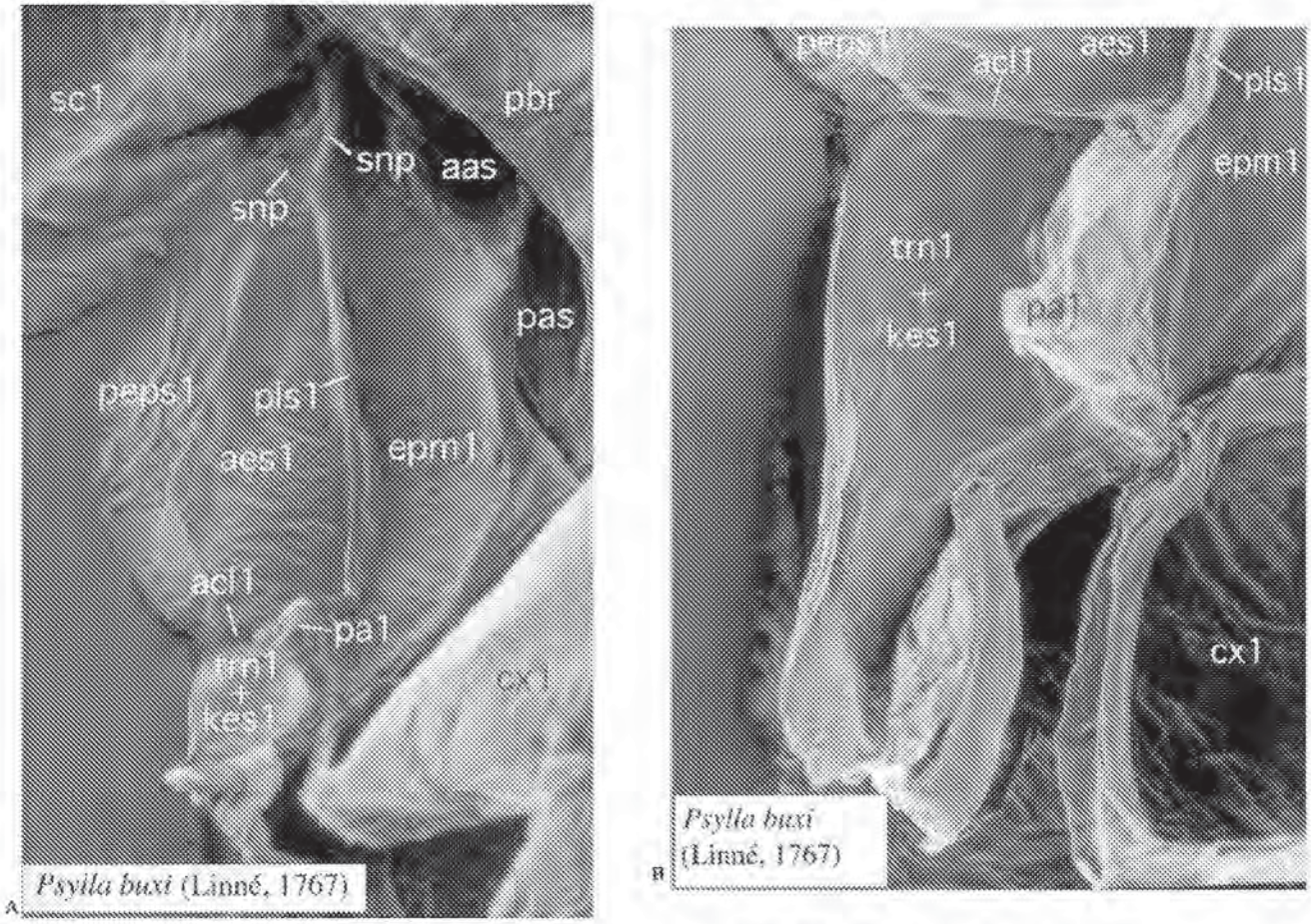

Fig. 5. Magnified scanning electron micrographs of **A:** the internal lateral region of the prothorax of *P. buxi*. *snp*, notopleural sulcus. **B:** The internal ventral region of the prothorax of *P. buxi*, lateral view.

sulcus. The boundary between the episternum and the anterior vertical wall of the pronotum is sometimes an infolding membranous structure and not a true sulcus.

Mesothorax. From an internal vantage, the prealar bridge extends anterodorsally from the episternum to the prescutum, but does not fuse with it. The internal aspect of the parapteron is disc-shaped, not bulbous as it appears externally. This pronator disc (*pdk*: Fig. 4; muscle disc of Snodgrass, 1908) is vertically oriented, anteriorly convex, and partially fused with the posterior edge of the prealar bridge.

The anterior margin of the internal mesepisternum is a narrow elongated sclerite, the preepisternum (*peps*: Fig. 4). This sclerite is not visible externally, positioned anterior to the visible external episternum, and is perpendicular to the body axis, forming a vertical wall. This sclerite is broad dorsally, sharply narrows ventrally, but does not contact the sternum.

The dorsal edge of the pleuron is internally folded, forming a roof-like structure. An elongate longitudinally oriented disc, referred to here as the anepisternal disc (*adk*: Fig. 4), is partially connected to this roof-like structure and serves as the base from which the basalare (*bas*: Fig. 3) projects. The anepisternal disc is a newly described structure that provides lateral support to the pleuron. Hence, as a result of functional constraints it serves as a morphological substitute for the incomplete pleural sulcus. The wing process is also folded on the margin in its posterodorsal angle.

The caudal limit of the mesepimeron is not delineated by a visible suture. Dorsally, this limit is visible posterior to the edge formed by the descending aspect of the wing process. Parallel and anterior to this posterior limit the transepimeral sulcus can be traced from the curve in the wing process to the coxa.

The pleural sulcus is incomplete and especially enlarged ventrally, where it meets a strongly developed pleural apodeme that projects internally. The trochantinal apodeme, ventral and anterior to the pleural apodeme, is relatively reduced and appears as a flattened finger-like protuberance. According to Snodgrass (1935), only one muscle, the "Tergal Pro-

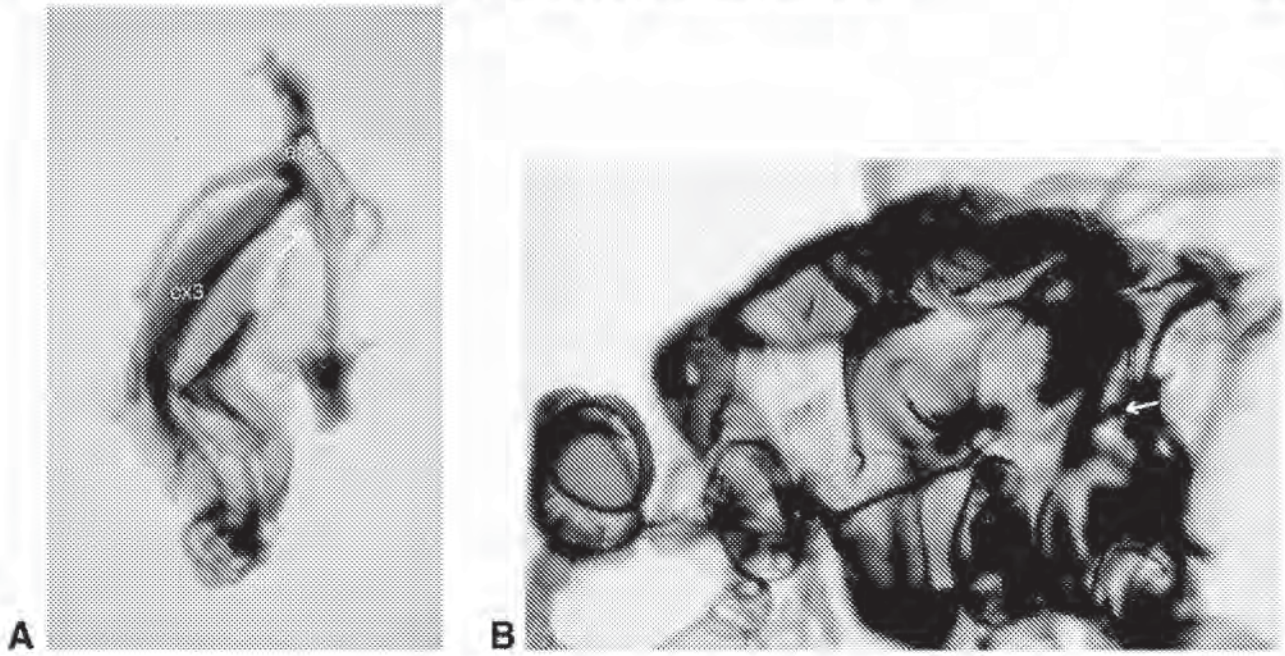

Fig. 6. Light micrographs of **A:** a dissected portion of the metathorax and metacoxa of *Diaphorina citri*, internal lateral view. Arrow indicates the metathoracic pleural apophysis. **B:** The thorax of *Apsylla cistellata*, left external lateral view. Arrow indicates the metathoracic pleural apophysis.

motor of the Leg," could have an insertion on this trochantinal apodeme, stretching from the tergum to the ventral extremity of the trochantin, if the trochantin is present. Weber (1929) describes the pleural muscles $IIpm_1$ and $IIpm_2$ as extending from the katepisternum (sternum sensu Weber 1929) to the dorsal edge of the episternum. These muscles serve to pronate and lower the wing. Emeljanov (1981) describes an episternal apodeme in "Auchenorrhyncha" other than Cercopoidea. In Cicadoidea, the muscles attached to the episternal apodeme extend to the trochantin and coxa and are presumably used in jumping. However, the absence of such an apodeme in the prothorax of psyllids might indicate that these muscles are actually involved in flight.

Metathorax. The origin of the metapleural wing process is visible as a vertical shaft which then curves anteriorly reaching the wing articulation sclerites above a fold in the cuticle. Internally, as externally, there is no noticeable demarcation between the pleuron and the postnotum. The posterior edge of the metepimeron is notable because three particular structures merge at this point: 1) the sulcus between the epimeron and the trochantin, 2) the origin of the extraordinarily developed metafurcae, and 3) the incomplete pleural sulcus, which is bordered dorsally by the pleural apophysis, particularly visible in *Diaphorina citri* (Fig. 6A). The condyle of articulation, between the metepimeron and metacoxa, and the pleural apophysis are the only available features for identifying the position of the metathoracic pleural sulcus.

The trochantin is relatively well developed, exhibits two large bulges on its ventral area, possesses a reduced trochantinal apodeme (*tna3*: Fig. 4), but does not extend to or contact the metacoxa. Weber (1929) described three metathoracic pleural muscles, $IIIpm_1$, $IIIpm_2$, and $IIIpm_3$. The pronator muscle to the hind wing, $IIIpm_1$, extends from the trochantin to the dorsal edge of the episternum, just ventral to the extremity of the pleural wing process. Whereas $IIIpm_2$ and $IIIpm_3$, the adductor muscles of the hind wing, extend posterior to the extremity of the pleural wing process.

DISCUSSION: A SCENARIO DESCRIBING THE EVOLUTION OF THE PSYLLID METATHORAX (FIG. 7)

For our discussion we chose *Apsylla cistellata* as a model to understand the complicated metathoracic pleuron of Psylloidea in relation to the generalized groundplan for insects.

Metathoracic Pleural Apophysis

Apsylla cistellata possesses a large internal apodeme proximal to the unique point of articulation of the pleurites with the coxa (Fig. 6B). We interpret this apodeme to be the metathoracic pleural apophysis (Ouvrard, 2000) for two reasons: 1) its connection with the condyle, and 2) its spatial relation with the internal furcae. As proposed by Brod-

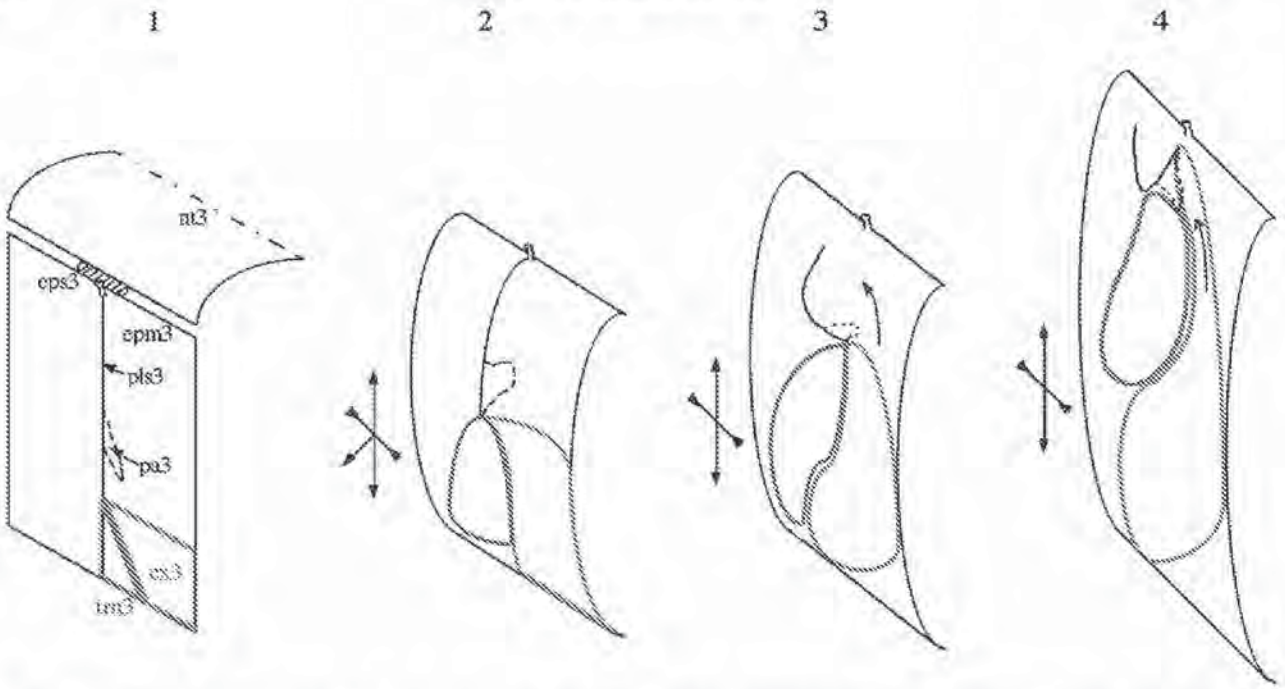

Fig. 7. Series of schematic diagrams proposing the main progressive evolutionary events in the expansion and migration of principal features of the metacoxa of the Psylloidea. Four main steps are proposed: 1) Generalized groundplan of the pleuron of a typical pterothoracic segment. 2) The pleuron expands three-dimensionally in the directions indicated by the arrows. Simultaneously, the trochantin (outlined in blue) and coxa (outlined in red) become enlarged. 3) The meron of the coxa extends upwards, pulling the trochantin dorsally. The pleural sulcus begins to rotate counterclockwise causing its dorsal end to draw away from the wing articulation. 4) As a result of the upward migration of the meron of the coxa the pleural apophysis (dotted outline) eventually rotates 180° and presses against the ventral edge of the metepimeron.

sky (1994), the pleural apophysis of a wing-bearing segment in most insects is closely associated with another apodeme, the sternal apophysis, of the same segment through common muscles. If one incinerates the insect so as to combust the muscles and leave the exoskeleton intact the junction of these apodemes is quite visible. This junction is characterized by the apices of these apodemes almost coming into contact. This junction is conspicuous in the mesothorax of Psylloidea, where these structures are in a common vertical plane, perpendicular to the body axis. In Cope (1940) this junction is used as a means to identify the pleural apophysis at the base of the prothoracic episternum in Psocoptera.

The pleural apophysis is visible in *Psylla buxi*, but it is very reduced (*pa3*: Fig. 3B), and compressed to the ventral edge of the metepimeron, as a result of the upward extension of the meron of the coxa (Fig. 7). As stated above, the condyle is the ventral origin of the pleural sulcus in the first and second segment. In the metathorax of *P. buxi*, as in most psyllid species, the pleural sulcus does not have the usual vertical orientation as in the other thoracic segments, because the coxo-pleural articulation is situated above the wing articulation. Thus, the pleural sulcus of the metathorax appears to follow a partial vertical course ventrad, fading immediately after fusing with the posterior margin of the episternum. It is at this point where this edge of the episternum thickens because of fusion with internal furcae. There are no other features available for inferring the putative course of the pleural sulcus until just near its articulation with the wing-base.

Pleural Sulcus

We inferred the positional relationships among the eupleuron, the trochantin, and the coxa in the meso- and metathorax by considering three major evolutionary changes, as follows: Step 1) an incomplete pleural sulcus; Step 2) a rotation of the sclerites from a subvertical to a horizontal position; Step 3) a dorsoventral elongation of the coxa. Interestingly, putative intermediate levels of these steps can be observed in the mesothorax of all extant specimens we observed. A complete pleural sulcus is only visible in the prothorax. This suggests each thoracic segment can evolve independently and can be "designed" as an evolutionary response to mechanical and/or functional constraints on appendages of the respective thoracic segment. The extraordinary modifications of the metapleuron, as described here for psyllids, are adaptations for the jumping aptitude of these insects because of restrictions on how

much the legs could adapt for jumping. In the mesothorax, constraints are not applied to the legs but on the wings. The topography of the mesopleuron is different than the metathorax, with the mesopleuron having a less-developed meron but a more modified dorsal epimeron. Lastly, for the prothorax, where there are no clear evolutionary constraints applied to adaptations of prothoracic appendages, the disposition of the pleuron is close to the groundplan for the generalized insect. However, a complete pleural sulcus may not be the ancestral state, in view of the observation by Snodgrass (1909) that this sulcus was incomplete prior to wing development.

Trochantin

The general migration of the trochantin, from the plesiomorphic state to the derived state in psyllids, appears to result from an upward elongation of the meron of the coxa in the third segment. Figure 7 shows how the metathoracic trochantin evolved from an ancestral state, in a ventral position, to a more dorsal position, as occurs in psyllids. If our explanation for this movement of the trochantin is correct, it suggests the trochantin has a coxal origin, supporting the contention of Barlet (1950).

CONCLUSION

The most notable and unique development observed in the psyllid thorax was the metapleuron, where the meron has evolved to accommodate a jumping aptitude, leading to reduction and rotation of the pleural sulcus. The evolutionary steps we proposed to explain the development of the psyllid metapleuron (Fig. 7) requires testing a 'history' for this trend on a phylogenetic basis (Grandcolas et al., 1997). We are currently in the process of performing such a test.

To date, very few morphological characters have been provided for inferring phylogenetic relationships among Psylloidea. Our study here describes a number of new features of the thorax, including designation of homologous structures, and provides the basis for improvising a new set of characters for phylogenetic studies. Such morphological characters, combined with molecular data (18S rRNA sequences) and other morphological features, will enable more robust inferences on psyllid phylogeny. Such a phylogeny will allow testing our proposed 'independent evolution' of individual thoracic segments in Psylloidea.

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APPENDIX

Glossary of Abbreviations and Definitions of Terms Used to Describe the Pleuron

Synonymous terms used elsewhere are provided.

aas—**Anterior accessory sclerite.*** Intersegmental sclerite of unknown origin posterior to the proepimeron and anterior to the posterior accessory sclerite in the membranous area delimited dorsally by the mesothoracic prescutum and the prealar bridge and ventrally by the peritrema. = proepimeron (Stough, 1910) = intersegmental plate = intersegmentalia (Crampton, 1914a) = part of peritreme (Brittain, 1922) = sclerite oblungo (Tremblay, 1965) = dorsal oblong sclerite (Matsuda, 1970; Journet and Vickery, 1978).

acl—**Anapleural cleft** Matsuda, 1970. Simple sulcus or membranous area dividing the episternum into a dorsal anepisternum and a ventral preepisternum and/or katepisternum. = Grenznaht zwischen Sternum und Pleura (Weber, 1929) = anapleural sulcus (Matsuda, 1970) = incisure anapleurale (Matsuda, 1979).

adk—**Anepisternal disc.*** Internal cuticular invagination or fold on the dorsal edge of the mesepisternum supporting the basalare.

aem—**Anepimeron** Crampton, 1909; Taylor, 1918. Dorsal portion of the epimeron, connected dorsally with the tergum and separated ventrally from the katepimeron by the posterior portion of the paracoxal suture sensu Matsuda (1970). = hyperepimeron = anaepimeron (Crampton, 1909) = pteropleurite (Crampton, 1914a,b) = epimetapleurium (Dicke and Howe, 1978).

aeps—**Anepisternum** Crampton, 1909; Taylor, 1918; Matsuda, 1970. Dorsal portion of the episternum separated antero-ventrally from the preepisternum + katepisternum by the anapleural cleft. = laterale (Crampton, 1909) = katopleure (Snodgrass, 1908) = preepisternum (Snodgrass, 1909) = lateropleurite = part of anepisternum (Crampton, 1914a,b) = hypopropleurium (Dicke and Howe, 1978) = surepisternum (Journet and Vickery, 1978).

bas—**Basalare** Crampton, 1914a; Snodgrass, 1935; Matsuda, 1970. An epipleurite of the wing articulation located between the pleural wing process and the prealar bridge. It is supported by the dorsal edge of the episternum (anepisternal disc) and overlaid by the anterior (membranous and axillary) part of the wing articulation. = Basalare *or* Episternalgelenkstück (Weber, 1929) = sclerite basal(ar)e dell'ala (Tremblay, 1965) = alipleurium anterius (Dicke and Howe, 1978).

epm—**Epimeron** Crampton, 1909, 1914a,b; Stough, 1910 *nec* proepimeron, Snodgrass, 1927, Journet and Vickery, 1978; Matsuda, 1970. Pleural plate forming the posterior part of the pleurae positioned posterior to or upon the pleural sulcus and the extremities of which are connected to the tergum dorsally and to the sternum ventrally. = épimère

(Audouin, 1824) = epimerum (Snodgrass, 1908, 1909; Brittain, 1922; Weber, 1929) = epimeron + postcoxale (Snodgrass, 1935) = metapleurium (Dicke and Howe, 1978).

eps—**Episternum** Audouin, 1824; Snodgrass, 1908, 1909, 1927, 1935; Crampton, 1909, 1914a,b; Stough, 1910 *nec* proepisternum, Brittain, 1922; Weber, 1929; Journet and Vickery, 1978; Matsuda, 1970. Anterior part of the pleuron, cephalad to the pleural sulcus, connected with the tergum dorsally and with the sternum ventrally. = episterno (Boselli, 1928; Ramírez-Gomez, 1955).

fpa—**Fossa of the pleural apophysis** Emeljanov, 1981. External cavity marking the pleural apophysis and a major external feature of the pleural sulcus.

ftna—**Fossa of the trochantinal apodeme.*** External cavity marking the trochantinal apodeme designating the trochantinal area.

hepm—**Heel of the epimeron** Emeljanov, 1981. A process extending from the posterodorsal portion of the epimeron connecting it to the lateral part of the pseudonotum. = astragalus (Emeljanov, 1981).

kcx—**Katepisternal complex** Crampton, 1909. Ventral area of the episternum corresponding to the partial or complete fusion between the katepisternum and the trochantin. = katepisternal complex = katepimeral complex p. 26 [sic] = pleuro-trochantin (Crampton, 1914b) = preepisternokatepisternum (Matsuda, 1970) = propleurosternium (Dicke and Howe, 1978) = *prothoracic* trochantinal process (Journet and Vickery, 1978).

kem—**Katepimeron** Crampton, 1909; Taylor, 1918; Matsuda, 1970. Ventral area of the epimeron, separated from the anepimeron dorsally by the paracoxal suture sensu Matsuda (1970) and connected ventrally to the sternum. = hypoepimeron (Crampton, 1908, 1914a,b) = kataepimeron (Taylor, 1918) = hypometapleurium (Dicke and Howe, 1978).

kes—**Katepisternum** Taylor, 1918. Ventral area of the episternum, separated from the anepisternum dorsally by the paracoxal suture sensu Matsuda (1970), and anterior to the front margin of the trochantin. = part of antecoxal laterale (Crampton, 1909) = part of laterosternite = antecoxale (Crampton, 1914a) = antecoxale = part of katepisternum (Matsuda, 1970) = infraepisternum (Journet and Vickery, 1978).

mcs—**Meracanthus** Fieber, 1875. Small spine-like process on the meron of the coxa, projecting caudally in nonheteropteran Hemiptera.

pa—**Pleural apophysis** Snodgrass, 1935; Emeljanov, 1981. Internal process originating on the ventral third of the internal pleural ridge and projecting towards a corresponding furcal apophysis. = adfurcal process (Crampton, 1909) = pleural ridge = pleural apodeme (Snodgrass, 1908; Crampton, 1914a) = lateral apodeme (Brittain, 1922) = pleural arm (Snodgrass, 1909, 1927; Matsuda 1970) = Pleuralhaken (Weber, 1929) = apodemas laterales de las pleuras (Ramírez-Gomez, 1955) = apodema pleurale (Dicke and Howe, 1978).

pas—**Posterior accessory sclerite.*** Intersegmental sclerite of unknown origin located between the anterior accessory sclerite and the anterodorsal edge of the metepisternum in the membranous area delimited dorsally by the prealar bridge and ventrally by the peritrema. = intersegmental plate = intersegmentalia (Crampton, 1914a) = accessory sclerite (Crawford, 1914; Journet and Vickery, 1978) = intertergite (Taylor, 1918; Brittain, 1922) = sclerite accessorio (Tremblay, 1965) = additional sclerite above the oblong sclerite (Matsuda, 1970).

pbr—**Prealar bridge** Crampton, 1914b; Snodgrass, 1927, 1935, Matsuda, 1970. Sclerotized arm anterior to the wing articulation extending ventrad from the prescutum to the episternum. = praesegmental sclerite (Crampton, 1909) = prealare (Crampton, 1914a,b; Taylor, 1918; Brittain, 1922; Snodgrass, 1935) = processo alungato (Boselli, 1928) = Tergalarm (Weber, 1929) = apofisis lateral del prescudo (Ramirez-Gomez, 1955) = junctura antealaris (Dicke and Howe, 1978) = prealar arm (Journet and Vickery, 1978) = bras préalaire préscutal (Matsuda, 1979).

pdk—**Pronator disk** Snodgrass 1909. Internal discoid process projecting inward from the the parapterum to which are attached a majority of the pronator muscles of the wing. = muscle disc (Snodgrass, 1908, 1909) = hebelartiger Fortsatz von Hautpolster der Flügelbasis (Weber, 1929).

peps—**Preepisternum** Snodgrass, 1909. Anterior or antero-ventral area of the episternum, separated caudally from the anepisternum and ventrally from the katepisternum. = katopleure (Snodgrass, 1908) = part of laterale (Crampton, 1909) = lateropleurite (Crampton, 1914a,c) = part of precoxale = part of precoxal bridge (Crampton, 1914b) = preepisternite (Duporte, 1965).

pls—**Pleural sulcus** Snodgrass, 1908, 1909, 1927; Crampton, 1909, 1914a; Crawford, 1914; Taylor, 1918; Brittain, 1922. Vertical or subvertical groove separating the episternum from the epimeron and extending dorsally (when complete) from the articulation condyle of the coxa to the wing articulation. Internally, the pleural sulcus is visible as a ridge bearing the pleural apophysis. = part of internal entopleurum (Snodgrass, 1909) = sutura pleurale (Boselli, 1928; Tremblay, 1965) = Pleuralnaht (Weber, 1929) = *prothoracic and mesothoracic* sutura pleural (Ramirez-Gomez, 1955) = *prothoracic* pleural sulcus (Matsuda, 1970; Journet and Vickery, 1978) = *mesothoracic* transanepisternal suture (Matsuda, 1970) = suture transépisternale secondaire (Matsuda, 1979).

pobr—**Postalar bridge** Crampton, 1914b, Taylor, 1918, Snodgrass 1935. A ventral extension of the postnotum of wing-bearing segments connecting to the posterio-dorsal area of the epimeron and to the phragma of the neighboring posterior segment. =

pleurophragmite (Crampton, 1914a) = postalare (Snodgrass 1935) = postalar bridge (Matsuda 1970) = junctura postalaris (Dicke and Howe, 1978).

pocx—**Postcoxal bridge** Crampton, 1914b; Taylor, 1918; Snodgrass, 1927, 1935. Sclerotized area (not always distinct) flanking the caudal edge of the coxa and joining the postero-ventral portion of the epimeron to the sternum. = postcoxale (Crampton, 1914a,b; Taylor, 1918; *only for the metathorax* Brittain, 1922; Snodgrass, 1935; Matsuda, 1970) = postcoxale Brücke (Weber, 1929) = *metathoracic* ponte postcoxale (Tremblay, 1965) = metapleurosternium = junctura postcoxalis (Dicke and Howe, 1978).

ppt—**Parapterum** Snodgrass, 1908. Ovoid epipleurite anterior to the tegula and posterior to the prealar bridge between the junction of prescutum and scutum dorsally and the dorsal edge of the episternum ventrally. = episternal parapterum = preparapterum (Snodgrass, 1909) = articulatory epideme (Stough, 1910) = parapteron (Crawford, 1914) = anterior basalare (Taylor, 1918; Brittain, 1922) = paraptero (Boselli, 1928) = Hautpolster der Flügelbasis (Weber, 1929) = tubercolo prealare (Tremblay, 1965) = prealar sclerite (Matsuda, 1970).

prcx—**Precoxal bridge** Crampton, 1914b, Taylor, 1918, Snodgrass, 1927. Junction between the episternum and the basisternum anterior to the trochantin; fusion of the katepisternal complex with the anepisternum dorsally, and the basisternum ventrally. = *for the prothorax of Psylla mali* Kehlplatte *or* Trochantinus = *for Apsylla* präcoxale Brücke (Weber, 1929) = regione epi-lateristernale (Tremblay, 1965) = prothoracic trochantin in *P. mali* (Matsuda, 1970).

ptm—**Peritreme** Snodgrass, 1909; Crampton, 1914a,b; Taylor, 1918; Snodgrass, 1935; Journet and Vickery, 1978. Sclerite surrounding the spiracle. = part of peritreme (Brittain, 1922) = stigma mesometatoracico (Boselli, 1928) = peritremo (Ramirez-Gomez, 1955) = ventral sclerotization surrounding the first thoracic spiracle (Matsuda, 1970).

pwp—**Pleural wing process** Snodgrass, 1908, 1909, 1927, 1935; Matsuda, 1970. Thin vertical process at the median dorsal edge of the pleural sulcus; acts as a fulcrum for wing movement during the flight. The pleural wing processes of the mesothorax and metathorax are termed here the anterior pleural wing process (*apwp*) and the posterior pleural wing process (*ppwp*), respectively = alar apophysis (Snodgrass, 1908) = alar process of the apodeme (Crampton, 1909) = pleuraler Flügelgelenkkopf (Weber, 1929) = apofisis de las alas (Ramirez-Gomez, 1955) = processo alare (Tremblay, 1965) = alipedium (Dicke and Howe, 1978).

tems—**Transepimeral sulcus.*** Sulcus running subvertically from the most dorsal point of the coxa upwards to the anterior angle of the pleural wing process in the mesothorax of Psylloidea. = ?sternepimeral carena Emeljanov, 1981.

tg—**Tegula** Kirby and Spence, 1826; Snodgrass, 1909; 1935; Crampton, 1914b,c; Weber, 1929; Tremblay, 1965; Matsuda, 1970. Reduced scale-like sclerite at the anterior membranous edge at the base of the forewing. = posterior basalare (Taylor, 1918; Brittain, 1922) = paraptero (Boselli, 1928) = Humeralplatte (Weidner, 1972).

tna—**Trochantinal apodeme.*** Internal apodeme of the meso- and metathoracic trochantins in Psylloidea. Probable insertion point of the III pleural muscle extending from the trochantin to the dorsal edge of the episternum (Weber, 1929). This muscle is one of the two "anterior pleurotrochantinal muscles" (p-ti (cx) 2 or 3) described by Matsuda (1970).

trn—**Trochantin** Audouin, 1824; Snodgrass, 1908, 1909, 1927, 1935; Crawford, 1914; Crampton, 1909, 1914a,b; Brittain, 1922; Matsuda, 1970, 1979. Sclerite anterior to the base of the coxa and articulating or fusing with the katepisternum dorsally.

*Structures defined only in Psylloidea.