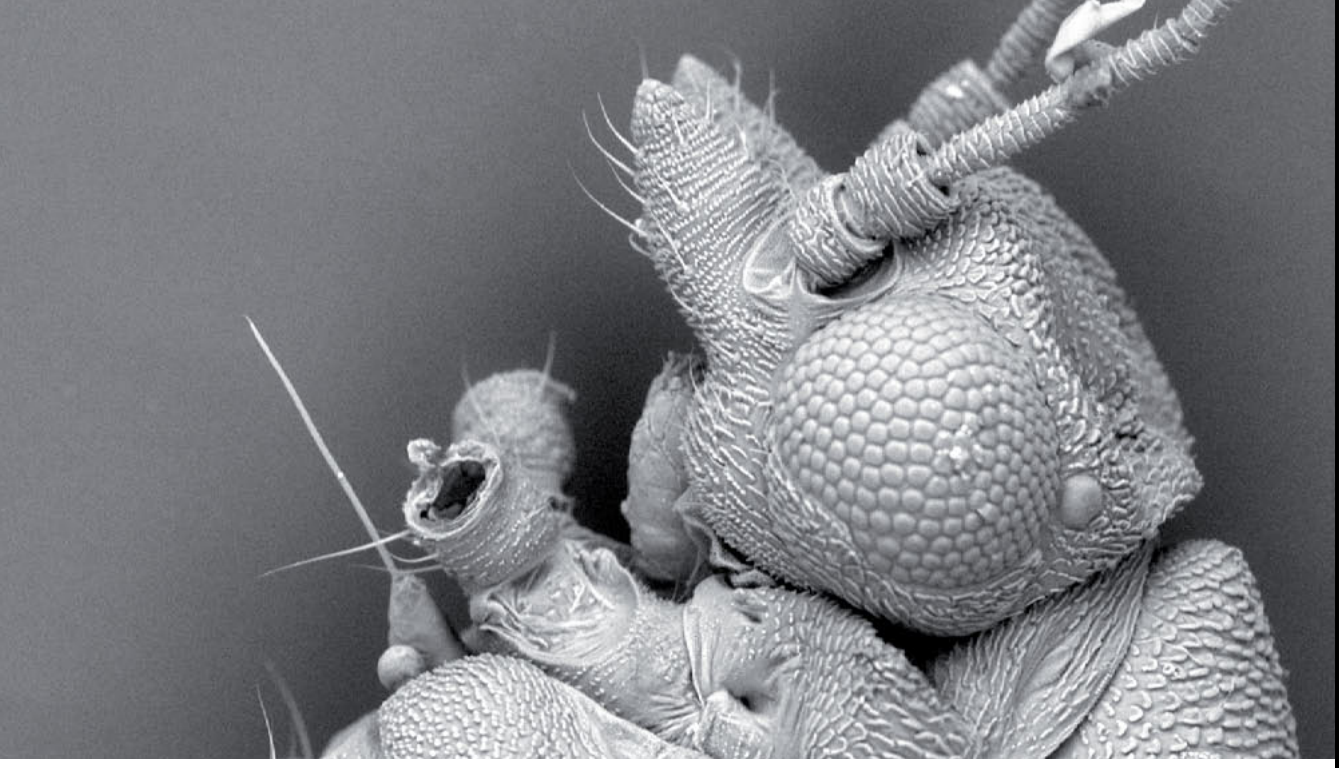

Thorax morphology and its importance in establishing relationships within Psylloidea (Hemiptera, Sternorrhyncha)

Jowita Drohojowska

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Abstract

The paper presents the description and documentation of the thorax structure in 59 species of psyllids – representatives of all families and subfamilies (with the exception of Atmetocraniinae, Metapsyllinae and Symphorosinae) within the Psylloidea superfamily in accordance with the classification introduced by Burckhardt and Ouvrard (2012). The paper also provides structural characteristics of that part of body in the Liadopsyllidae fossil family regarded as the ancestors of modern psyllids and the Aleyrodoidea insects, a group regarded as a sister group within the Sternorrhyncha suborder. Both groups have been applied as outgroups.

Based on the paleontological criterion as well as comparisons within and outside of groups, an analysis has been conducted regarding the directions of changes of the elements of thorax structures including the appendages. The polarization of characters has also been determined. The determination of phylogenetic relations based on the morphology of the thorax and its appendages has been conducted by means of cladistic analysis. The relations between the analyzed taxa have been presented in cladograms. The phylogenetic relations between the taxa of psyllids have been reviewed based on the analysis of the thorax including the appendages in comparison with other proposals of this group's phylogeny. The monophyly of five families has been confirmed: Carsidaridae, Homotomidae, Psyllidae, Phacopteronidae and Triozidae. In the structure of the thorax and the appendages, no synapomorphy confirming the monophyly of the following families has been established: Aphalaridae, Calophyidae and Liviidae. The characteristics of families and subfamilies have been complemented with new characters identified within the thorax. Based on the above, a key has been created for the identification of psyllids from individual subfamilies of the world fauna of psyllids.

Keywords: morphology, thorax, Hemiptera, Sternorrhyncha, Psylloidea

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Introduction

The morphological studies regarding insects from the Psylloidea superfamily conducted up to now focused mostly on the morphology of the head, forewings, legs and genitalia. In comparison to their total body dimensions, the thorax of psyllids is relatively large, yet not much information concerning its morphology is given in professional literature. It may thus be considered the least studied body part of these insects. Most information pertains to characters of diagnostic significance, and little characters of that kind have been found in the morphology of the thorax so far. It should not also be neglected that the thorax is a truly complex tagma of the body, which is difficult to mount. No studies of thorax in representatives of all higher taxonomic units have been conducted up to now (families, subfamilies or tribes of psyllids). Neither has any set of characters of the thorax which could serve as a determinant of affiliation of a given species to these units been distinguished. What is more, the morphological characters of the thorax have not been used in phylogenetic discussions regarding the Psylloidea. It has thus been decided to conduct a morphological analysis of the thorax in all families, subfamilies and tribes as well as to determine the feasibility of the distinguished characters for the determination of phylogenetic relations within the Psylloidea superfamily.

Review of previous studies of thorax morphology of psyllids

Audouin (1824) was the author of the first work regarding thorax morphology in insects. In his work, Audouin proposed a nomenclature for individual sclerites of the thorax of all orders of insects, as well as developed a topological definition for each of the sclerites constituting the thorax. Many of the contemporarily used terms relating to morphological structures and the thorax, such as episternum or trochantin, are derived from that particular work.

The first information regarding the structure of the thorax of psyllids have been provided by Witlaczil (1885), who studied the structures of the thorax in *Psyllopsis fraxinicola* (Foerster, 1848). That work, however, concerned mostly the anatomy of psyllids, so the information regarding the thorax was scarce and mostly related to the segmentation of the thorax into prothorax, mesothorax and metathorax.

In his works, Snodgrass (1908, 1909) has provided descriptions of numerous structures and has introduced names for individual structures of the thorax in insects, which are commonly used until present, also in the Psylloidea group. He has characterized and presented the drawings of the parapteron (Lat. *parapterum*), the peritreme (Lat. *peritrema*), the pleural sulcus (Lat. *sutura pleuralis*), the pleural wing process (Lat. *processus anterior alae*) and the preepisternum (Lat. *proepisternum*).

The thorax of psyllids was described in detail by Stough (1910) in his work regarding the species *Pachypsylla celtidismamma* (Fletcher, 1883). Based on Audoin's (1824) work referred to above, Stough (1910) has characterized the individual tagmata of the psyllids' thorax by describing and drawing all the constituent sclerites. While Stough (1910) has only provided information regarding a single species, the subsequent work written by Crawford (1914) has reviewed 7 species of different genera of New World psyllids. The author attempted to indicate homology between the individual elements of the thorax and to interpret their function and origin. He has given special attention to the three additional sclerites between the prothorax and mesothorax, the incompletely developed mesopleural sulcus, the meso- and metasternum, as well as the metapleurae. At the same time, he disagreed with the interpretation of sclerites proposed by Stoug (1910) and has complemented his descriptions with structures which were not included earlier. Moreover, he has illustrated the internal structure of the thorax of psyllids. In that same year, a series of works by Crampton (1914a, b, c) was published, in which the author has discussed the structure of the thorax of winged insects, at the same time introducing a number of morphological terms applied in descriptions of insects including psyllids until present.

Taylor (1918), while studying the *Euglyptoneura robusta* (Crawford, 1914) and *Apsylla cistellata* (Buckton, 1896) species, attempted to reinterpret the illustrations, notions and conclusions drawn from the structure of the psyllids' thorax by Crawford (1914) while resorting to the works of Crampton, referred to above. In the work, the author has also included conclusions regarding the thorax morphology of 8 contemporarily distinguished families within the Homoptera suborder and 17 families within the Heteroptera suborder. Based on these conclusions, he has developed a general structural plan of Heteroptera and Homoptera. He has also proposed relationships within the Hemiptera order based on the thorax structure and provided proper schematic illustrations.

Subsequent researchers such as Brittain (1922) and Minkiewicz (1924), who based their research on the *Psylla mali* Schmidberger, 1836 or Bosselli (1928), studying the thorax morphology of the *Homotoma ficus* (Linnaeus, 1758), did not go beyond the scheme provided by Crawford (1914) in their works.

It was only Weber (1929) who described the *Psylla mali* head and thorax structure while providing a series of new data regarding that part of the body. Weber's monograph is an accurate study of *P. mali,* in which the author characterized the external and internal structures of the head and thorax and supplemented the detailed descriptions with excellent drawings. He presented the dimensions and shapes of individual sclerites and the occurring structures, as well as the courses of most muscles, their proximal and distal attachment points at the prothorax, mesothorax and metathorax apodemes. He was the first to indicate the trochantinal apodeme at the meso- and metathorax and the mode of attachment and course of the "pleurotrochantinal muscles" which make psyllids capable of jumping. His work included a comparison of the muscular system of individual sections of the thorax and the mechanics of the psyllids' muscles with other insects – both jumping (Auchenorrhyncha) and ones that lack this capability (Aphidoidea, Lepidoptera). Although it was published nearly a century ago, the drawings from this work are commonly copied by modern researchers, especially in descriptions of the psyllids' muscular system.

Pflugfelder (1941) published a monograph of insects classified in the contemporary Psyllina suborder, in which he has presented the structure of the psyllids' thorax while quoting descriptions and reproducing drawings from the works of Crawford (1914) and Weber (1929). This work also included a systematic part, in which the author provided the morphological characteristics of species classified in all 7 contemporarily distinguished subfamilies of the Psylloidea family from the Psyllina suborder. In case of species from 4 subfamilies (Liviinae Löw, Aphalarinae Löw, Psyllinae Löw and Triozinae Löw), the

author pointed out a differing shape of the pronotum in each subfamily as a defining character.

A unique approach towards the analyses of psyllids' thorax morphology was presented by Heslop-Harrison (1951), who was looking for morphological characters of adult specimens that would be useful for creating a natural taxonomic system of the Psylloidea. Within the thorax, he has only found such characters in the prothorax, while regarding the remaining two tagmas – the mesothorax and metathorax – as devoid of such characters. The author analyzed the episternal sclerites and has noted the number and distribution of stigmas at the peritremes.

In the introduction regarding morphology in his monograph of psyllids fauna of contemporary Czechoslovakia, Vondraček (1957) provided a graphical presentation of the dorsal and lateral *Arytaina genistae* (Latreille, 1804) tagma of a species that has not been studied before, in the form of general drawings devoid of several significant morphological elements such as the pleural sulci (Lat. *sutura pro-*, *meso-*, *metapluralis)*, the additional sclerites (Lat. *scleritum accessorium*) or the metathorax pleurites (*metaepimerum, metaepisternum)*.

In his work regarding the taxonomic system of the contemporary Psyllodea infraorder, Klimaszewski (1964) analyzed the structure of the thorax for the purposes of comparing higher taxonomic units – families. The author analyzed the morphology of 13 species of psyllids and proved that the relations between the pronotum, mesopraescutum and mesoscutum may be used for inferring lineages and relations between species from individual families. He pointed out the wide pronotum and relatively even development of the mesopraescutum and mesoscutum as plesiomorphic characters and undermined the common opinion that the development of the meracanthus is an apomorphic character. The author based his conclusions mostly on his own research, including his own descriptions and drawings, and on the data of two species described in the literature (Crawford 1914, Weber 1929). It was the first comparative analysis of thorax morphology of psyllids classified in individual families distributed all over the world, whereas Crawford (1914) only based his work on Nearctic material.

Also the work by Tremblay (1965) is significant in the view of studying the thorax of psyllids. The author was the first to describe the *Trioza tremblayi* Wagner, 1961 and to adapt the nomenclature concerning the morphology of the thorax of insects provided earlier by Snodgrass (1908, 1909, 1927, 1935). It was the first time that Snodgrass' terminology was applied in describing psyllids.

Apart from describing the morphology of the thorax of insects classified in 30 orders, Matsuda (1970) also discussed the probable evolution of individual elements of the thorax, homologies between its respective parts and the main evolutionary changes in the muscular system of imago and nymphs. He also introduced new morphological terms used up to now, such as the anapleural cleft (Lac. *sutura anapleuralis*), that is the cleft dividing the pleura into the dorsal and ventral parts. For that purpose the author used the drawings of tergites and pleurites from the work by Weber (1929).

Based on the nomenclature provided by Matsuda, Journet and Vickery (1978) conducted a study of the morphology of adult insects and Nearctic larvae of species classified as *Craspedolepta* Enderlein, 1921. They presented their own drawings of individual elements of the segments in concern, which has contributed to the general knowledge of their morphology.

Further developments in discovering the thorax structure were due to the works by Hodkinson and White (1979), Brown and Hodkinson (1988), Ossiannilsson (1992). In the introductions to their works, the authors discussed the morphological structure of psyllids, thus standardizing the terminology used in describing psyllids. In all works referred to above, however, the authors neglected the ventral side.

In their work, Ouvrard et al. (2002) described the structure of the pleuron in 7 species from 3 selected families – with consideration given to both internal and external sides. The authors pointed out the elements of the thorax which are characteristic only to psyllids, such as the transepimeral sulcus in the mesothorax, the

fossa of the trochantinal apodeme or the anapisternal disc. They also described the probable manners of shifting and forming of the pleuron elements, especially in the metathorax. What is more, they compared all the morphological terms used earlier by various authors. In their work regarding the wing base articulation (Ouvrard et al., 2008), the authors have characterized and illustrated all the elements and structures allowing for the movement of wings in psyllids, as well as presented the dorsal thorax sclerites.

In recent years, Drohojowska has taken up studies of variation in the morphology of the thorax of psyllids. The results of the studies have been published in three works (Drohojowska 2009a, b, 2013). For the first time, the thorax of male and female specimens has been compared (8 species from various families and genera) and it became clear that the shape and proportions of individual thorax pleura are similar and the differences only concern sizes (Drohojowska, 2009b). In her work of 2013, the author has studied the thorax of species of the *Cacopsylla* Ossiannilsson, 1970 genus classified as three subgenera, and indicated the characters which may be used in their diagnostics.

In the introduction to his monograph containing descriptions and redescriptions of over 3.500 species of psyllids of China, Li (2011) has provided a description of the thorax based on the *Cacopsylla chinensis* Yang, Li, 1981 species. Despite the great number of analyzed species, the author did not include the description or drawings of the dorsal and ventral sides of the thorax.

In the papers based on fossil material, where the Psylloidea superfamily is relatively well represented, there is little information regarding the thorax of psyllids. Except for Klimaszewski (1997), Ouvrard et al. (2010) and Drohojowska (2011), no descriptions of the thorax part may be found. Similarly, little information is provided in the works regarding the modern fauna of psyllids. While, as far as the fossil material is concerned, the above may be understood due to the preservation condition of specimens, it should not cause difficulties in case of modern material.

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Streszczenie

Praca zawiera opis i dokumentację budowy tułowia 59. gatunków koliszków, przedstawicieli wszystkich rodzin i podrodzin (za wyjątkiem Atmetocraniinae, Metapsyllinae, Symphorosinae) w obrębie nadrodziny Psylloidea wg klasyfikacji Burckhardt, Ouvrard (2012). Przedstawiono także charakterystykę budowy tego odcinka ciała dla owadów z kopalnej rodziny Liadopsyllidae uważanej za przodków współczesnych koliszków oraz owadów z rodziny Aleyrodoidea, grupy uznanej za siostrzaną w obrębie podrzędu Sternorrhyncha. Obie te grupy zostały wykorzystane jako grupy zewnętrzne. Opierając się na kryterium paleontologicznym, porównaniach wewnątrzgrupowych oraz porównaniach pozagrupowych, przeprowadzono analizę kierunków zmian elementów budowy tułowia i jego przydatków oraz wyznaczono polaryzację cech. Ustalenie filogenetycznych relacji w oparciu o budowę morfologiczną tułowia i jego przydatków wykonano przy pomocy analizy kladystycznej, z wykorzystaniem programu komputerowego TNT 1.1 (Goloboff et al., 2008). Relacje pomiędzy analizowanymi taksonami zostały przedstawione na kladogramach. Omówiono relacje filogenetyczne pomiędzy taksonami koliszków w oparciu o analizę tułowia i jego przydatków w porównaniu z innymi propozycjami filogenezy tej grupy. Potwierdzono monofiletyczność pięciu rodzin: Carsidaridae, Homotomidae, Psyllidae, Phacopteronidae oraz Triozidae. W budowie tułowia i jego przydatków nie znaleziono synapomorfii potwierdzających monofiletyczność rodzin: Aphalaridae, Calophyidae i Liviidae. Uzupełniono charakterystyki rodzin i podrodzin o nowe cechy zidentyfikowane w obrębie tułowia. Na ich podstawie stworzono klucz do oznaczania gatunków z poszczególnych podrodzin światowej fauny koliszków.

Jowita Drohojowska

Die Morphologie des Thoraxes und deren Bedeutung für Festsetzung der stammesgeschichtlichen Verwandtschaft innerhalb der Superfamilie *Psylloidea* (*Hemiptera*, *Sternorrhyncha*)

Zusammenfassung

Die Arbeit beinhaltet die Charakteristik von der Morphologie des Thoraxes und den Nachweis dafür bei 59 Arten der Blattflöhe, Vertretern aller Familien und Unterfamilien (mit Ausnahme von *Atmetocraniinae*, *Metapsylllinae*, *Symphorosinae*) innerhalb der Superfamilie *Psylloidea* nach der Klassifizierung von Burckhardt; Ouvrard (2012). Die Verfasserin präsentiert die Charakteristik von dem Körperteil für Insekte aus der als Vorfahren der heutigen Blattflöhe geltenden fossilen Familie *Liadopsyllidae* und für Insekte aus der innerhalb der Unterordnung *Sternorrhyncha* als eine Schwestergruppe geltenden Familie *Aleyrodoidea*. Die beiden Gruppen dienten als äußere Gruppen. In Anlehnung an paläontologisches Kriterium, an das Gruppeninnere betreffende Vergleiche und Außergruppenvergleiche wurde erforscht, in welcher Richtung sich die einzelnen Elemente von der Morphologie des Thoraxes und dessen Anhänge veränderten und wie sich diese Eigenschaften differenzierten. Stammesgeschichtliche Verwandtschaftsverhältnisse wurden anhand der Morphologie des Thoraxes und dessen Anhänge mittels phylogenetischer Analyse mithilfe des Computerprogramms TNT 1.1 (Goloboff et al., 2008) festgestellt. Die Wechselbeziehungen zwischen den zu untersuchten Taxa wurden an Kladogrammen dargestellt. Phylogenetische Verhältnisse zwischen den Taxa von Blattflöhen wurden anhand der Analyse des Thoraxes und dessen Anhänge untersucht und mit anderen Vorstellungen von der Phylogenese der Gruppe verglichen. Es hat sich bewahrheitet, dass folgende fünf Familien: *Carsidaridae*, *Homotomidae*, *Psyllidae*, *Phacopteronidae* und *Triozidae* monophyletisch sind. In der Morphologie des Thoraxes und dessen Anhänge wurde keine Synapomorphie festgestellt, die eine Monophylogenese von den Familien: *Aphalaridae*, *Calophyidae* und *Liviidae* bestätigen würde. Die Verfasserin vervollständigte außerdem die Charakteristiken von den einzelnen Familien und Unterfamilien mit den im Bereich des Thoraxes neu identifizierten Merkmalen. Auf der Grundlage wurde ein Bestimmungsschlüssel entwickelt, mit dessen Hilfe die aus den einzelnen Unterfamilien stammenden und heutzutage lebenden Arten der Blattflöhe bestimmt werden können.

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