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GENERAL MORPHOLOGY OF LEAFHOPPER NYMPHS OF THE SUB-FAMILY DELTOCEPHALINAE (HEMIPTERA: CICADELLIDAE)

Dmitry A. DMITRIEV

Zoological Institute, Russian Academy of Sciences, Universitetskaya nab. 1,
St. Petersburg 199034, Russia. E-mail: hemipt@zin.ru

Abstract – Although morphology of adult leafhoppers has been relatively well studied, works on morphological characters of their larvae remain very scarce. This refers especially to the family Cicadellidae with similar larvae difficult to identify. However, with careful study of larval characters, we could better comprehend phylogenetic relations among the taxa. This article gives the description and comparative analysis of morphological characters of larvae of the subfamily Deltocephalinae. Characters such as the borders between the vertex, clypeus and frons, in terms of their relative positions, were found to be the most important characters of the head. The degree of development of wing pads indicates the age of the larvae and also development of wings in imagos. On the legs both usual setae and platellae can be found. Pretarsi of larvae of different species are very similar. The abdomen is usually covered with setae. Ten patterns of abdominal chaetotaxy are distinguished in species of the subfamily Deltocephalinae. The pygofer is longer than other segments of the abdomen. Below the pygofer, the abdomen bears 3 pairs of gonapophyses (rudimental genitalia) that are useful for definition of the larval sex. Female gonapophyses are similar while male gonapophyses vary in shape.

KEY WORDS: Hemiptera, Cicadina, Deltocephalinae, leafhoppers, nymphs, larvae, morphology.

Izvleček – SPLOŠNA MORFOLOGIJA NIMF ŠKRŽATKOV IZ PODDRUŽINE DELTOCEPHALINAE (HEMIPTERA: CICADELLIDAE)

Čeprav je morfologija odraslih škržatkov relativno dobro proučena, ostajajo dela o morfoloških znakih njihovih ličink zelo redka. To še posebej velja za družino Cicadellidae s podobnimi, težko določljivimi ličinkami. S skrbnim proučevan-

jem znakov pri ličinkah bi lahko filogenetske odnose med taksoni boljše razumeli. Ta članek je posvečen opisu in primerjalni analizi morfoloških znakov pri ličinkah poddružine Deltocephalinae. Znaki, kot so položaji robov med temenom, klipejem in čelom, so se izkazali za najpomembnejše znake na glavi. Stopnja razvitosti krilnih lusk kaže na starost ličink in tudi na razvitost kril pri odraslih. Na nogah lahko najdemo tako običajne dlake kot tudi luskice. Končni členi stopalc ličink različnih vrst so si podobni. Zadek je običajno pokrit z dlakami. Deset vzorcev odlakanosti zadka lahko razločimo pri vrstah poddružine Deltocephalinae. Pigofor je daljši od drugih členov zadka. Pod pigoforjem ima zadek tri pare gonapofiz (zametkov genitalij). Gonapofize so uporabne za določanje spola ličink. Ženske gonapofize so si podobne, moške pa so različnih oblik.

KLJUČNE BESEDE: Hemiptera, Cicadina, Deltocephalinae, škržatki, nimfe, ličinke, morfologija.

Introduction

Although the morphology of adult leafhoppers has been relatively well studied, works on morphological characters of their larvae remain very scarce. This refers especially to the family Cicadellidae with similar larvae difficult to identify. There are only a few publications with comparative morphological data and keys for leafhopper larvae. In 1975 and 1978, S. Walter published two papers dedicated to the leafhopper larvae of the tribe Athysanini and some species from the nearest tribes. These articles contain descriptions of some Central European larvae of the Athysanini, keys for their identification, and detailed material on comparative morphology of all instar larvae.

M.R. Wilson made an essential contribution to the knowledge of leafhopper larvae. His first work (Wilson, 1978) was dedicated to the larvae of British leafhoppers of the subfamily Typhlocybinae; the species of the genus *Iassus* were described in his second article (Wilson, 1981); and the key for larvae of Cicadina, associated with rice in South East Asia, is given in the third work (Wilson, 1983).

The paper of J. Vilbaste (1987) is the most comprehensive in terms of the number of included species. This work is dedicated to the nymphs of the North European Cicadelloidea.

There are also more than two dozen of papers with descriptions of larvae of individual species (Melichar, 1897; Kirkaldy, 1906, 1907; MacGill, 1932; Silvestri, 1934; Evans, 1947; DeLong, 1948; Oman, 1949; Wagner, 1950, 1964; Esaki, Miyamoto, & Ishihara, 1959; Mochida, 1970; Mitjaev, 1971; Müller, 1974, 1979, 1987, 1988, 1994; Linnavuori & DeLong, 1977; Lee, 1979; Hegab, Orosz, & Jenser, 1980; Ossiannilsson, 1981, 1983; Linnavuori & Al-Ne'amy, 1983; Meyer-Arndt & Remane, 1992; Hamilton, 1995; Szwedo, 1996; Theron, 1996; Guglielmino & Virla, 1997; Tishechkin, 1999; Dmitriev, 1999, 2001). Notes on comparative morphology

of larvae can be found in the works of Kershaw & Muir (1922), Wagner (1951), Mochida (1970), Kathirithamby (1974a, 1974b), Walter (1975, 1978), Vilbaste (1982), Wilson (1983), Dmitriev (2000a, 2000b).

The significance of the study of larvae is evident. First, this would enable us to determine species when only their larvae are present in collections. Second, the larvae provide complementary characters for the description of higher taxonomic groups. Eventually this could help us to better comprehend the phylogenetic relations among the taxa.

Methods

This work is dedicated to the leafhopper nymphs of the subfamily Deltocephalinae, the most diverse subfamily of Cicadina. In contrast to the previous investigators, the work was done based only on dry material. For more reliable identification, if it was possible and if sufficient material was available, nymphs that were ready to molt into imagos or only their abdomens were boiled in a solution of caustic soda. Then the developed male genitalia were used for identification. In many cases, this method allowed us to avoid mistakes and also to find some in the works of previous investigators.

The system of Cicadina is based mainly on characters of the male genitalia. However, this method cannot be used for larvae. Previous authors used a scanty set of characters for their description, mainly such as the pattern of coloration and chaetotaxy of the abdomen, and a few other striking characters. In some cases, however, they were inadequate for the description of suprageneric and even generic taxa.

The author had an opportunity to examine larvae of about 200 species from the subfamily Deltocephalinae. This was the material kept in the Zoological Institute (St. Petersburg) collected mostly by the author, by A.F. Emeljanov, and V.M. Gnezdilov. Some specimens were provided by my colleagues G.A. Anufriev and H. Nickel.

General morphology of leafhopper nymphs

Cicadina are hemimetabolic insects and their larvae are generally similar to imagos (Figs. 1–2). They are small or middle-sized insects. The head is usually longer than one of imagos, and, in some cases (in species of the tribes Scaphytopiini and Drabescini), it bears a long apical projection lacking in adult insects (Figs. 47–48). A more or less developed carina often passes along the fore-edge of the head. This carina is usually considered the border between the vertex and clypeus, but the actual border of the vertex lies below this carina. Best of all, as a suture, this border is marked in representatives of the tribes Macrostelini, Grypotini, and also in 3rd–4th instar larvae of some other groups. In other cases the suture is invisible, but the existence of the border can be indicated by some indirect attributes such as the depres-

sion of the face (for example, in species from the tribes Doraturini and Selenocephalini), or differences in the colour patterns. The frons is small, triangular, situated above the clypeus. Sometimes it is marked by the colour and/or depression, but more often, it is indistinct. The upper part of the head, termed a macrocoryphe by Anufriev & Emeljanov (1988), and its lower part – the face – can be separated either by a carina (for example, in larvae of the tribe Drabescini, Selenocephalini, Hecalini) or the transition is rounded as occurs in species of Athysanini, Goniagnathini and some other tribes. In the last case, the border between the face and the macrocoryphe is usually marked by a suture which is usually slightly bent on the upper side of head and from above is similar to two arches. The part of the vertex that approximates the facial surface, is named the metope (after Anufriev & Emeljanov, 1988). The heads of representatives of some groups (such as Doraturini, Paralimnini and some others) can have a secondary carina but it passes somewhat distally to the primary border between the face and macrocoryphe. Besides the borders, just as had been written, the T-shaped molting suture is well developed on the upper side of larval head of all groups. The transverse part of this suture passes at some distance from the fore edge of the head. This suture, together with the suture or carina passing along the fore-edge of the head, borders on a triangular sclerite – an acrometope (after Anufriev & Emeljanov, 1988). All sutures in question are more or less developed not only in larvae of the tribe Deltocephalinae, but also in other subfamilies of Cicadellidae. They are practically indistinct in leafhopper imagos, but well developed in adults of Fulgoromorpha (Figs. 4–5).

The clypeus takes up most of the facial surface. It is subdivided into two parts by a transverse suture: the upper part is the postclypeus, the lower is the anteclypeus. Species of the tribes Scaphytopiini and Drabescini often possess a longitudinal carina in the upper part of the postclypeus. Its shape is strongly varied in different groups. It can be either parallel-sided, or narrowing, or widening toward the apex. Lora lie on each side of the clypeus. They can be either as wide as the anteclypeus or somewhat narrower, either bordered or not bordered with the postclypeus.

The pronotum is transverse, either with or without lateral carinae. The pterotorax (this is mesonotum + metanotum) bears two pairs of wing pads. Previous authors (beginning with Mochida (1970) and Kathirithamby (1974b)) used the comparative length of wing pads as an indication of larval age (Figs. 6–10). In nymphs, the apices of the forewing pads extend to the apices of the hind wing pads (Fig. 10), but *Anoterostemma*, *Doratuopsis*, and the species of the subtribe Acheticina (the tribe Opsiini), with reduced wings in imagos and wing pads in larvae, are an exception to this rule (Figs. 56, 57, 60). The degree of development of larval wing pads is correlated with wing development of adult insects. Macropterous imagos emerge from larvae with wing pads 1.5–2.0 times as long as the pterothorax medially; if the wing pads are 1.2–1.3 times as long as the pterothorax, imagos are subbrachypterous; if wing pads are about as long as the pterothorax, imagos are brachypterous; and in the case of extremely brachypterous imagos, the apices of forewing pads don't reach the apices of hindwing pads, even in nymphs.

The legs are densely covered with setae. All setae are arranged in rows and groups. Rakitov in his paper (Rakitov, 1998) developed the nomenclature of the leg chaetotaxy. The hind legs provide the majority of characters. Femora bear setae only on the dorsal side at the apex. The possible numbers of setae are either 2+1, or 2+2+1, or 2+2+1+1. Tibiae bear 4 longitudinal rows of setae, namely: anterodorsal, posterodorsal, anteroventral and posteroventral. Dorsal rows consist of 6–16 macrosetae and a few shorter setae between them. Ventral rows consist of numerous setae; their size increases toward the apex of the tibia. At the apex there is a transverse row of 7 setae (Figs. 19–24). All setae are usual, but in species of the genus *Balclutha* a part of setae is modified into platellae—short wide setae with rounded apices. This term is used after Howe (1930) (Fig. 20).

Hind tarsi are two-segmented. The first tarsomere bears 2 longitudinal rows of setae on the ventral side (Figs. 19–24). The setae are usual ones, but in the genera *Balclutha*, *Grypotes*, *Opsius*, and *Allygus* the anteroventral row consists of platellae (Figs. 19–21). The first tarsomere bears a transverse row of setae at the apex. The majority of them are platellae; the last seta is often a usual one (Figs. 21, 23), only in the tribe Deltocephalini is the first seta a usual one (Fig. 22).

Pretarsi of different species are very similar (Figs. 25–34). They are about as long as wide. The arolium is usually well developed and overlaps the unguis, but in larvae of the genera *Tamaricades* and *Aconura* the pretarsi have strongly elongated unguis and a reduced arolium (Figs. 31–32).

The abdomen consists of 8 segments, a pygofer, and anal tube (Fig. 1). The first two segments are reduced. The rest of abdomen is more or less covered with setae. Chaetotaxy of the abdomen is one of the most important features of the group. It is possible to distinguish 10 types of abdominal chaetotaxy (Dmitriev, 2000b). A regressive evolution is characteristic for them.

Type I: numerous setae cover the whole body, not only the abdomen. There are also some macrosetae among them. They arise from the hind margins of abdominal tergites. This type of chaetotaxy is observed in representatives of 3 tribes: Drabescini, Hecalini, Tetartostylini, and Macrostelini. In all other cases setae arise only from the hind margins of tergites III–VIII, from the hind angles of tergites VII–VIII, and from the pygofer, or the setation is more or less reduced.

Type II: each tergite bears numerous setae. The fore tergites bear 8–14 setae, the number of setae usually decreases backwards. This pattern was found in representatives of the tribes Opsiini and Athysanini.

Type III – 6 setae on each tergite.

Type IV is the most common one in the subfamily: 4 longitudinal rows of setae and additional setae in the hind angles of tergites VII–VIII.

Type V can be defined as a decrease in the number of setae on tergite VII and often VIII.

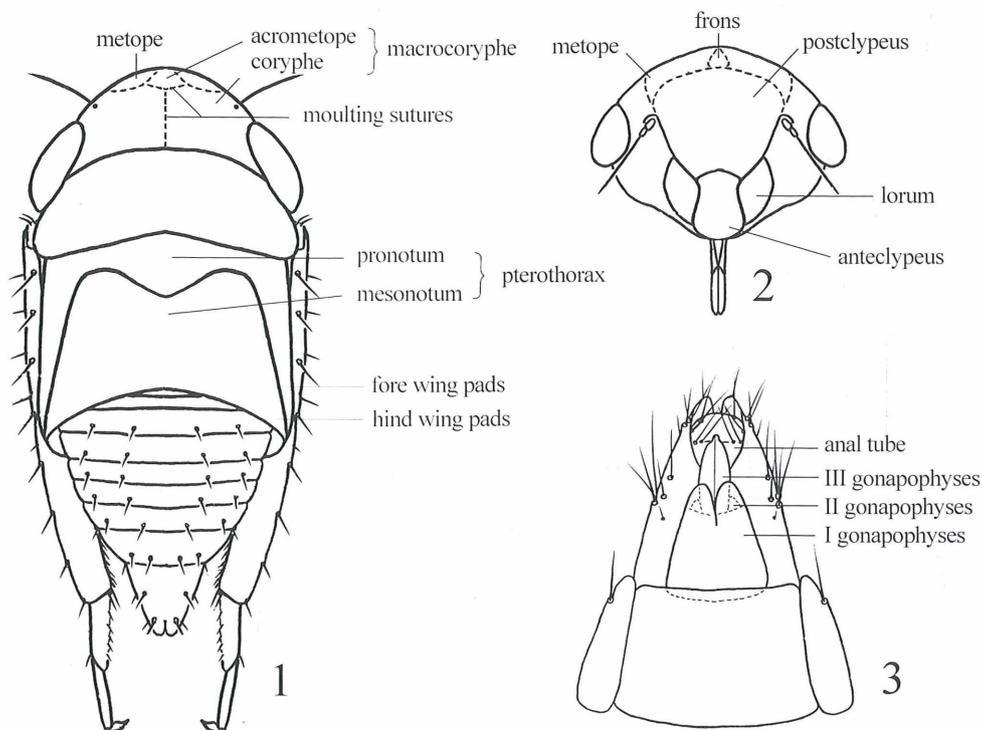
Type VI: median rows of setae are absent; there are only lateral rows. This pattern was found in species of the genus *Platymetopius* and the tribe Fieberiellini.

Types VII–IX are the stages of further evolution of chaetotaxy. Setae arise from tergites VII and VIII (type VII of the chaetotaxy), from tergite VIII (type VIII), and finally from the pygofer only (type IX).

Type X is the total absence of setae on the abdomen. This setation was found only in larvae of the genus *Chiasmus* (the tribe Doraturini).

The distribution of patterns of chaetotaxy among the tribes of the subfamily Deltocephalinae is shown in the table. It should be noted that types III and IV take place in many tribes. This provides evidence of the parallel changes of this character in different tribes.

The last segment of the abdomen is the pygofer (Figs. 1, 3). It is usually about 1.5 times as long as the preceding segments, but in representatives of the tribes Scaphytopiini, Drabescini, Fieberiellini the pygofer is often strongly elongated, in some cases it is about as long as the rest of the abdomen. On top of the pygofer there is a longitudinal cut, about 1/3 of its length. The pygofer of Drabescini significantly differs from the pygofers of other species. It is divided in more than 2/3 of its length,



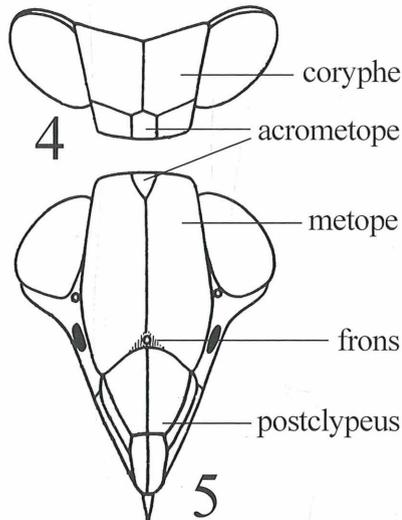
Figs. 1–3: General morphology of nymphs of leafhoppers, 1: above view; 2: face, from below; 3: apex of male abdomen, from below.

and the lobe bases are widely apart from one another (Fig. 47). The pygofer is covered with setae denser than other abdominal segments. There are two lateral groups of setae, each usually formed by 3 setae. On the ventral side the setae form an irregular row, passing along the lower margin of the pygofer.

Below the pygofer, the abdomen bears triangular projections: rudimental genitalia or gonapophyses, and also an anal tube (Fig. 3). Gonapophyses of both sexes consist of 3 pairs of triangular plates more or less covering each other. The degree of their development together with that of the wing pads is useful to designate the age of larvae (Figs. 6–18). Shape of gonapophyses can also be used for designation of sex. Females have very similar gonapophyses; the left and the right parts of external plates are separated from one another along their whole length. In adults, gonapophyses I, II, and III turn into outer and inner processes and the ovipositor sheath, respectively.

In contrast with females, the external male gonapophyses are divided no more than half their lengths and strongly vary in shape (Figs. 35–46). They are usually triangular, with rounded or pointed apices; sometimes the apices are strongly elongated (for example in the species of *Cicadula*). Gonapophyses I usually completely cover gonapophyses II and III, but in some cases they only somewhat overlap them (for instance, in the majority of species of the tribe Stirellini). In adults larval gonapophyses turn into genital plates, the aedeagus and stili respectively.

The anal tube is situated nearer to the apex of the pygofer (Fig. 3). It is covered by the pygofer, and only its apex is seen from above. The apex is usually rounded,

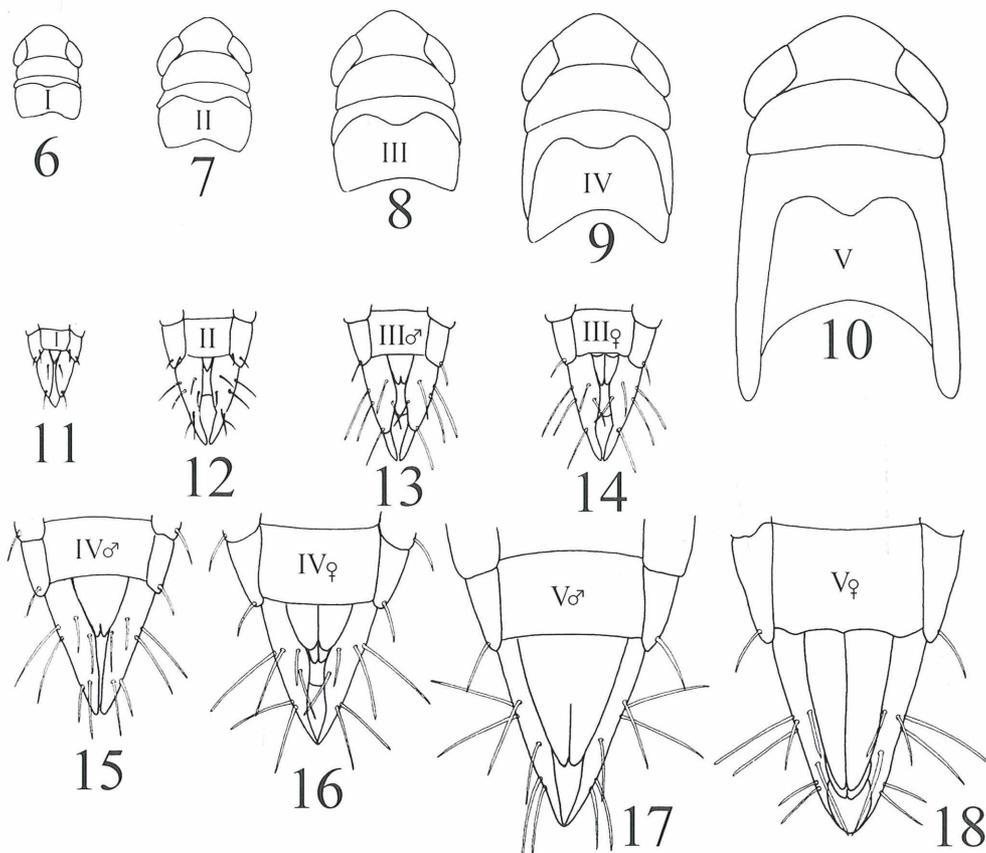


Figs. 4–5: Head of Delphacidae and Cixiidae (Fulgoromorpha), general view (after Anufriev & Emeljanov, 1998), 4: head, from above; 5: face.

but in larvae of Drabescini, Scaphytopiini, Hecalini, and Fieberilini, it bears a large pointed tooth. Near the apex the anal tube bears 4 pairs of setae. The only species which usually has more than 4 pairs of setae is *Grypotes puncticollis* H.-S.

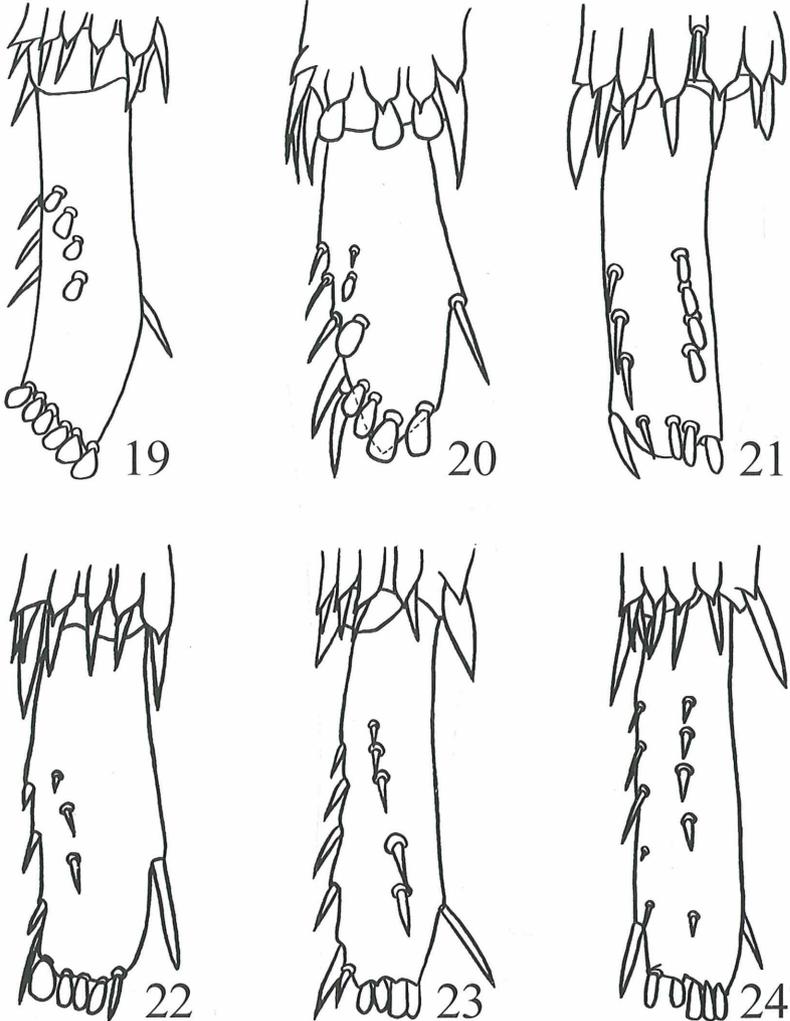
Peculiarities of leafhopper larvae of Palaearctic tribes

The tribe Drabescini (Fig. 47). The larvae of this group strongly differ from the other species. Usually, they have elongated heads with a longitudinal carinae on the postclypeus and on the acrometope. The head is often significantly longer than the heads of imagos. The body is densely covered with setae, not only the abdomen. The pygofer of larvae of the tribe Drabescini bears two long projections widely apart from one another. The coloration is brownish, without a specific pattern.



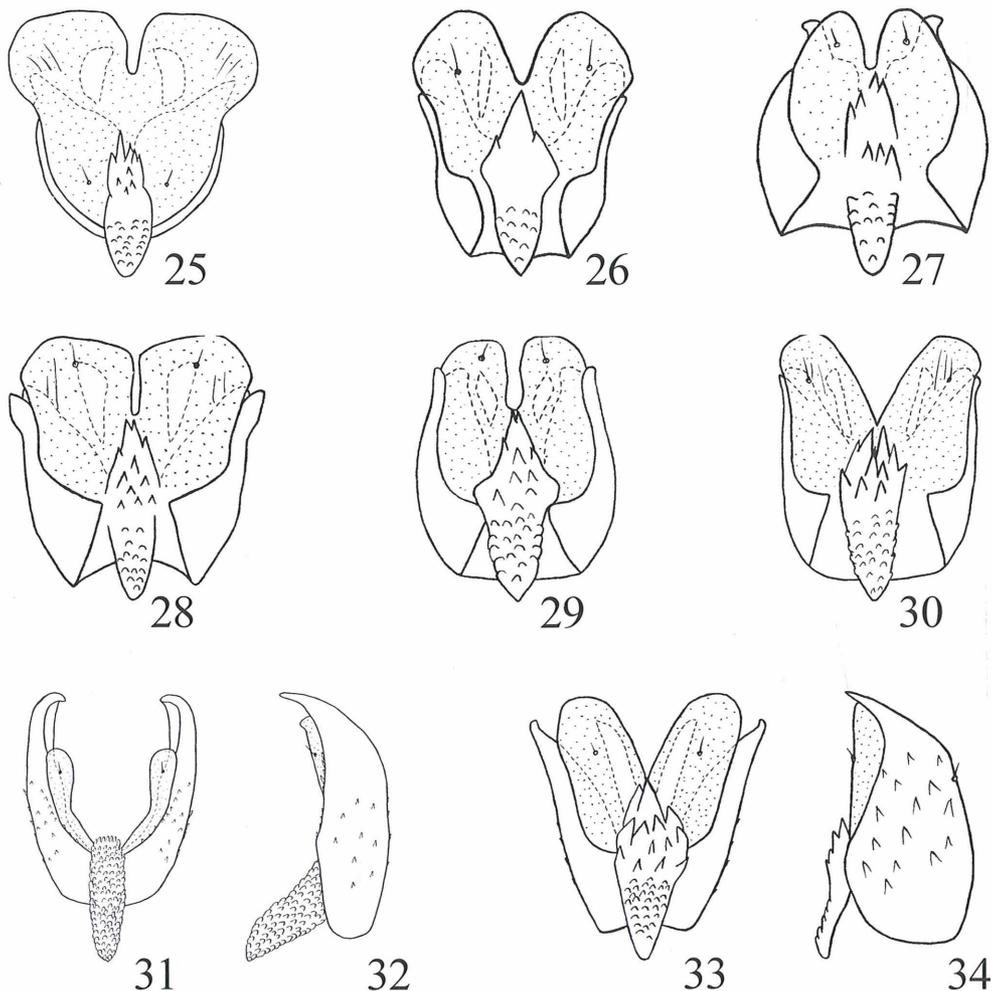
Figs. 6–18: Development of wing pads and gonapophyses (after Wilson, 1983, modified), 6–10: development of wing pads; 11–18: development of gonapophyses.

The tribe Scaphytopiini (Figs. 48–49). This group is also easily recognizable. The head of species from this tribe is usually elongated, but without a longitudinal carina on the acrometope; on the postclypeus, the carina is usually present. The pygofer is elongated, often strongly so. The abdomen bears 4 or 6 longitudinal rows of setae. The coloration pattern usually consists of longitudinal stripes.



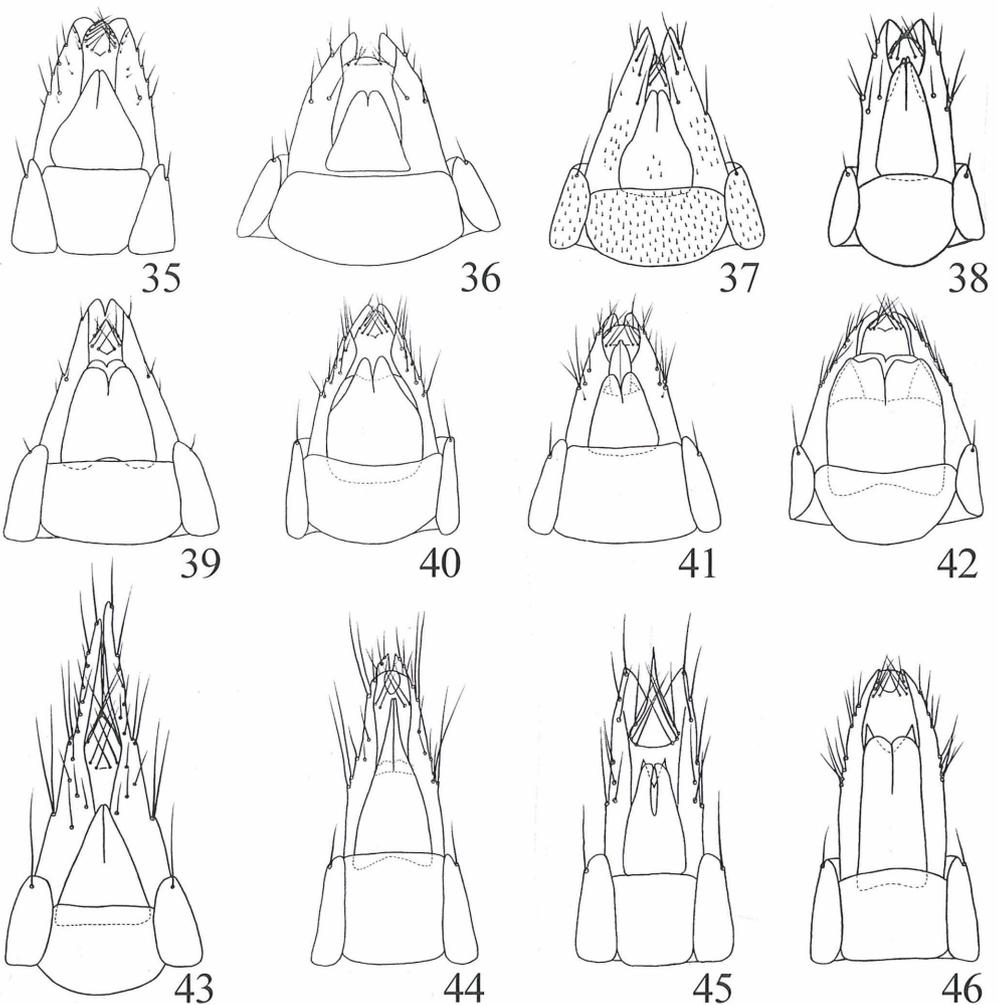
Figs. 19–24: Apices of hind tibiae and the first metatarsomeres of some leafhopper larvae of the subfamily Deltocephalinae, 19: *Grypotes puncticollis* H.-S.; 20: *Balclutha punctata* F.; 21: *Opsius pallasi* Leth.; 22: *Deltocephalus pulicaris* Fall.; 23: *Tamaricades decoratus* Hpt.; 24: *Paralimnus zachvatkini* Em.

Tribe Fieberiellini (Fig. 50). The most significant feature of this group is the chaetotaxy of the abdomen. There are only 2 longitudinal rows of setae, and additional setae in the hind angles of tergites VII and VIII. Mayer-Arndt & Remane (1992) in their work wrote that only the genus *Ericotettix* with 6 setae on tergite VIII, does not fall into this pattern. The common representatives of the tribe, the species



Figs. 25–34: Pretarsi of some leafhopper larvae of the subfamily Deltocephalinae, 25: *Grypotes puncticollis* H.-S.; 26: *Balclutha punctata* F.; 27: *Macrosteles cyane* Boh.; 28: *Elymana kozhevnikovi* Zachv.; 29: *Cicadula albingensis* Wgn.; 30: *Doratura homophyla* Fl.; 31–32: *Tamaricades decoratus* Hpt.; 33–34: *Goniagnathus rugulosus* Hpt.

of the genera *Fieberiella* and *Synophropsis* have elongated pygofers. Coloration is greenish, rarely brownish. The pattern consists of black dots.

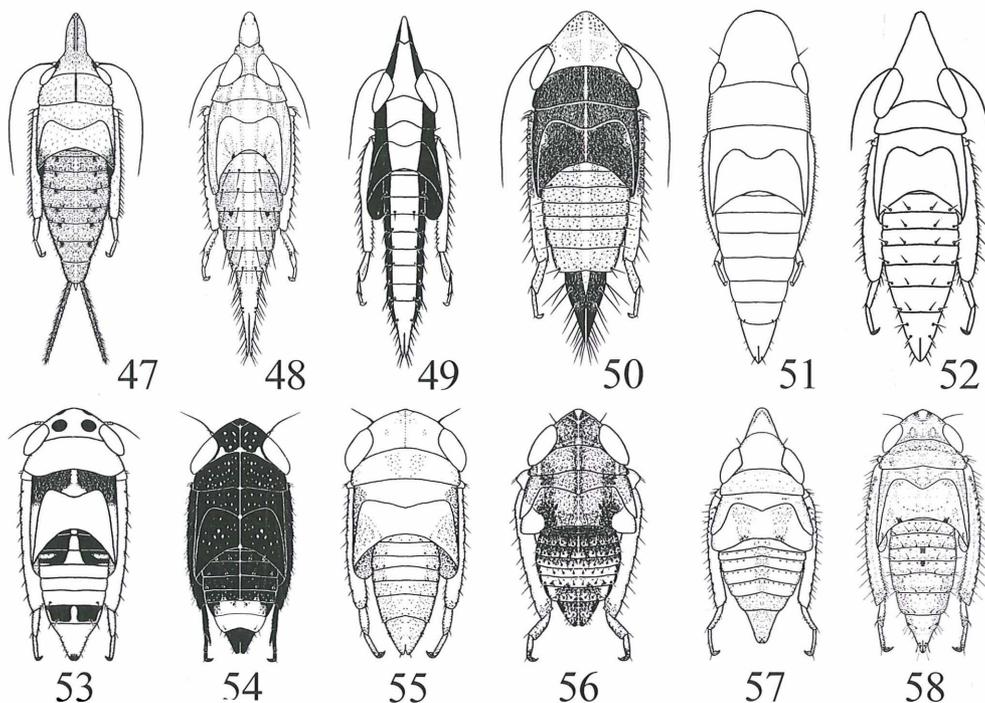


Figs. 35–46: Apices of male abdomens of some leafhopper larvae of the subfamily Deltocephalinae, 35: *Grypotes puncticollis* H.-S.; 36: *Goniagnathus rugulosus* Hpt.; 37: *Tetartostylus* sp.; 38: *Macrosteles viridigriseus* Edw.; 39: *Doratura homophyla* Fl.; 40: *Eremophlepsius sexnotatus* Kusn.; 41: *Stirellus* sp.; 42: *Diplocolenus abdominalis* F.; 43: *Fieberiella septentrionalis* Wgn.; 44: *Cicadula quadrinotata* F.; 45: *Japananus hyalinus* Osb. (with broken apices); 46: *Enantiocephalus cornutus* H.-S.

Tribe Hecalini (Fig. 51). Insects of this tribe have spade-shaped head. The body is somewhat flattened. Antennae are very short. Coloration is greenish or brownish, often with 4 longitudinal stripes.

Tribe Stirellini (Fig. 52). The peculiarity of this group is the shape of the gonapophyses. Gonapophyses II are significantly elongated, pointed, and usually well seen from below (Fig. 41). Hind femora bear only 2+1 setae. European species of the genus *Stirellus* have greenish coloration, the Asiatic and tropic representatives are often bright, with longitudinal stripes.

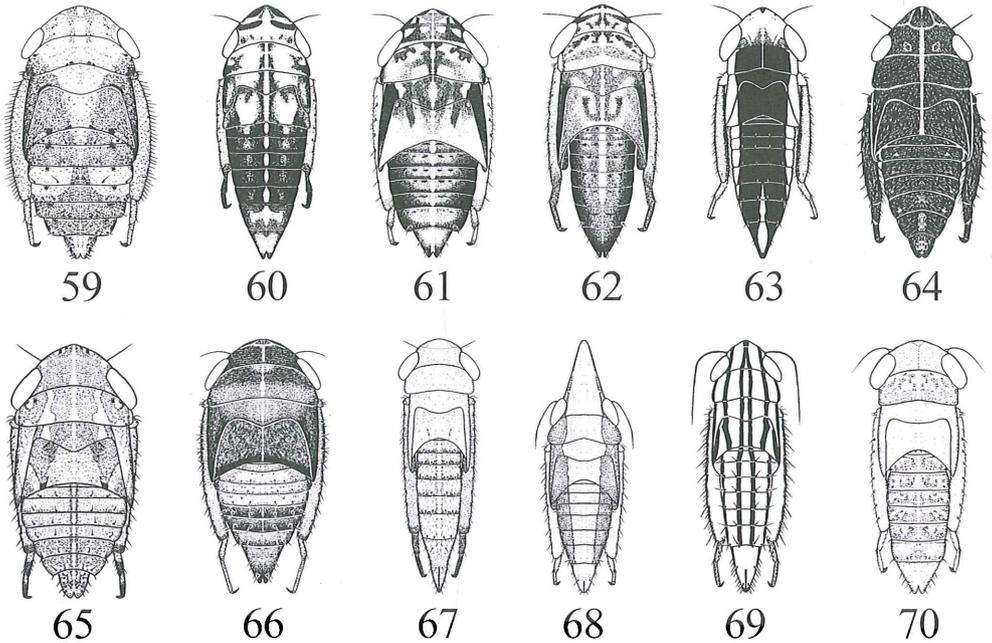
Tribe Macrostelini (Fig. 53). It is strongly detached group. The species don't have the suture between acrometope and metope; on the contrary the suture between the metope and postclypeus is well developed.



Figs. 47–58: Larvae of some species of leafhoppers of the subfamily Deltoccephalinae, 47: tribe Drabescinae – *Drabescus ochrifrons* Vilb.; 48–49: tribe Scaphytopiini, 48: *Stymphalus rubrostriatus* Stål, 49: *Proceps acicularis* M.R.; 50: tribe Fieberilini – *Fieberiella septentrionalis* Wgn.; 51: the tribe Hecalini – *Hecalus glaucescens* Fieb.; 52: tribe Stirellini – *Stirellus* sp.; 53: tribe Macrostelini – *Macrosteles laevis* Rib.; 54–58: tribe Opsiini, 54: *Nealiturus fenestratus* H.-S.; 55: *Opsius pallasi* Leth.; 56: *Zapycna eremita* Em.; 57: *Chlidochrus tristis* Em.; 58: *Pseudophlepsius binotatus* Sign.

Tribe Opsiini (Figs. 54–58). This tribe is subdivided into several subtribes, and the representatives of them are very differed from each other (for example, in the setation of the abdomen). Species of the subtribe Achaeticina have up to 14 longitudinal rows of setae. Species of the subtribe Circuliferina have 4 incomplete rows of setae. In the subtribe Opsiina species also have 4 rows of setae, but they are very short, and practically indistinct. Coloration varies: most of species have black spots at the hind margin of the metanotum.

Tribe Selenocephalini (Fig. 59). The species have stumpy body, a wide head with a sharpened fore-edge. Abdomen with additional carinae besides the carinae that subdivide the dorsal parts of tergites and ventral laterotergites; these carinae pass along lateral rows of setae. Coloration is brownish, with numerous black dots.



Figs. 59–70: Larvae of some species of leafhoppers of the subfamily Deltocephalinae, 59: tribe Selenocephalini – *Selenocephalus pallidus* Kbm.; 60–62: tribe Limotettigini, 60: *Anoterostemma ivanoffi* Leth.; 61: *Ophiola decumana* Kontk.; 62: *Limotettix striola* Fall.; 63–64: tribe Doraturini, 63: *Doratura salina* Horv.; 64: *Chiasmus conspurcatus* Per.; 65–66: Goniagnathini, 65: *Goniagnathus bolivari* Mel.; 66: *Tamaricades decoratus* Htp.; 67: the tribe Tetartostyliini – *Tetartostylus* sp.; 68–69: tribe Athysanini, 68: *Platymetopius rostratus* H.-S.; 69: *Taurotettix beckeri* Fieb.; 70: tribe Grypotini – *Grypotes puncticollis* H.-S.

Tribe Limotettigini (Figs. 60–62). 3 genera *Anoterostemma*, *Limotettix*, and *Ophiola* were closed and placed into the tribe Limotettigini (Dmitriev, 2000b). All of them have similar pattern of abdominal chaetotaxy and coloration not characteristic for the tribe Athysanini.

Tribe Doraturini (Figs. 63–64). The representatives have a specific head shape. Coloration varies; the bases of abdominal setae are usually surrounded by dark color while in the majority of the groups they are surrounded with palor.

Tribe Goniagnathini (Figs. 65–66). One of the most significant features of this tribe is the elongated ungui with a reduced arolium (Figs. 31–34), especially in the species of the genus *Tamaricades*. External male gonapophyses with very short cleft (Fig. 36). Coloration is brownish or greenish with numerous brown or pink dots.

Tribe Tetartostylini (Fig. 67). Whole body of species of this tribe are covered with numerous setae, not only the abdomen. The pygofer is often elongated. Coloration is brownish with numerous black dots.

Tribe Athysanini (Fig. 68–69). This is large and varied group. It is to be subdivided into several tribes or subtribes, but at present this is very difficult because different groups of genera have many similarities.

Tribe Grypotini (Fig. 70). It is possible that the tribe Grypotini is closely related with the tribe Macrostelini. They have the same sutures on the head as the species of the tribe Macrostelini. The abdomen has setae on tergites VII and VIII only. There are often more than 4 pairs of setae at the apex of the anal tube.

Tribe Deltocephalini. The peculiarity of this tribe is the specific setation of the first metatarsomere (Fig. 22): the first seta in the apical row is a simple one; in species of all other tribes, the first seta is a platella.

Tribe Paralimnini. Almost all representatives have similar chaetotaxy of the abdomen: 4 longitudinal rows of setae, with additional setae in hind angles. Head with angled fore edges. The anteclypeus narrows toward the apex. Pattern of coloration usually consists of longitudinal stripes.

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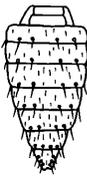
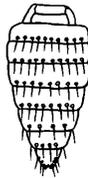
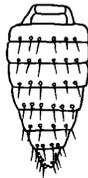
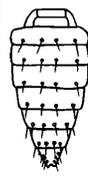
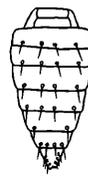
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Tab. I: Abdominal chaetotaxy of leafhoppers of the subfamily Deltocephalinae

| Tribes |  I |  II |  III |  IV |  V |  VI |  VII |  VIII |  IX |  X |
|-----------------|--|---|--|---|--|---|--|---|---|--|
| Drabescini | + | | | | | | | | | |
| Scaphytopiini | | | + | + | + | | | | | |
| Hecalini | + | | | | | | + | | | |
| Fieberilini | | | | | | + | | | | |
| Selenocephalini | | | | | + | | | | | |
| Tetartostyliini | + | | | | | | | | | |
| Doraturini | | | + | + | | | + | + | + | + |
| Deltocephalini | | | | + | + | | | | | |
| Paralimnini | | | + | + | | | | | | |
| Stirellini | | | | + | + | | + | | | |
| Opsiini | | + | + | + | + | | | + | + | |
| Athysanini | | + | + | + | + | + | + | + | + | |
| Goniagnathini | | | | + | + | | | | | |
| Limotetigini | | | | | | | | + | + | |
| Macrostelini | + | | | | | + | + | + | + | |
| Grypotini | | | | | | | + | + | + | |

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Autor(en)/Author(s): Dmitriev Dmitry A.

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