Entomological Review 75(9):134-150.

UDC 595.754

Entomological Review, 75 (9), 1996

On the Question of the Classification and Phylogeny of the Delphacidae (Homoptera, Cicadina), with Reference to Larval Characters*

A. F. YEMEL'YANOV

Zoological Institute, Russian Academy of Sciences, St. Petersburg

Abstract. A new, more detailed classification of the lower representatives of Delphacidae formerly assembled in the subfamily Asiracinae is elaborated. Four tribes and a new genus in the tribe Eodelphacini trib. n. are described. Subfamily Ugyopinae Fennah, stat. n. (Ugyopini Fennah, 1979) is distinguished, comprising *Neopunanini* trib. n., *Egyopinae* Fennah, stat. n. (*Ugyopini* Fennah, 1979) is distinguished comprising is restricted to the tribes *Tetrasteirini* trib. n., *Platysystatini* trib. n., *Asiracini Motschulsky s. str., and subfamily* Delphacinae which includes the tribes *Vizcayini* Asche, stat. n. (*Vizcayinae* Asche, 1990), *Kelisiini* Wagner, stat. n. (*Kelisiinae* Wagner, 1963), *Stenocranini* Wagner, stat. n. (*Stenocraninae* Wagner, 1963), *Plesiodelphacini* Asche, stat. n. (*Plesiodelphacinae* Asche, 1985), *Tropidocephalini* Muir, 1915, *Saccharosydnini* Vibaste, 1968, *Delphacini* Leach, 1815, the first four of which Asche considers distinct subfamilies, and the last 3 he combines in the *Delphacinae*. Larval characters are widely used to make the classification and substantiate the phylogeny; a more detailed terminology of larval structures is suggested. A scheme of the lower *Delphacidae* phylogeny; a more detailed terminology of larval structures is suggested. A scheme of the lower *Delphacidae* phylogeny to the tribal level is suggested complementing the one worked out in detail by Asche for the higher delphacids.

Key words: Delphacidae; phylogeny; classification; larval characters.

In the last 10-15 years the systematics of the Delphacidae has undergone considerable progress. The various works of Asche (1985, 1990, etc.) and then the publications, rich in facts, of Yang and other Taiwanese Cicadina specialists (Wu and Yang, 1985; Yang and Yang, 1986; Yang, 1989; Yang and Yeh, 1994) and also of Wilson et al. (Wilson and McPherson, 1981; Wilson, 1985; Calvert and Wilson, 1986; Wilson and Wheeler, 1986; Tsai and Wilson, 1986; Calvert, Tsai, and Wilson, 1987; Calvert, Wilson, and Tsai, 1987) are the most important. The accumulated materials make it possible to improve the systematics and elucidate the phylogeny of the Delphacidae.

CLASSIFICATION OF THE FAMILY AND NEW TAXA

Here I propose a modified classification of the family, diverging from the classification of Asche (1985) in distributing ranks differently and in describing several new tribes. I am dividing the subfamily Asiracinae into two: the Ugyopinae, which corresponds to the tribe Ugyopini of Asche, and the Asiracinae. The subfamilies composing the Eudelphacida of Asche, I propose considering tribes of a single subfamily of the Delphacidae, preserving the rank of tribes as well for the Tropidocephalini and

*Originally published in Entomologicheskoye Obozreniye, Vol. 74, No. 4, 1995, pp. 780-794

ISSN0013-8738/96/0009-0134

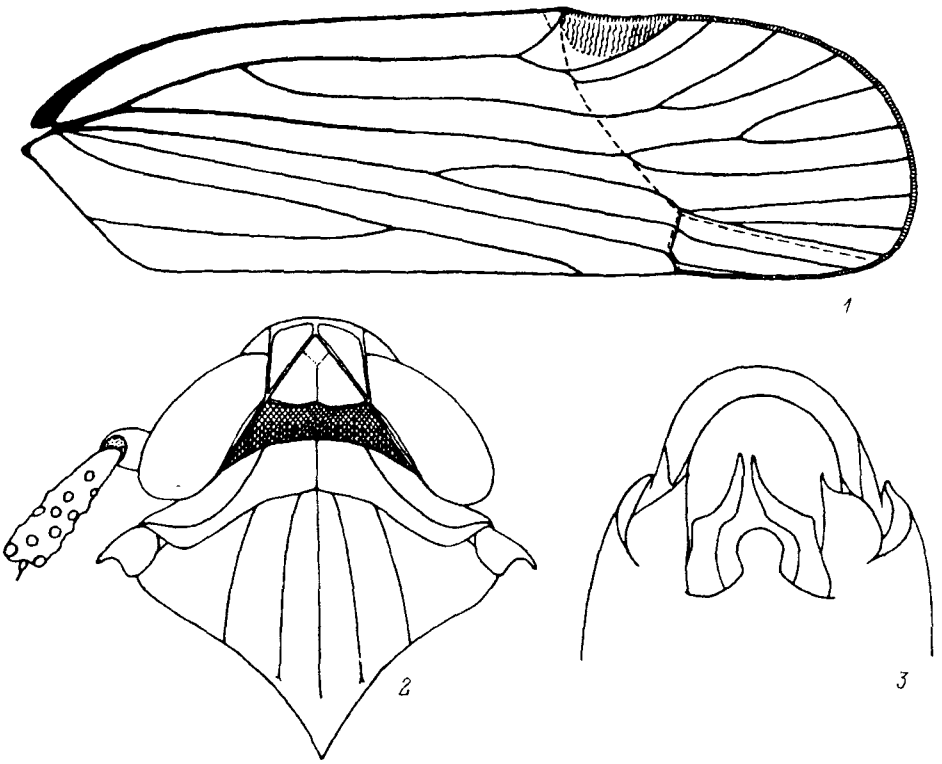


Fig. 1. *Prolivatis gorochovi* gen. et sp. n.: *1*) forewing, *2*) anterior part of body, dorsal view, *3*) genital segment of ♂, ventral view.

Saccharosydnini. The subfamilies Ugyopinae and Asiracinae together I propose calling the association Protodelphacida.

The subfamily Ugyopinae Fennah, 1979, stat. n. contains three tribes: Neopunanini trib. n. (*Neopunana* Asche, 1983), Eodelphacini trib. n. (*Eodelphax* Kirkaldy, 1901; *Ostama* Walker, 1857; *Paranda* Melichar, 1903; *Melanesia* Kirkaldy, 1907; *Punana* Muir, 1913; *Livatiella* Fennah, 1956; *Prolivatis* gen. n.) and Ugyopini Fennah, 1979 (*Ugyops* Guerin-Meneville, 1834; *Canyra* Stål, 1862; *Ugyopana* Fennah, 1950; *Melanugyops* Fennah, 1956; *Notuchus* Fennah, 1969).

The subfamily Asiracinae Motschulsky, 1863 contains four tribes: Tetrasteirini trib. n. (*Tetrasteira* Muir, 1926), Platysystatini trib. n. (*Platysystatus* Muir, 1930; *Equasystatus* Asche, 1985), Asiracini Motschulsky, 1863 (*Asiraca* Latreille, 1796; *Copicercus* Schwartz, 1802; *Elaphodelphax* Fennah, 1949; *Fennasiraca* Asche, 1985), Idiosystanini Asche, 1985, stat. n. (*Idiosystatus* Berg, 1883; *Idiosemus* Berg, 1883; *Pentagramma* Van Duzee, 1897).

Subfamily **UGYOPINAE** Fennah, 1979, stat. n.

Tribe **Neopunanini** Emeljanov, trib. n.

The tribe is characterized by having a wide, short head, absence of a distinct median eumetopic*

Transl. note. Use of the terms *metopa*, *eumetopa*, *corypha* and *macrocorypha* are explained below in the original text. Generally, metopa is used to indicate the frons and corypha the vertex.

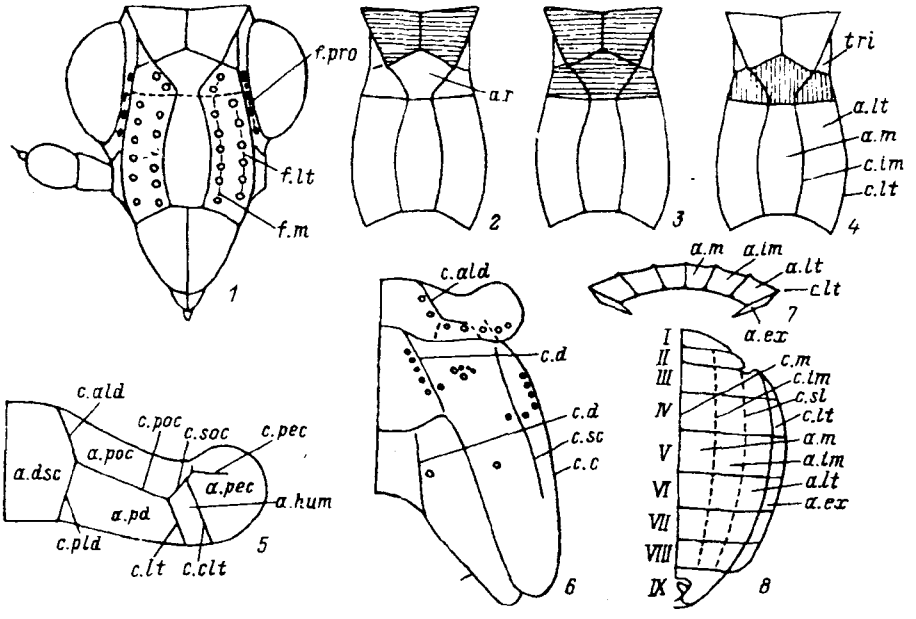
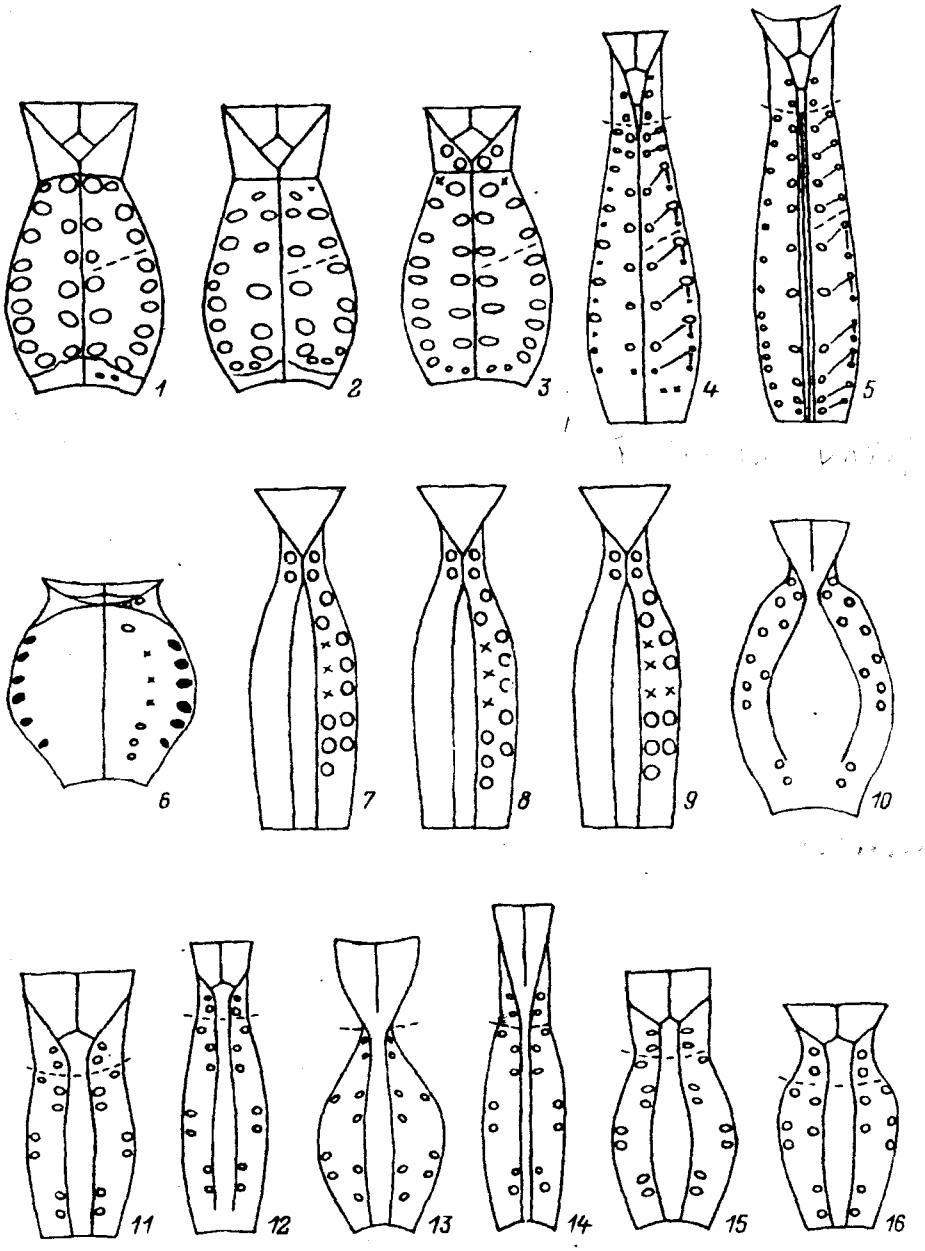


Fig. 2. Terminology of larval structures: *1*) representation of the head, anterodorsal view; *2-4*) representation of the anterovertical part of the head (as in Fig. 1): *2*) corypha shaded, metopa clear, *3*) macrocorypha shaded, eumetopa clear, *4*) acrometopa shaded; *5*) representation of pronotum, right half; *6*) representation of tergal parts of nymphal thorax (5th instar), right half; *7*) representation of an abdominal tergite, posterior view; *8*) representation of tergal part of abdomen, right half. *a* - area, *a. dsc.* - discal area, *a. ex.* - extralateral area, *a. hum* - humeral area, *a. im* - intermediate area, *a. lt* - lateral area, *a. m* - median area, *a. pd* - paradiscal area, *a. pec* - pectoral area, *a. poc* - postocular area, *ar* - areolet, enlarged apical callus, *c. ald* - anterolaterodiscal carina, *c. c* - costal carina, *c. clt* - collateral carina, *c. d* - discal carina, *c. im* - intermediate carina, *c. lt* - lateral carina, *c. pec* - pectoral carina, *c. pld* - posterolaterodiscal carina, *c. poc* - postocular carina, *c. sc* - subcostal carina, *c. soc* - subocular carina, *f. lt* - lateral row of metopic pits, *f. m* - median row of metopic pits, *f. pro* - preocular row of pits, *tri* - trigon. Roman numerals identify the number of the abdominal tergites.

Fig. 3. Arrangement of sensory pits on the head in 5th-instar larvae (nymphs). Schematic representation—the metopa and corypha are spread ut in the same plane. The dotted line shows the boundary between the macrocorypha and eumetopa, in *1-5* only on the right side is the boundary between the upper and lower parts of the metopa also shown. *1*) *Punana annulata* Dist., based on traces in the adult; *2*) *P. brunnea* Muir, based on traces in the adult; *3*) *Prolivatis gorochovi* gen. et sp. n., based on traces in the adult; *4*) *Eucanyra* sp., based on traces in the adult; *5*) *Ugyops* sp., 4th-instar larva; *6*) *Equasystatus breviceps* Muir, left side, based on traces in the adult (only traces of the lateral pits were retained), right side, hypothetical reconstruction of the entire complex of pits; *7*) *Elapchodelphax* sp., based on traces in the adult; *8*) *Copicercus irroratus* Schwartz, 5th-instar larva; *9*) *Asiraca clavicornis* F., 5th-instar larva; *10*) *Pentagramma longistylata* Penner, 5th-instar larva; *11*) *Kelisia brucki* Fieb., 5th-instar larva; *12*) *Stenocranus major* Kmb., 5th-instar larva; *13*) *Tropidocephala brunnipennis* Sign., 5th-instar larva; *14*) *Saccharosydne* sp., 5th-instar larva; *15*) *Chloriona* sp., 5th-instar larva; *16*) *Stobaera concinna* Stal, 5th-instar larva. *1, 2, 6* - after Asche, 1983; *5, 11, 12, 14, 15* - after Asche, 1985; *13* - after Yang, 1989; *16* - after Calvert et al., 1987.


1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16

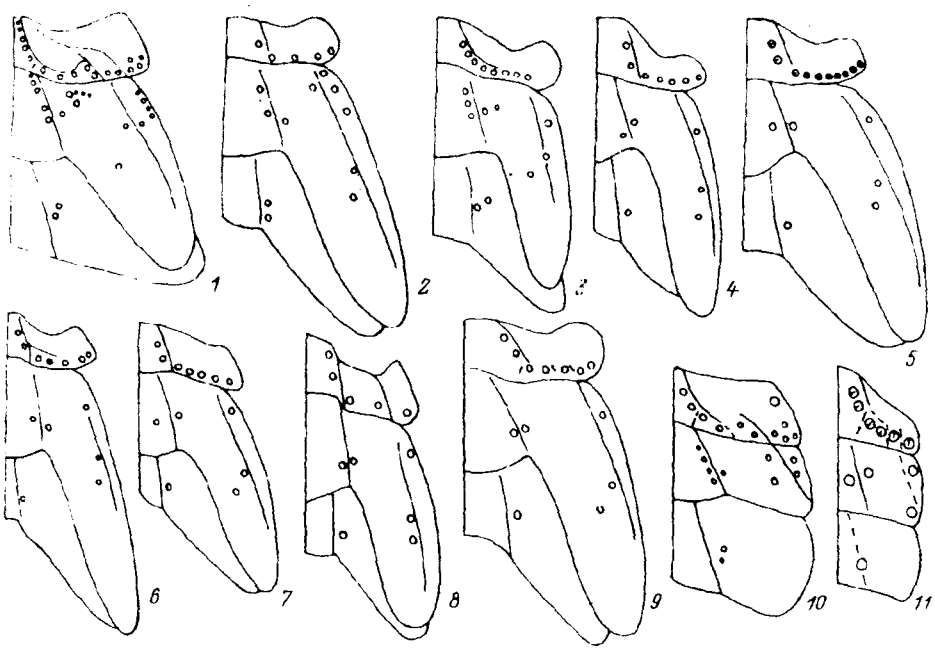


Fig. 4. Arrangement of sensory pits on the thorax in larvae (dorsal view; prothoracic paranota bent to the side). *1-9*) 5th-instar larvae (nymphs); *10, 11*) 1st-instar larvae. *1*) *Ugyops tripunctatus* Kato, *2*) *Asiraca clavicornis* F., *3*) *Pentagramma longistylata* Penner, *4*) *Kelisia brucki* Fieb., *5*) *Stenocranus major* Kmb., *6*) *Saccharosydne* sp., *7*) *Purohita taiwanensis* Muir, *8*) *Tropidocephala brunnipennis* Sign., *9*) *Delphax crassicornis* Panz., *10*) *Ugyops tripunctatus* Kato, *11*) generalized representation for the tribe Delphacini (orig.). *1, 7, 8, 10*) After Yang and Yang, 1986; *3*) after Wilson and Wheeler, 1987; *4-6*) after Asche, 1985.

carina, S-shaped bend in the distal segment of the penis when its basal part is curved to the right, an even row of 4 teeth on the second segment of the hindtarsus, presence of sinus on the margin of the hindwings opposite the tip of *CuP*, in having the tips of *CuP* and *Pcu* approximated, and in having the intermediate carinae of the mesonotum developed throughout the entire length and undulating.

Tribe **Eodelphacini** Emeljanov, trib. n.

The tribe is characterized by the simple structure of the head with one simple median eumetopic carina, by having the distal segment of the penis arched clockwise (from the base curved to the left), a row of teeth on the second segment of the hindtarsi, in which the marginal teeth are considerably longer than all others, the presence of the sinus on the hindwings opposite *CuAP*, absence of postnodal transverse veins on the forewings, well defined bend of the membrane when the wings are folded, and by the straight intermediate carinae of the mesonotum.

Genus ***Prolivatis*** Emeljanov, gen. n.

Type species *Prolivatis gorochovi* sp. n.

In terms of external appearance and most characters it is close to the genus *Punana* Muir

Macrocorypha slightly longer than wide, corypha with areolet in form of isosceles triangle, median carina not well defined. Eumetopa with convex lateral margins, greatest width shifted to lower 1/3. Antennae simple, of average length, 2nd segment 3 times as long as 1st, 1st segment about 1.5 times as long as wide. Anterodiscal carinae of pronotum smoothly move into postorbital and then into lateral one, lateral lobes of upper surface of pronotum short since the postorbital carina runs close to posterior margin. Mesonotum with 5 distinct carinae, paired ones slightly arcuate. Forewings compact, leathery, fairly densely covered with setiferous tubercles accompanied on both sides by longitudinal veins. Nodal break runs like arch from nodulus to anterior cubital vein at level of tip of clavus, where arch runs almost parallel to vein and at app. right angle connects with posterior transverse part of break, which terminates just in back of tip of clavus. Vein *ScR* split before actual nodal break. On membrane *RA*2 simple, *RP* with 2 tips, media with 3 tips in posterior comb, anterior branch of *CuA* with 3 tips in anterior comb. Legs of usual structure, hindtibiae with 3 lateral teeth, 2nd segment of hindtarsi with 3 teeth.

Pygophor of ♂ ventrally with median projection, lateral to which lies pair of wide lanceolate lobes with tapered prolonged tips, styli fairly slender, both together lyrate, weakly projecting back past tips of lobes of pygophor. Anal tube with short lobes twisted anteriorly and inward as in *Livatiella* Fenn.

Prolivatis gorochovi Emeljanov, sp. n. (Fig. 1, *1-3*).

Brown, with paler carinae. On face with light transverse stripe along clypeal margin of metopa and light specks at location of larval sensory pits. Forewings with darker longitudinal veins and pale setiferous tubercles. Lower surface of body paler, pigmentation often increased at sutures, legs with dark brown transverse bands, 2 bands, on fore- and midtibiae, 3 on hindtibiae.

Length of ♂ 5.0, ♀ 4.9 mm.

Material. Vietnam, Zyalay-Kontum Prov., 20 km N of Buonloy, 21-30.XI.1988, 1 ♂ - holotype, 1 ♀ (Gorokhov).

Tribe **Ugyopini** Fennah, 1979

Tribe characterized by having narrow head with extended eumetopa, median carina of which is partially or entirely divided, penis of same type as in the Eodelphacini, slanted row of 3-4 teeth on the second segment of the hindtarsi, sometimes with a tooth extended basally as on the first segment, absence of sinus on the posterior margin of the hindwings in the area of the vannus, loss of bend in membrane with retention of the nodal line of the veins.

Subfamily **ASIRACINAE** Motschulsky, 1863

Tribe **Platysystatini** Emeljanov, trib. n.

Tribe characterized by having short and wide head with or without simple median carina, absence of morphologically defined areolet, presence of 5 carinae on mesonotum with undulating intermediate ones, straight row of teeth at tip of second segment of hindtarsi, notch on posterior margin of hindwings opposite the tip of *CuP*, as in *Neopunana* Asche.

Tribe **Tetrasteirini** Emeljanov, trib. n.

Tribe is characterized by a short, narrow corypha, extended, fairly narrow metopa with simple

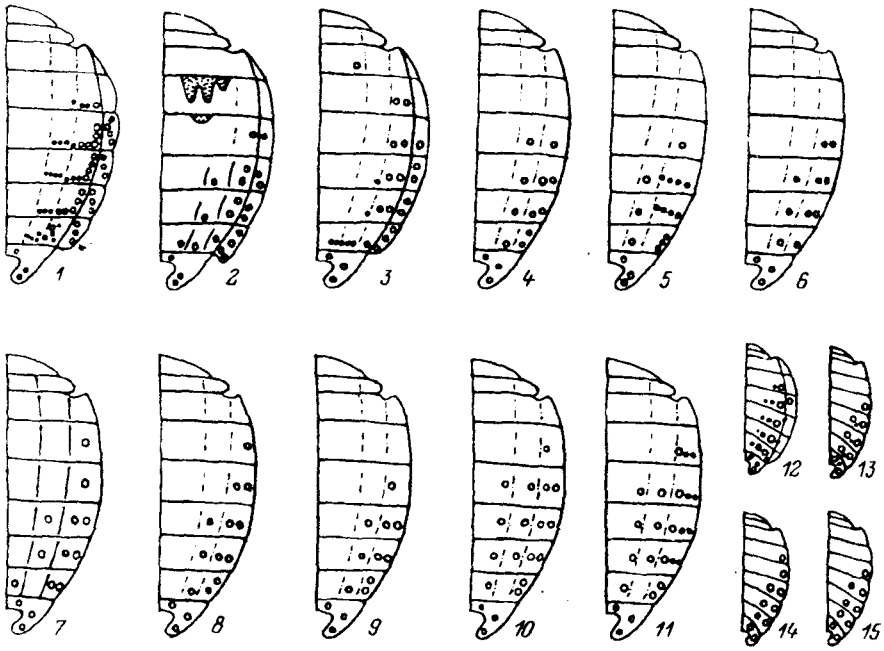


Fig. 5. Arrangement of sensory pits on the abdomen in larvae (representation, dorsal view, extralateral areas in *1-3* are bent laterally). *1-10*) 5th-instar larvae (nymphs). *12-15*) 1st-instar larvae. *1*) *Ugyops tripunctatus* Kato. *2*) *Asiraca clavicornis* F., *3*) *Pentagramma longistylata* Penner, *4*) *Kelisia brucki* Fieb., *5*) *Stenocranus major* Kmb., *6*) *Saccharosydne* sp., *7*) *Tropidocephala brunnipennis* Sign., *8*) *Chloriona vasconica* Rib., *9*) *Delphax crassicornis* Panz., *10*) *Achorotile albosignata* Dahlb., *11*) same (adult), *12*) *Ugyops tripunctatus*, *13*) *Stenocranus lautus* V. D., *14*) *Chloriona unicolor* H. S., *15*) *Delphacodes bellicosa* Muir et Giff. (*1, 7, 12* - after Yang and Yang, 1986; *3* - after Wilson and Wheeler, 1987; *4-6, 8* - after Asche, 1985; *13* - after Calvert and Wilson, 1986; *14* - after Lindberg, 1939; *15* - after Wilson, 1985).

median carina, absence of areolet, small flattened antennae, presence of 4 evenly arcuate mesonotal carinae, oblique row of teeth on the tip of the second segment of the hindtarsi, and notch on the posterior margin of the hindwings opposite the tip of CuP.

Morphological Features of the Larval Stage as Material for Elucidating Phylogeny

Morphological features of the larval stage provide abundant and very incompletely used material for phylogenetic reconstructions. In putting together morphological series of the transformation of individual characters it is important to understand on what basis they are derived and which conditions are the starting point for these transformations.

The family as a whole is characterized by a distinct synapomorphy in the form of a saltatorial spur at the tip of the hindtibia. This spur differentiates in the 1st, 2nd, or 3rd instar and is formed from one of the apical teeth characteristic of all Fulgoroidea (Lindberg, 1939; Wilson and McPherson, 1981; Asche, 1985; etc.). Development of the spur in turn slows differentiation of the tarsus, which in the higher Delphacidae becomes tri-segmented not in the 4th instar but in the 5th instar. The genus *Ugyops*

Increase by instar in the number of rhinaria in delphacids

Species	Instar					Author
	I	II	III	IV	V	
Asiraca clavicornis	0	1	3	10	15	Asche, 1985
Pentagramma longistylata	?	?	5	13	25	Wilson and Wheeler, 1986
Stenocranus lautus	0	0	4	9	14-15	Calvert and Wilson, 1986
Megamelus davisi	0	2	4	8	14	Wilson and McPherson, 1988
Peregrinus maidis	0	2	4	6	9	Tsai and Wilson, 1986
Delphacodes bellicosus	0	2	4	6	9	Wilson, 1985
Chloriona unicolor	0	2	4	6	9	Lindberg, 1939
Chloriona vasconica	0	2	4	7	11	Asche, 1985
Delphacodes nigrifacies	0	2	3-5	6-8	10-12	Calvert, Tsai, and Wilson, 1987
Stobaera concinna	0	2	4-6	6-8	12-14	Calvert, Wilson, and Tsai, 1987

G.-M. is special in that the posterior tarsus becomes tri-segmented as early as the 2nd instar (Yang and Yang, 1986).

Another, particularly larval synapomorphy of the family is a group of sensory pits in the preocular area.

Delphacid larvae on the whole are weakly flattened dorsoventrally, active, lead an open way of life, jump well and are characterized by primary absence of wax gland areas on the abdomen (secondary exception is the advanced tribe Saccharosydnini).

The larvae of a fairly large number of representatives are described, but a complete larval ontogenesis is unknown for many tribes and, in particular, for virtually all Ugyopinae, except *Ugyops* (Yang and Yang, 1986), and Asiracinae, except for *Pentagramma* V. D. (Wilson and Wheeler, 1986). In *Asiraca clavicornis* Asche (1985) described in all instars only the antennae and legs.

The Delphacidae is the first family in the phylogenetic series of the Fulgoroidea, in representatives of which there are so-called sensory pits—a combination of a recess with a seta lying in it parallel to the body surface (Ymel'yanov, 1980). This structure was first described in detail by Šulc (1928, 1929) in the Cixiidae and Flatidae.

Very important for elucidating the phylogeny of the Delphacidae is the change in the arrangement of larval sensory pits, which, fortunately, in a number of cases can also be recognized in the adult from coloration—the place of the pits often is occupied by light specks.

Head. On the head of the Delphacidae (Fig. 2, *1-4*), as in the Cixiidae, there are two types of boundary along which runs the division into the vertical and facial sides, if we ignore the location of the areolet and homologous apical callus. The first, retained in more advanced families, runs between the corypha and metopa, the second divides the metopa into the acrometopa and eumetopa. The acrometopa, uniting with the corypha, forms the macrocorypha, which is found only in the Delphacidae and Cixiidae (Anufriyev and Yemel'yanov, 1988). On the corypha sensory pits never occur, and this leads to the thought that in terms of origin, it may be the occiput and not the vertex.

On the metopa, on each side, there are two rows of sensory pits along the carinae—the outer

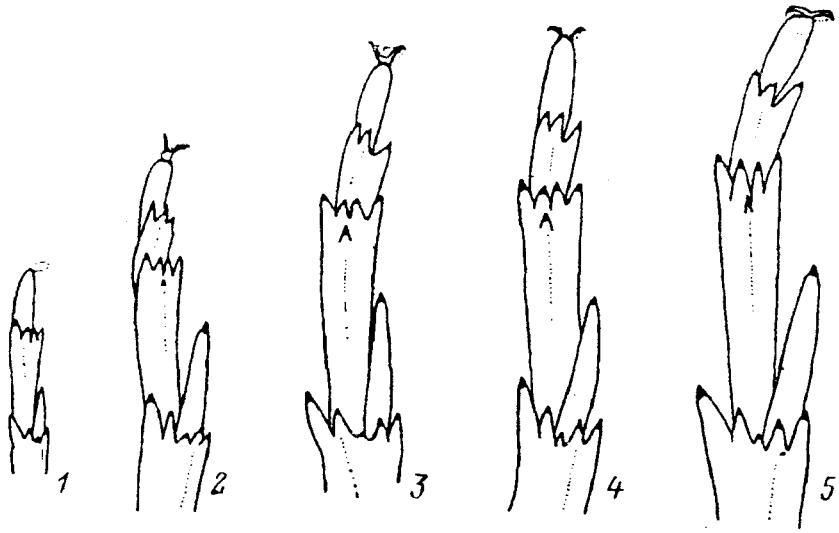


Fig. 6. *Ugyops tripunctatus* Kato. Hindtarsi and tip of the tibia in the 1st-5th instars (after Yang and Yang, 1986).

ones are located around the lateral carinae, and inner ones around the intermediate carinae (Fig. 3), which in delphacids are often contiguous or coalesce into a single median carina that in terms of composition does not entirely correspond to the median carina of the higher Fulgoroidea. If the intermediate carinae are disconnected, then there is no median carina in delphacid larvae, as is also the case with most adults.

In the subfamily Ugyopinae interspecific variation is observed in the number of pits on the metopa from 6-8 to 12 and more in each row; however, there is a base number, from which we can simply derive a classification for the arrangement of pits in all further advanced tribes of all the subfamilies, and cases of exceeding this number among the Ugyopini may be interpreted as polymerization. The base number is 8 pits in the median row and 6 in the lateral. Normally, on the acrometopa there are only 2 pits from the median row[1], and sometimes a third pit appears (*Ugyops*, *?Vizcaya*). On the eumetopa in both rows there are 6 pits; judging from all things, the lateral row primitively was shifted upward a half step with respect to the median row. Each pit in its row may be shifted independently upward or downward up to one step, but if the shift is great then the adjacent pits are also shifted in the same direction as if giving up the location. Often it is evident that in the middle part of the eumetopa the distances between the pits in the rows are greater than at the ends. Pits on the metopa are described in the Protodelphacida—in polymerized representatives of the genus *Ugyop* (Asche, 1985; Yang and Yang, 1986), in the genus *Asiraca*, and in the genus *Pentagramma* (Wilson and Wheeler, 1986) from the advanced tribe Idiosystatini. Valuable information about the pits is provided by speckles in adults at their location, which are illustrated by Asche (1985) or elucidated from collective material: *Punana*, *Prolivatis* (Ugyopinae, Eodelphacini), *Eucanyra* (Ugyopini), *Equasystatus* (Asiracinae, Platysystatini), and *Elaphodelphax* (Asiracini). In *Equasystatus* the speckles show a full set of 6 pits in the lateral row; the median row is not indicated. In *Punana* all pits appear on the eumetopa, the median row is completely defined, and in the lateral row pits corresponding to the three lower ones of the median row are duplicated. In *Prolivatis*, on the other hand, the median pits are

[1]Everywhere only one side of the head, and later the thorax and abdomen, is characterized.

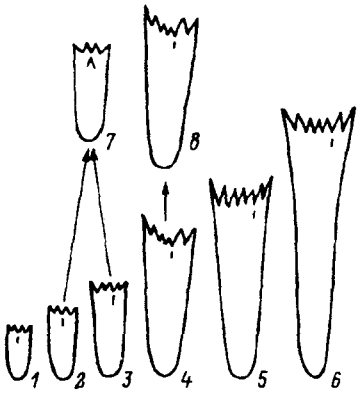


Fig. 7. Transformations of the first segment of the hindtarsi (ventral view, schematic representation). *1-6*) *Asiraca clavicornis* F. from the 1st instar (*1*) to adult (*6*), *7*) *Ugyops* variation, *8*) *Delphax* variation, from *3 to 7*) the transition of the middle (fifth) tooth in the second row with subsequent stop in development, from *4 to 8*) development stopped (*1-6* - after Asche, 1985).

duplicated in the upper half of the eumetopa. Within the subfamily Asiracinae, in *Equasystatus* the lateral row is completely defined. In the Asiracini (*Asiraca, Copicercus*) the first losses are found—in the median row the 4th and 5th pits counting from below disappeared, and in the lateral row the 3rd. In *Pentagramma* the losses are somewhat different—there is no 3rd, 4th, and 6th median pits and no 1st and 2nd lateral. In all higher Delphacidae, that is in the Eudelphacida, besides *Vizcaya*, there is only one difference from the arrangement of the pits in *Pentagramma*—the 6th median pit is defined, and the 5th lateral one disappeared, as if one pit had jumped to the opposite row. The case of *Vizcaya* is unfortunately not described (Asche, 1990) clearly enough, and I could not construct a map showing the arrangement of pits.

In the subfamily Delphacinae the arrangement and number of pits are very stable, significant deviations are characteristic of most representatives of the tribe Tropidocephalini, where only the genera *Malaxa* and *Bambusiphaga* retain a typical plan; among the Delphacini remarkable deviations are sometimes found, as, for example, in *Stobaera* or *Eoeurysa*, but they are fairly rare.

The names of the groups of pits proposed at the time by Vilbaste (1968) do not work and are inconvenient since they are applicable only to representatives of the subfamily Delphacinae and not to all pits of the metopa (frons): above the pits called, after Vilbaste, the upper pits, there are another 3 nameless pits.

In two closely related genera of the tribe Delphacini—*Achorotile* Fieb. and *Laccocera* V. D.—sensory pits are retained in the adult; in *Achorotile* the median area of the metopa is also retained, and in *Laccocera* it is not, and the intermediate carinae fuse into a single median carina. The close affinity of these genera, in particular, is suggested by the similarity in the structure of the genitalia (cf. Scudder, 1963; Anufriyev and Yemel'yanov, 1980), and it is difficult to agree with Asche (1985: 77), who believed they were not closely related.

In all cases, except *Ugyops*, when the complete ontogenesis is elucidated, the number of pits on the head from instar to instar does not change. The case of *Ugyops* is described, unfortunately, incompletely.

The ocular group of pits is most numerous in *Ugyops*: here, besides the pits in the main row, there are pits in a second row and even individual ones in a third row. The number of pits in the main row now reaches 14. In other groups the number of pits is usually 4-5, and sometimes reaches 8: a row is entire or divided into two parts (*Stenocranus, Saccharosydne*).

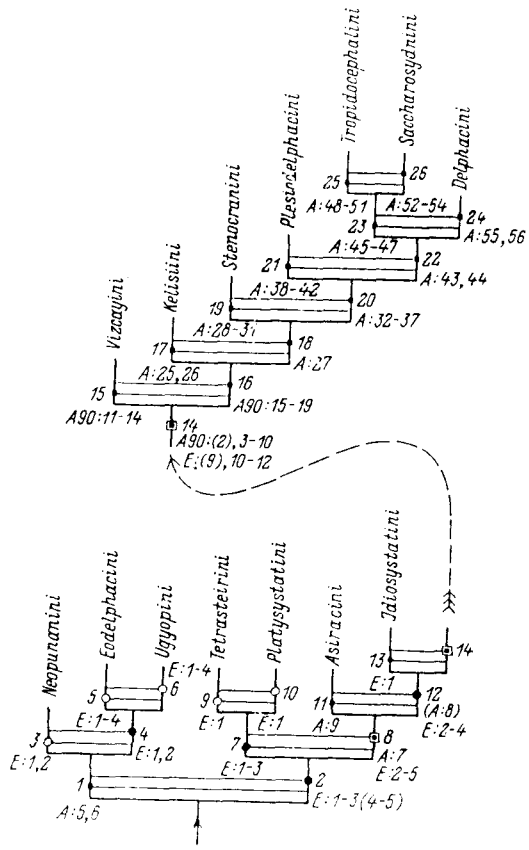


Fig. 8. Cladogram of the family Delphacidae to the tribe level. Nodes are numbered, next to the number of the node its apomorphies are provided; after the letter *A* apomorphies reported by Asche (1985) are provided with his numbers, after the *A*90 index apomorphies from an article by Asche (1990) are provided; after the letter *E* new apomorphies proposed in this article are provided with corresponding numbers. Designations for nodes: small square - node based only on apomorphies of Asche; large square - node based on Asche, but additional new apomorphies are provided; small circle - node based on Asche, but apomorphies cited by Asche are not accepted, other (new) apomorphies are given; large circle - node not found in Asche.

Thorax (Fig. 4). The sensory pits are most numerous and differentiated into groups in *Ugyops*. On the pronotum in this genus the lateral and collateral carinae are developed, with the latter separating the two groups of paranotal pits. The dorsal surface of the pronotum bears a row of 7-8 (up to 10) pits along the entire anterodiscal-postocular carina. There are 2 humeral pits, 4 pectoral. In the 1st instar the discal-paradiscal row consists of 4 pits, the humeral of 2, the pectoral of 5: besides a posterior group there is a large isolated anteropectoral pit, which is already absent in the 2nd instar. Humeral and posteropectoral pits are stable in all instars, the discal-paradiscal group doubles into the 2nd instar and then almost does not increase. In other delphacids, including the Ugyopinae (*Punana*, *Equasystatus*, *Neopunana*), pronotal pits form a single row from the discal to pectoral pits that is not divided by carinae; sometimes only the posterodiscal carina, setting off the discal pits, is defined. The discal-paradiscal group is easily identified by the orientation of the setae in the pits: they are directed backward while in the humeral-pectoral group they are directed forward. In Protodelphicida, because of the small number of examples the evolutionary pattern of the number and arrangement of pits is not

clear; in the Eudelphacida, on the contrary, the main plan is fairly clear: the discal-paradiscal group consists of 4 pits (2 in each), the humeral of 1, and the pectoral of 2. In rare cases the humeral-pectoral group increases to 4 or 5-6 pits (*Kakuna, Stenocranus*). In the 1st instar the discal-paradiscal group consists of 4 pits, and the humeral-pectoral group is represented by only 2.

The mesonotum in most Ugyopinae and in the Platysystatini bears a longitudinal row of pits interior to the discal carina and one pit on the outside opposite the posterior pit of the inner row; there is also a scapular group of 4-5 pits (only in *Ugyops*); in addition, there is a pit interior to the subcostal carina and a group of pits in the costal area (4 pits: 3+1). The metanotum of *Ugyops* has only 2 pits in an oblique row on the outside of the discal carina.

The evolution of the thoracic pits is primarily one of oligomerization and simplification; the lateral and collateral carinae of the pronotum disappear, the number of pits on average decreases, but often a posterodiscal carina is developed that separates a single row of pits into two parts, often the 3rd pit of this row interrupts the posterodiscal carina. On the mesonotum the discal row is reduced to 2-3 pits in the Asiracinae (*Equasystatus* 4, *Asiraca* 2, *Pentagramma* 3) and to 1 in the Eudelphacida. In the costal area 1 pit is retained in front and 2 pits in the obliquely longitudinal row in the middle part of the wing rudiment. On the metathorax in all described Protodelphacida (*Ugyops, Asiraca, Pentagramma*) there are 2 pits and 1 pit in the Eudelphacida.

Abdomen (Fig. 5). Besides *Ugyops*, the extralateral area is sclerotized and provided with sensory pits on segments V-VIII also in *Asiraca* and *Pentagramma*, that is, in the Protodelphacida. In the Eudelphacida it is membranous and correspondingly without pits. In *Ugyops* the sensory pits median to the lateral carina are arranged like a corner along the posterior and lateral margins, as in the Cixiidae, in the longitudinal part there are up to 4 pits, and in the transverse part up to 5 (total of 8); evidently, these rows correspond to the two primitive pits of the longitudinal median and transverse lateral series. In *Ugyops* and *Pentagramma*, unlike all other delphacids, there is also a transverse row of pits on the 4th segment. In *Asiraca* already the number of pits is close to the minimum characteristic of the Eudelphacida, but the lateral pits as before form a longitudinal row. In the higher Delphacidae there are also usually 3 pits, but in the transverse row. An exception is the Stenocranini, where the lateral group often is polymerized to 3-4 and slightly slanted, and on the 8th segment lies longitudinally; longitudinal arrangement of pits on the 8th segment is also found among the Delphacini (*Chloriona* and others). In the Kelisiini the pits are not polymerized, but on the 8th segment 2 lateral ones lie in a longitudinal row. On the 5th segment there is only 1 pit in the lateral group. in the Tropidocephala all areas of the tergite are separated by carinae, and in addition there are lateral pits on the 4th segment, and the median pit of the 8th segment is shifted from the intermediate area to the median (in *Asiraca* here there is also a pit, but there is also an intermediate area).

In 1st-instar larvae usually on the posterior segments (VI-IX) 2 pits are developed, on the anterior ones 1 pit (V or IV-V), in *Stenocranus* between two well developed a small third one appears. In *Ugyops* the pattern is quite similar, here on tergites V-VIII there are 3 pits each; in addition, there is another pit around the lateral carina, the position of which varies: it is either in the lateral or extralateral area; in later instars the pits of the extralateral area correspond to it.

Antennae. Appearance and increase by instar in rhinaria on the second antennal segment occurs in various groups of delphacids differently (see Table).

The arrangement of rhinaria has been examined only in the Delphacidae (Asche, 1985) and Dictyopharidae (Yemel'yanov, 1980); on the first ring in delphacids 7 rhinaria are counted, and in dictyopharids 5. The small number of examples still provides a basis for postulating that lower and higher Delphacidae differ in the pattern of increase in the number of rhinaria in early instars.

Legs. In connection with the transformation on the lateral apical tooth of the hindtibia into a spur in delphacids great disparity is observed in changes from instar to instar in the imaginal features in the supporting area of the hindlegs. In higher delphacids the tooth transformed into the spur from the 1st or 2nd instar, and the tarsus becomes tri-segmented only in the last, the 5th, instar, while at the same time in all other fulgoroids, including tettigometrids, the tarsus becomes tri-segmented in the penultimate the 4th, instar. In higher delphacids, thus, there is a compensatory slowing in the differentiation of the tarsus in connection with the increased role of the spur. Among lower delphacids, in *Asiraca* the standard situation is retained in which the tarsus is tri-segmented in the last two instars And, evidently, the primary moment in transformation of the tooth into a spur is with the molt to the 3rd instar. It is different in *Ugyops*, in which the spur is differentiated in the 1st instar, and the tarsus becomes tri segmented as early as the 2nd instar, and in further molts only increases in size without changing with respect to the number and shape of the teeth (Fig. 6). Such increased imaginization in the development of the hindlegs undoubtedly is secondary and, most likely, an apomorphy of the genus *Ugyops* or the tribe Ugyopini, but the ontogenesis of other representatives of the subfamily Ugyopinae is presently unknown.

The arrangement of teeth on the tip of the basal segment of the hindtarsus in the Delphacidae occurs in three main variations: an even gently arcuate row, angulate concave row consisting of two slanted parts, and an even row with one tooth in the middle that is significantly shifted basally. Asche (1985) considers plesiomorphic the single even row of teeth from which derives two independent apomorphies (diapomorphy): the angulate variation—*Delphax*, *Idiosystastus*, and the variation with the basally shifted tooth—*Ugyops*. In my view, these three variations are three conditions that are macroevolutionarily mutually transitional as parts of one homologous series, and therefore cannot be unconditionally treated as apomorphies or plesiomorphies. The arcuate and angulate rows pass into each other even in the ontogenesis of delphacids, and this transition makes it possible also to understand the formation of the variation with the tooth turned basally. A continuous row in ontogenesis is formed from two parts, each starting as one tooth, to which medially are added new teeth; when there are 6 teeth the row is joined together. If one half of the row develops with a bias (lateral ones grow more rapidly, and the median ones slowly) then the *Dephax* variation is obtained; if the next (5th) tooth is shifted to the second row, the *Ugyops* variant is obtained. In *Asiraca* (Asche, 1985) the row of teeth on the metabasitarsus in the 4th instar clearly embodies the *Delphax* variation, and in the 5th acquires the same appearance as the *Asiraca* variation (Fig. 7).

Most likely, the morphogenetic system of the successive formation of the teeth is even more complex since the row of teeth by origin is paired or may be transformed into a paired row by the appearance of new teeth in the spaces between already existing ones, but slightly more basally. This mechanism may be seen in the appearance of the teeth of the tip of the tibia in the Tettigimetridae: it is also manifested in the formation of the third tooth on the tip of the hindtibiae in the inner group in the Dictyopharidae and Fulgoridae.

It is easiest to postulate, as Asche does, that in the formation of the teeth on the basal segment of the hindtarsus first an even row arose and then two groups with the outer skewed and, finally, a row with the tooth moved back. Then, despite the views of Asche, through adaptive requirement and for other reasons, any of the three passed-through (acquired) variations for the arrangement of the teeth by reversion became possible. Thus, in the evolution of the Delphacidae any of the three variations may have been primitive, including that of *Ugyops*, which again appears in higher delphacids (Plesiodelphacini) clearly after the *Delphax* variation. In those cases (as in the discussed morphotype of the ugyopoid metabasitarsus) when a character is stable and delimits fairly discrete groups it is possible to consider it for each group separately a dependent synapomorphy that arose as a result of reversion.

Not quite so simple is the question of the primitive condition of the chaetotaxy of the metatibial saltatorial spur: are the setae distributed randomly, uniformly or are they arranged in rows (4 rows). Asche considers the random variation plesiomorphic. It seems to me, however, that a random setal cover and one arranged in longitudinal rows are the two final conditions of a single morphogenetic mechanism. We shall examine the arrangement of setae on the legs (particularly on the tibiae and tarsi). In ontogenesis in the first instars there are fewer setae, and here they more often are arranged in rows. Random cover with polymerization of setae arises through lateral growth of setae in rows with loss of uniform distancing, including misalignment and a checkered, but not strict, arrangement. We should not decide the question of the primitive density of the setal cover (in particular on the legs) for the Fulgoroidea or for insects, but as a minimum for the primitive Tracheata. At the same time it is evident that a morphogenetic mechanism for ordering and disordering the arrangement of setae formed and repeatedly and easily switched directions.

We can see with respect to the Fulgoroidea that in the Tettigometridae the random variation with multitude of smaller setae dominates, and in the Cixiidae there is a more ordered variation with fewer and larger setae.

We now examine the apical teeth of the hindtibiae and the delphacid spur that is derived from such a tooth. The teeth bear setae only on the lower surface; the upper surface is bare. On the spur the setae are situated on all sides. Did the setae gradually creep from the sides and then meet above based on the random variation or did the lower row induce (in-line metatopy) 3 other rows—lateral ones and an upper one? Four rows of setae (ribs) are also part of the main structure of the tibia. These four rows may also be transferred to the chaetotaxy of the teeth, that is, they are repeated on each tooth by means of metatopy when the teeth reach a significant size.

The question of the primitive chaetotaxy of the spur is closely associated with the question of the future of the chaetotaxy of the hindlegs of the immediate ancestor of the first delphacids. Until the opposite is proved, I believe that the primitive spur had intertwined, indistinct rows, from which formed as a diapomorphy conditions with distinct rows (apomorphy of the Ugyopinae) and with a completely disorganized chaetotaxy (apomorphy of the Asiracinae, which Asche considers a plesiomorph).

BASIS OF THE PHYLOGENETIC REPRESENTATION

Below we provide the basis of the phylogenetic representation of the Protodelphacida at the tribe level. In the list of apomorphies and in the cladogram (Fig. 8) all nodes are numbered and the reading of the apomorphies follows the nodes. Apomorphies cited by Asche (1985) are additionally marked in the list with the letter *A* and by those numbers used by Asche. The Eudelphacida cladogram proposed and substantiated by Asche is provided only to complete the picture without changes and without listing apomorphies that can be found in the study of Asche.

1.1. (*A*.5). Four-faced posttibial spur with 4 rows of setae along the ribs.

1.2. (*A*.6). Ugyopoid metabasitarsus: 4 teeth in a row and a fifth, middle one, shifted proximally there from the row.

2.1. Random setae on spur (in Asche this is plesiomorph *A*.5).

2.2. Complete fusion of *MP* and *CuA* on the hindwings.

2.3. Evening out in continuous row of teeth at the tip of the metabasitarsus (in Asche this is plesiomorph *A*.6).

(2.4.) Disruption of uniformity of distribution of pits on the metopa—*Asiraca* variation (see 8.2).

(2.5) Proboscis tri-segmented in adult (see 8.3).

3.1. On hindwings tips of *CuA* and *Pcu* approximated.

3.2. No median carinae on metopa.

4.1. Distal segment of penis arched clockwise: from the base it is turned to the left (the opposite in *Neopunana*, *Equasystatus* and *Asiraca*).

4.2. On hindwings sinus opposite tip of *CuP* disappeared (present in *Neopunana* and *Platysystatus*).

5.1. Hindwings with sinus opposite tip of *CuAp*.

5.2. Second segment of hindtarsus with differentiation into long marginal teeth and short intermediate ones.

5.3. Straight intermediate mesonotal carinae.

5.4. No postnodal transverse veins on forewings.

6.1. Nodal fold lost, membrane ceases to inflect.

6.2. Median carina of metopa bifurcate (in the adult the median area of the larva is retained, partial or entire).

6.3. Sinus on wing margin in area of *M-CuP* disappeared.

6.4. Sloped row of teeth on tip of second segment of hindtarsus.

7.1. Hindwings with sinus opposite tip of *CuP*.

7.2. Anterior margin of wing concave in area of pterostigma.

7.3. Median carina of corypha continued through region of the areolet to the eumetopa.

8.1. (*A.7*). Appearance of genal carina.

8.2. On metopa in larvae there are 5 lateral and 6 median pits (see also 2.4.). *Asiraca* variation.

8.3. Proboscis in adult tri-segmented (see also 2.5).

8.4. Not more than 3 pits on mesonotal disk in larva.

8.5. Three pits on forewing rudiment of larva.

9.1. Clavus with blunt tip. Tetrasteirini.

10.1. Head shortened and expanded. Platysystatini.

11.1. (*A.9*). First antennal segment strongly elongate, more or less flattened and with distinct carinae on dorsal, ventral and frontal sides.

11.2. Glands on 3rd and 4th abdominal tergites in larva.

12.1. (*A.8*). Distal teeth of metabasitarsus divided into outer and inner groups, outer group sloped.

12.2. Pits on metopa in larva: 4 lateral and 5 median (see 8.2 and 2.4)—*Pentagramma* variation Ventrally 1 median pit (upper?) of the lower group and 2 lateral pits lost, the upper pit of the middle median group is absent, being replaced by an opposing pit in the lateral row.

12.3. On metanotum of larvae near the lateral carina of the disk there ar 2 pits in the transverse row (plesiomorph—in the longitudinal).

12.4. In the lateral area of larval abdominal tergites II-VII? only pits of the transverse row are retained, the pit anterior to the row by the lateral carina disappears.

13.1. Intermediate carina of metopa broadly spread and more or less parallel.

14.1-14.5: *A.16, 18, 19, 20, 21.*

14.6 (*A.22*). On metopa, 18 pits in characteristic order.

14.7. (*A.23*). 14.8 (*A.24*).

14.9. Early differentiation of posttibial spur—from 1st-2nd instar.

14.10. Hindtarsus in 4th instar bi-segmented.

14.11. On metanotum of larvae there is 1 pit near the lateral margin of the disk.

14.12. Extralateral area on abdominal tergites disappeared in larvae.

14.13. Median carina on abdominal tergites disappeared. In larvae?

CONCLUDING REMARKS

Current knowledge of the Protodelphacida is far from complete; their mode of life and habitats are very poorly known (almost unknown), and their genus and species composition are clearly incompletely known. It is therefore difficult to provide a general picture of their evolution (evolutionary scenario). Of course, the basis for the cladogram provided here leaves many doubts, but I considered it useful to provide a schematic representation that includes all (even if poorly known) tribes of this main division of the family.

LITERATURE CITED

ANUFRIYEV, G. A., and A. F. YEMEL'YANOV. 1980. On the systematics and faunistics of genus *Achorotile* Fieb. (Homoptera, Delphacidae) of the Palearctic. [In Russ.]. Entomol. Obozr. 59(1): 118-127.

ANUFRIYEV, G. A., and A. F. YEMEL'YANOV. 1988. Suborder Cicadinea (Auchenorrhyncha). [In Russ.]. In: Opredelitel' Nasekomykh Dal'nego Vostoka SSSR. Vol. 2. Nauka, Leningrad: 12-495.

ASCHE, M. 1983a. Zur Kenntnis der Gattung *Platysystatus* Muir, 1930 (Homoptera, Auchenorrhyncha, Fulgoromorpha, Delphacidae). Marbuger Entomol. Publ. 1(8): 107-126.

ASCHE, M. 1983b. Aufgliederung der Asiracinen-Gattung *Punana* Muir, 1913; *Equasystatus* gen. nov. aus Equador und *Neopunana* gen. nov. von den Karibischen Inseln (Homoptera, Auchenorrhyncha, Fulgoromorpha, Delphacidae). Marburger Entomol. Publ. 1(8): 127-166.

ASCHE, M. 1985. Zur Phylogenie der Delphacidae Leach, 1815 (Homoptera Cicadina Fulgoromorpha). Marburger Entomol. Publ. 2(1-2): 1-910.

ASCHE. M. 1990. Vizcayinae, a new subfamily of Delphacidae with revision of *Viscaya* Muir (Homoptera: Fulgoroidea), a significant phylogenetic link. Bishop Mus. Occas. Papie 30: 154-187.

CALVERT, P. D., J. H. TSAI, and S. W. WILSON. 1987. *Delphacodes nigrifacies* (Homoptera: Delphacidae): field biology, laboratory rearing and descriptions of immature stages. Florida Entomologist 70(1): 129-134.

CALVERT, P. D., and S. W. WILSON. 1986. Life history and descriptions of the immature stages of the planthopper *Stenocranus lautus* (Homoptera: Delphacidae). J. N. Y. Entomol. Soc. 94(1): 118-125.

CALVERT, P. D., S. W. WILSON, and J. H. TSAI. *Stobaera concinna* (Homoptera: Delphacidae):

field biology, laboratory rearing and descriptions of immature stages. J. N. Y. Entomol. Soc. 95(1): 91-98.

LINDBERG, H. 1939. Der Parasitismus der auf Chloriona-Arten (Homoptera, Cicadina) lebenden Strepsiptere *Elenchinus chlorionae* n. sp. sowie die Einwirkung derselben auf ihren Wirt. Acta Zool. Fenn. 22: 1-179.

SCUDDER, G. G. E. 1963. Studies on the Canadian and Alaskan Fulgoromorpha (Hemiptera). I. The genera *Achorotile* Fieber and *Laccocera* Van Duzee (Delphacidae). Canad. Entomol. 95(2): 167-177.

ŠULC, K. 1928. Die Wachsdrüsen und ihre Produkte bei den Larven der Cixiinen (Homoptera). Publ. Biol. Ecole Hautes Etudes Veterin. Brno, 7, 13, B108: 1-32.

ŠULC, K. 1929. Die Wachsdrüsen und ihre Produkte bei den Larven fon Flata (Phromnia) marginella d'Oliver. Biol. Spisy Ac. Veter., 8, 2, B112: 1-23.

TSAI, J. H., and S. W. WILSON. 1986. Biology of *Peregrinus maidis* with descriptions of immature stages (Homoptera: Delphacidae). Ann. Entomol. Soc. Amer. 79(3): 395-401.

VILBASTE, YU. 1968. Preliminary key for the identification of the nymphs of North European Homoptera Cicadina. I. Delphacidae. Ann. Entomol. Fenn. 34(2): 65-74.

WILSON, S. W. 1985. Descriptions of the immature stages of *Delphacodes bellicosa* (Homoptera: Fulgoroidea, Delphacidae). Pan.-Pac. Entomol. 61(1): 72-78.

WILSON, S. W., and J. E. MCPHERSON. 1981a. Life history of *Megamelus davisi* with descriptions of immature stages. Ann. Entomol. Soc. Amer. 74(4): 345-350.

WILSON, S. W., and J. E. MCPHERSON. 1981. Ontogeny of the tibial spur in *Megamelus davisi* (Homoptera: Delphacidae) and its bearing on delphacid classification. Great Lake Entomol. 14(1): 49-50.

WILSON, S. W., and A. G. WHEELER, JR. 1986. *Pentagramma longistylata* (Homoptera: Delphacidae): descriptions of immature stages. J. N. Y. Entomol. Soc. 94(1): 126-133.

WU, R.-H., and CH.-T. YANG. 1985. Nymphs of Delphacidae from Taiwan (I) (Homoptera: Fulgoroidea), J. Taiwan Mus. 38(2): 95-112.

YANG, CH.-T. 1989. Delphacidae of Taiwan (II) (Homoptera: Fulgoroidea). National Sci. Council Rep. China Spec. Publ. 6: 1-334.

YANG, CH.-T., and W.-B. YEH. 1994. Nymphs of Fulgoroidae (Homoptera: Auchenorrhyncha) with descriptions of two new species and notes on adults of Dictyopharidae. Chinese J. Entomol. Spec. Publ. 8: 1-188.

YANG, J.-T., and CH.-T. YANG. 1986. Delphacidae of Taiwan (I). Asiracinae and the tribe Tropidocephalini. Taiwan Mus. Spec. Ser. 6: 1-79.

YEMEL'YANOV, A. F. 1980. Phylogeny and evolution of the dictyopharid subfamily Orgeriinae (Homoptera, Dictyopharidae). [In Russ.]. In: Chteniya Pamyati N. A. Kholodkovskogo: 1-96.

YEMEL'YANOV, A. F. 1990. Attempt to construct a phylogenetic tree for the Fulgoroidea (Homoptera, Cicadina). [In Russ.]. Entomol. Obozr. 69(2): 353-356.