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Dorso-abdominal scent glands and metathoracic evaporatoria in adults of central European Rhopalidae (Hemiptera: Heteroptera), with a discussion of phylogeny and higher systematics

JITKA DAVIDOVÁ-VILÍMOVÁ[1], MARKÉTA NEJEDLÁ[1] and CARL W. SCHAEFER[2]

[1] Department of Zoology, Charles University, Viničná 7, 128 44 Praha 2, Czech Republic; e-mail: vilim@natur.cuni.cz

[2] Department of Ecology and Evolutionary Biology, University of Connecticut, U-43, Storrs, CT 06269-3043, USA; e-mail: schaefer@uconnvm.uconn.edu

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Abstract. The reservoirs of dorso-abdominal scent glands and the occurrence of the metapleural scent gland evaporatoria in the adults of nine central European and one North American species in the family Rhopalidae (Hemiptera) were studied. All published data about the persistence of the dorso-abdominal scent glands in rhopalid adults are reviewed, and systematic and phylogenetic implications are derived from the patterns of variation.

GENERAL CONSIDERATIONS

Detailed studies of the dorso-abdominal scent glands of Western Hemisphere adults of the heteropteran family Rhopalidae have been reported in a number of papers. Formerly, authors commonly recorded completely reduced larval abdominal glands in heteropteran adults and their replacement by the metapleural scent glands (MTGs). However, several recent studies have reported the persistence of abdominal glands in adults. At least one gland, usually the anteriormost, has been found to be functional (Davidová-Vilímová, in prep., and Table 1).

Dupuis (1953) first mentioned the persistence of the abdominal glands in rhopalid adults: "...two orifices of dorso-abdominal glands, medially on segment IV–V and V–VI." He illustrated the abdominal dorsum with two conspicuous dorsal gland ostioles in two Rhopalini (Rhopalinae), *Corizus hyoscyami* (L., 1758) and *Rhopalus* (*Aeschyntelus*) *maculatus* (Fieber, 1837). Similarly, Schaefer (1965) illustrated the abdominal dorsum with two unpaired ostioles of three species, *C. hyoscyami*, *Harmostes reflexulus* (Say, 1832) (Rhopalinae: Harmostini), and *Boisea trivittata* (Say, 1825) (as *Leptocoris trivittatus*) (Serinethinae); other examples are in Table 1.

Later, Aldrich et al. (1979) described the adult abdominal glands of *Niesthrea louisianica* Sailer, 1961 (Rhopalinae: Niesthreini) and *Jadera haematoloma* (Herrich-Schaeffer, 1847) (Serinethinae). Schaefer & Chopra (1982) used these data, the persistence of two adult functional abdominal glands, to characterize Serinethinae. Aldrich et al. (1990a) mentioned scent glands in *Jadera haematoloma* and *J. sanguinolenta* (F., 1775), and Aldrich et al. (1990b) described in detail the adult abdominal glands of eight rhopalid species. The character "one gland, anterior, retains in the adults" was used to characterize the subfamily Rhopalinae, based on the study of one representative, *N. louisianica*. The authors described glands of two serinethine genera, *Boisea* Kirkaldy, 1910 (two spp.) and *Jadera* Stål, 1862 (five spp.).

Aldrich (1988) studied the chemistry of adult scent glands of *Leptocoris isolatus* (Distant, 1914) (Serinethinae), and of species in *Niesthrea* Spinola, 1837 and *Jadera*. He (1995) also mentioned briefly the Rhopalidae in his review of scent glands of Pentatomomorpha. Putshkov (1986), in his study of Palaearctic Rhopalidae, described briefly, and illustrated, the position of the adult dorso-abdominal scent gland ostioles in several species (see Table 1). Moulet (1995) mentioned generally the persistence of two dorso-abdominal scent glands, with open ostioles, in adults of Rhopalidae.

MTGs are generally developed, as autapomorphic structures, in adult heteropterans. However, the English name for Rhopalidae, scentless plant bugs, suggests an absence of MTGs. But this state is not general for all rhopalids. Chopra (1967) first summarized the states of MTGs in Rhopalidae, and used them in a new higher classification of the family. His opinion on anagenesis of MTG was later corroborated by Schaefer & Chopra (1982). The primitive state is represented by a separated metathoracic epimeron and episternum and a distinct ostiole, with a well-developed evaporatorium and/or peritreme (Rhopalinae: Niesthreini, Rhopalini). Reduction and loss of an externally visible ostiole and associated structures are more advanced stages. Reduction proceeded as follows: Fusion of epimeron and episternum accompanied by reduction of peritreme, and ostiole hidden between meso- and metacoxa (Rhopalinae: Chorosomatini); loss of peritreme (Rhopalinae: Harmostini, Maccevethini); loss of an externally visible ostiole, the gland opening into the coxal cavity (independently Rhopalinae: Corizomorphini and Serinethinae). This strong reduction of the MTG is correlated with retention of functional larval abdominal glands in serinethine adults (e.g., Aldrich et al., 1990b). Schaefer (1972) mentioned loss or

TABLE 1. The persistence of the adult dorso-abdominal scent glands in the Rhopalidae. Median gland – gland between terga 4–5; posterior gland – gland between terga 5–6, glands and ostioles unpaired; + – presence of gland, and/or gland reservoir; il. – only illustration; sex. dim. – gland reservoir sexually dimorphic. All cited references report original data except for Schaefer & Chopra (1982) who quote already published data.

Taxon	Ostioles	Median gland	Posterior gland	Reference
RHOPALIDAE	two			Dupuis (1953)
		+		Aldrich et al. (1978)[1]
		generally persistence	generally persistence	Aldrich et al. (1979)
		+	+	Moulet (1995)
Rhopalinae		+		Aldrich et al. (1990a)
Niesthreini				
Niesthrea louisianica		+		Aldrich et al. (1979), Aldrich (1988)
		+	inactive	Aldrich et al. (1990a)
Rhopalini				
Corizus hyoscyami	two			Dupuis (1953, il.), Schaefer (1965, il.), Putshkov (1986)
		+, sex. dim.	+	present paper
Liorhyssus hyalinus	two			Putshkov (1986)
		+, small	+, small	present paper
Rhopalus curtulus	two			Putshkov (1986)[2]
Rhopalus maculatus	two			Dupuis (1953, il.)
		+, large	+, large	present paper
Rhopalus subrufus		+	+	present paper
Rhopalus tigrinus	two			Putshkov (1986)[3]
		+	+	present paper
Chorosomatini				
Chorosoma schillingi	two			Putshkov (1986)
		+	+	present paper
Myrmus miriformis	two			Putshkov (1986)
		+, large	+, large	present paper
Agraphopus viridis	two			Putshkov (1986)
Maccevethini				
Maccevethus caucasicus		+, large	+, large	present paper
Maccevethus corsicus	two			Putshkov (1986)
Stictopleurus abutilon		+, large	+, large	present paper
Harmostini				
Harmostes reflexulus	two			Schaefer (1965, il.)
Corizomorphini				
Corizomorpha janowskyi	two			Putshkov (1986)
Serinethinae		one or two glands persistent		Aldrich (1988)
		+	+	Aldrich et al. (1979), Schaefer & Chopra (1982)
Boisea		reduced	+, functional	Aldrich (1995)
B. rubrolineata		reduced	+, functional	Aldrich et al. (1990a)[4]
B. trivittata	two			Schaefer (1965, il.)[5]
		reduced	+, functional	Aldrich et al. (1990a)[6]
		+	+	present paper
Jadera		+	+	Aldrich (1988[7], 1995)
J. antica		+, functional	+, functional	Aldrich et al. (1990a)
J. hinnulea		+, functional	+, functional	Aldrich et al. (1990a)
J. haematoloma		+, functional	+, functional	Aldrich et al. (1979, 1990a, b), Aldrich (1995)
J. obscura		+, functional	+, functional	Aldrich et al. (1990a)
J. sanguinolenta		+, functional	+, functional	Aldrich et al. (1990a, b)
Leptocoris isolatus		reduced	+	Aldrich (1988)

[1]mentioned as III–IV, sic!; [2]as *Limacocarenus curtulus*; [3]as *Brachycarenus tigrinus*; [4]as *B. rubrolineatus*; [5]as *Leptocoris trivittatus*; [6]as *B. trivittatus*; [7]chemistry of secretion of median gland.

strong reduction of MTGs in the entire family Rhopalidae, but this conclusion is too generalized. Göllner-Scheiding (1978) used summarized data about the development of the external structures associated with MTGs in her taxonomic revision of the Rhopalinae. The structures are developed in Niesthreini and Rhopalini, not developed in Chorosomatini, Harmostini, and Maccevethini (Corizomorphini not considered).

The higher classification of the Rhopalidae, suggested by Chopra (1967), has been basically accepted (e.g., Schaefer, 1994): Two subfamilies, Serinethinae and Rhopalinae, the latter with six tribes. Schaefer (1993) summarized data on the distribution of all the rhopaline tribes. He discussed centres of origin of individual tribes, in respect of Chopra's (1967) phylogeny and classification, their present distribution, and the Rhopalidae invasion of the New World.

The subfamily Serinethinae is generally considered the most advanced taxon of Rhopalidae (e.g., Chopra, 1967; Schaefer & Chopra, 1982; Putshkov, 1986). Ahmad & Afzal (1978) suggested that the data on MTG indicate that Serinethinae are more primitive than Rhopalinae. The former subfamily possesses a paired MTG reservoir, occurring also in the most primitive Heteroptera, combined with an advanced character, the MTG ostiole opening in the coxal cavity. However, Schaefer & Chopra (1982) did not consider this character as primitive, and agreed with many other authors that the paired condition is derived from the single condition.

Schaefer (1978), in a comprehensive morphological study of the Rhopalidae pygophore, did not find any pygophoral character clearly separating Serinethinae and Rhopalinae, and he suggested basing the classification of Rhopalidae on the tribal rather than subfamilial level. Putshkov (1986) mostly agreed with Chopra's (1967) conclusions, but he recommended also using characters of the eggs and larvae. Contrary to Chopra's (1967) conclusions, Putshkov (1986) considered the Eastern Hemisphere to have been the centre of the origin of Harmostini, which thus was the source area for dispersal to New World. Putshkov (1986) further supposed a closer relationship of Maccevethini to Rhopalini + Niesthreini than to Corizomorphini + Harmostini. He did not agree with close relationship of the genera classified in the tribe Maccevethini since their eggs and larvae are very different from each other. Putshkov classified these genera in the tribe Rhopalini, he thus synonymized Maccevethini with Rhopalini.

Schaefer & Chopra (1982) analyzed the Rhopalidae cladistically and suggested one change in Chopra's (1967) cladogram: The clade Serinethinae is not a sister group of all other Rhopalidae (= Rhopalinae), because there is no apomorphy separating Rhopalinae from Serinethinae. On the contrary, Maccevethini and Serinethinae share obvious synapomorphies (the number of conjunctival phallic appendages). However, in this conception Rhopalinae is paraphyletic. Schaefer & Chopra (1982) concluded that the tribes Rhopalini and Niesthreini are closely related and distinctly isolated from the other clades. Therefore, it would be possible to lump them into one taxon. The Serinethinae should be reduced to a tribe, but the authors preferred to leave the higher classification suggested by Chopra (1967) because of the amount of anagenesis the clade Serinethinae has undergone.

The most recent study of rhopalid higher classification was published by Li & Zheng (1994). The developed peritreme represents a plesiomorphic character, and it is retained in the monophyletic tribe Rhopalini and in representatives of the tribe Niesthreini. The absence of the MTG ostiolar peritreme and even the ostiolar opening are apomorphies. This advanced state (reduction) evolved in Maccevethini and Chorosomatini; the most advanced state (loss) in Harmostini and Serinethinae (the tribe Corizomorphini was not studied). The authors elaborated the higher classification of Rhopalidae based on almost 40 somatic and genital characters. The genera *Stictopleurus* Stål, 1872 and *Maccevethus* Dallas, 1852 were classified by Chopra (1967) in a new tribe Maccevethini. Later, Putshkov (1986) did not accept this tribe and classified both genera in Rhopalini. These two genera were not placed in the same clade in the cladogram of Li & Zheng (1994), they were far distant from each other. Their classification is therefore still open. The serinethine genera are closely related to Chorosomatini; the former taxon is highly advanced, but if classified as a subfamily then the Rhopalinae becomes a paraphyletic taxon. Therefore the authors suggested that all clades in Rhopalidae, including Serinethini, be considered only tribes. Generally, the results of Li & Zheng (1994) correspond with the tribal classification of Chopra (1967), except for the distant relationship of the two Maccevethini genera.

The reservoirs of dorso-abdominal glands and their ostioles, and the presence or absence of evaporatoria of the metapleural scent glands, were studied by one of us (MN, particularly in her Master's thesis) in the adults of both sexes of nine central European Rhopalidae: *Chorosoma schillingii* (Schilling, 1829), *Corizus hyoscyami*, *Liorhyssus hyalinus* (F., 1794), *Maccevethus caucasicus* (Kolenati, 1845), *Myrmus miriformis miriformis* (Fallén, 1807), *Rhopalus* (*Aeschyntelus*) *maculatus, Rhopalus* (*Rhopalus*) *subrufus* (Gmelin, 1790), *Rhopalus* (*Brachycarenus*) *tigrinus* (Schilling, 1829), and *Stictopleurus abutilon* (Rossi, 1790); and the North American *Boisea trivittata.* The results we present here include both a survey and analysis of the literature on these glands throughout the Rhopalidae, as well as the first acount of the glands in the Rhopalini. The results of our study can support some published phylogenetic conclusions, however, we recognize that no final conclusion can be drawn from study of a single character.

In the present paper, we review persistence of the reservoirs of dorso-abdominal scent glands in adult Rhopalidae and development of the evaporatoria of the metapleural scent glands. Our aim is to evaluate the pattern of phylogenetic variation in these characters, and to employ the data obtained in considering the higher classification of the family.

MATERIAL AND METHODS

Material examined

RHOPALINAE

Rhopalini

Corizus hyoscyami: Moravia mer., Podyjí National Park, July 1994: 3♂, 4♀.

Liorhyssus hyalinus: Albania, Smolethina, July 1960: 1♂, 1♀; Bulgaria or., Nesebar, August 1961: 1♂, 1♀.

Rhopalus (*Aeschyntelus*) *maculatus*: Bohemia mer., Ruda nr. Veselí nad Lužnicí, May 1994: 6♂, 5♀.

Rhopalus (*Brachycarenus*) *tigrinus*: Bohemia c., Praha env., May 1994: 2♂, 2♀.

Rhopalus (*Rhopalus*) *subrufus*: Bohemia c., České Středohoří, Mt. Lovoš, May 1976: 2♂, 2♀.

Chorosomatini

Chorosoma schillingii: Moravia mer., Podyjí National Park, June 1994: 2♂, 2♀.

Myrmus miriformis miriformis: Moravia mer., Podyjí National Park, June 1994: 2♂, 2♀.

Maccevethini

Maccevethus caucasicus: Slovakia mer., Štúrovo, May 1953: 1♂, Kováčov, June 1965: 1♀.

Stictopleurus abutilon: Moravia mer., Podyjí National Park, June 1994: 4♂, 4♀.

SERINETHINAE

Boisea trivittata: USA, IL, Jackson Co., Carbondale, March 1967: 1♂, 1♀.

Methods

The dry specimens were boiled for about 5 min in 10% KOH. They were removed to and dissected and drawn in distilled water. The abdomen was separated, the abdominal cavity was opened up laterally, and all tissues surrounding the gland reservoirs were removed with watchmaker forceps. The external structures associated with the metapleural glands (evaporatorium, ostiole, groove) were studied and illustrated on dry specimens, with the second and third pairs of legs removed.

The nomenclature and higher classification of the Rhopalidae follow Göllner-Scheiding (1983) and Henry & Froeschner (1988).

Terminology

Three dorso-abdominal scent glands are generally developed in Heteroptera. However, only two glands occur in Rhopalidae; the topographical median and posterior ones. We modify the terminology of Aldrich et al. (1990b) ("anterior" and "posterior" glands) to *median* and *posterior* glands, for those between terga 4–5 and 5–6, respectively. The anterior gland, of the three functional in other heteropteran larvae, lies between terga 3–4, and is not functional in Rhopalidae.

The following terms are used for the structures associated externally with the metapleural glands: *Ostiole* (e.g., Hepburn & Yonke, 1971; Ahmad & Afzal, 1978), for the external opening of gland. *Peritreme* (all authors of studies on metapleural glands mentioned), for ostiolar groove, running from the ostiole, mostly laterally. *Evaporatorium* (as "evaporative area," e.g., Chopra, 1967; Schaefer, 1972), for a part of external surface of metapleura, connected with the ostiole, and covered with a specific, complex, mushroom-like structure. *Groove-like structure,* for a part of the border between the mesothorax and metathorax, where the sclerites are separated from one another and form lateral walls of the groove-like structure, covered by the same structure as the evaporatorium.

The terms used for the dorso-abdominal glands are as follows: *Gland reservoir*, for the membranous structure, mostly sac-shaped, on the ventral surface of the abdominal dorsum, beneath the *ostiole*, a chink-shaped opening, surrounded by elevated, roughly ring shaped cuticle.

RESULTS

Reservoirs of dorso-abdominal scent glands in adults (Figs 1–9)

The number and position of the reservoirs in adults of studied Rhopalidae are the same as in their larvae (unpubl. data). Two unpaired reservoirs are developed, each with an unpaired ostiole and surrounded by a sclerotized cuticular ring. The ostiole of the median gland is located between abdominal segments 4–5, that of the posterior gland between segments 5–6. Abdominal tergum 5 is narrowed between the ostioles (Figs 1–5, 7–9), except in *Chorosoma* (Fig. 6).

The reservoirs are small in relation to body size, but conspicuous, and roughly sac-shaped; either both reservoirs are of the same shape, or the posterior one has two small lateral appendices giving a trilobate outline to the reservoir. The reservoirs are colorless and almost transparent, probably because the studied material was dried.

Rhopalini

Corizus hyoscyami (Fig. 1). Median reservoir shaped as a longitudinally elongated sac, slightly larger in male than in female. Posterior reservoir in both sexes globular, of the same size as female's median one.

Liorhyssus hyalinus (Fig. 2). Median and posterior reservoirs very small but distinct in both sexes, developed only as small globular sacs beneath ostioles, only slightly larger than ostiolar diameter.

Rhopalus maculatus (Fig. 3). Median and posterior reservoirs larger than their ostioles, conspicuous, slightly longitudinally elongated and sac-shaped, of same size in both sexes.

Rhopalus subrufus (Fig. 5). Median reservoir larger than posterior, longitudinally elongated and sac-shaped in both sexes. Posterior reservoir almost globular.

Rhopalus tigrinus (Fig. 4). Median reservoir small, almost globular in both sexes. Posterior reservoir larger than median, trilobate.

Chorosomatini

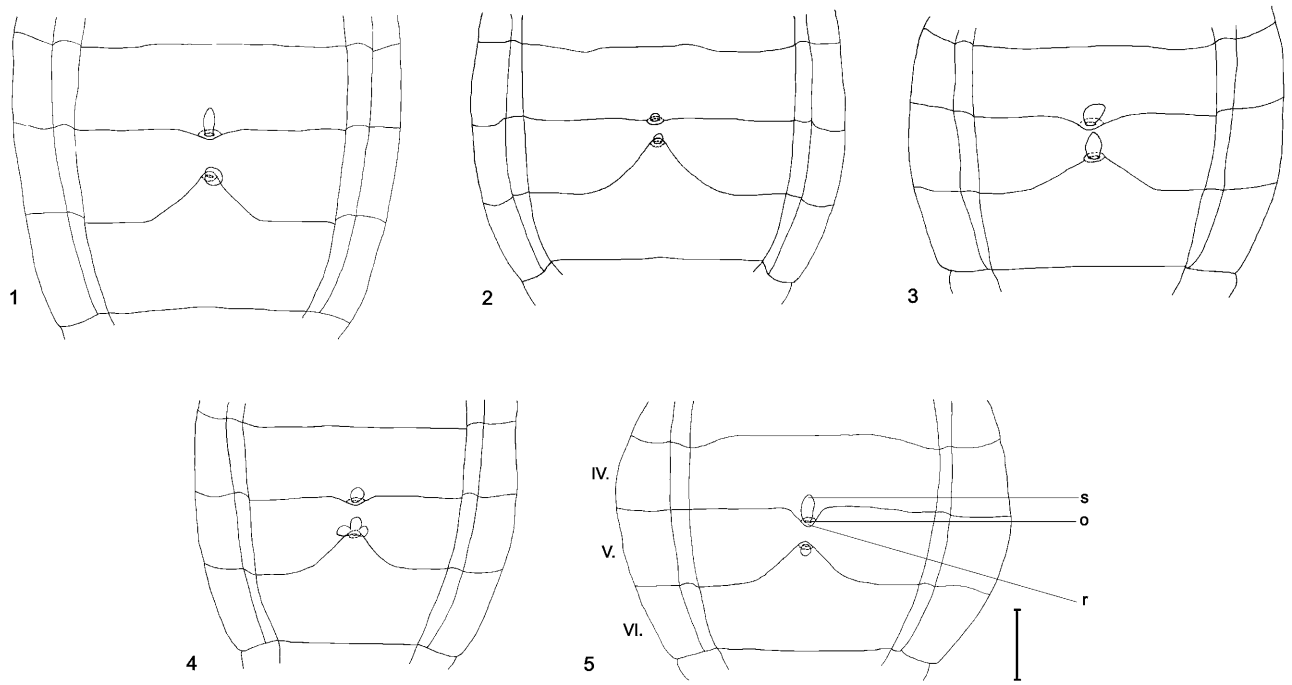
Chorosoma schillingii (Fig. 6). Median and posterior reservoirs small, longitudinally elongated and sac-shaped; median reservoir slightly larger than posterior.

Myrmus miriformis (Fig. 7). Median and posterior reservoirs conspicuous, larger than their ostioles, longitudinally elongated and sac-shaped in both sexes; median slightly larger than posterior.

Maccevethini

Maccevethus caucasicus (Fig. 8). Median and posterior reservoirs conspicuous, larger than their ostioles; median slightly longitudinally elongated and sac-shaped in both sexes, posterior trilobate.

Stictopleurus abutilon (Fig. 9). Both reservoirs conspicuous, larger than their ostioles. Median reservoir sac-



Figs 1–5: Dorsum of abdomen, ventral view. 1 – *Corizus hyoscyami*, male (for female see description); 2 – *Liorhyssus hyalinus*; 3 – *Rhopalus* (*Aeschyntelus*) *maculatus*; 4 – *Rhopalus* (*Brachycarenus*) *tigrinus*; 5 – *Rhopalus* (*Rhopalus*) *subrufus*. o – ostiole; r – sclerotized ring; s – reservoir of scent gland; IV.–VI. – abdominal segment. Scale: 1 mm.

like, only slightly elongated, slightly smaller than posterior in both sexes; in female of variable size, from one half to double of size in male. Posterior reservoir trilobate, larger than median in both sexes.

Serinethinae

Boisea trivittata (not illustrated). Median and posterior reservoirs very small, globular in both sexes, posterior a little larger than median.

Metapleural scent gland evaporatoria (Figs 10–14)

The species were examined with respect to the presence of an externally visible ostiole and peritreme, and the development of the evaporatorium, including groove-like structure.

The ostiole and associated evaporatorium were found only in Rhopalini, *Corizus hyoscyami* (Fig. 10), *Liorhyssus hyalinus* (Fig. 11), *Rhopalus maculatus* (Fig. 12), *Rhopalus tigrinus* (Fig. 13), and *Rhopalus subrufus* (Fig. 14). They were absent in the other rhopaline tribes and in Serinethinae.

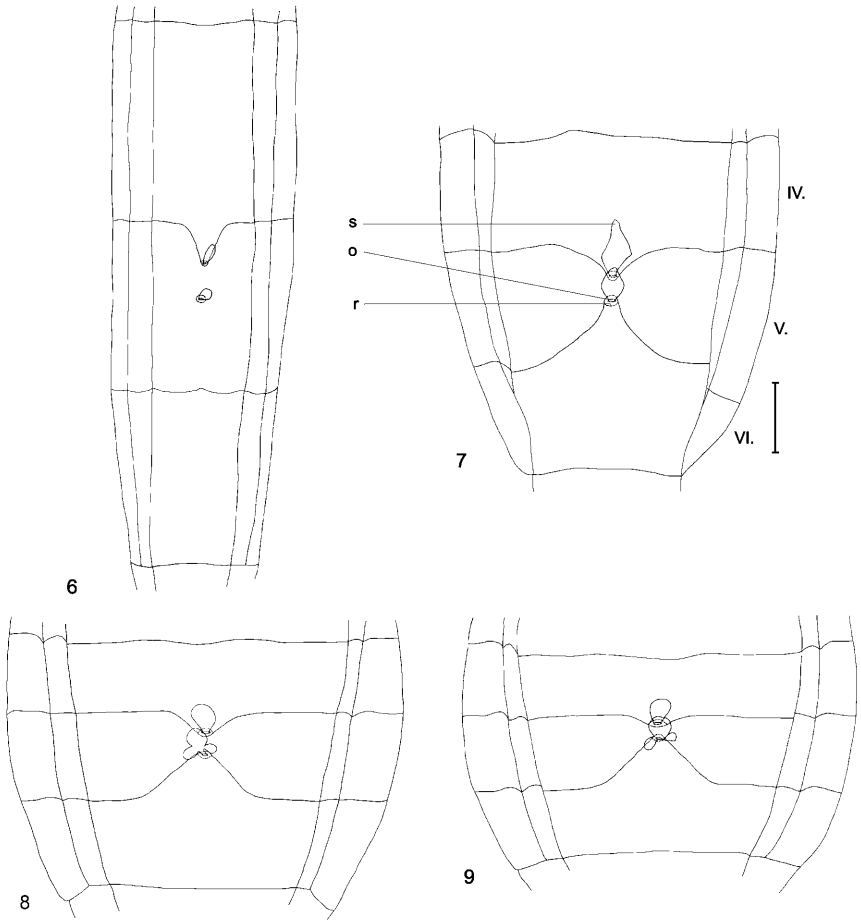
In Rhopalini, one pair of ostioles is developed ventrally on the metathorax. Each ostiole lies between the mesocoxa and metacoxa, not visible ventrally. The peritreme is not developed. The evaporatorium covers only a small median part of the epimeron, and a larger part of the episternum (median area, and a narrow anterior area running along the metapleural anterior margin). The evaporatorium also extends as a very narrow strip on the posterior mesopleural margin. Groove-like structure developed.

CONCLUSIONS AND DISCUSSION

It is difficult to decide conclusively without histological study if the dorso-abdominal scent glands (= DAGs) are functional in the adults studied. We can only estimate functionality from the size of the gland reservoir and the presence of its ostioles. We assume that when both reservoirs persist as sacs of the same size, connected with ostioles, they are functional.

The abdominal glands of *Boisea trivittata* (Serinethinae) were also studied by Aldrich et al. (1990b). They found two unpaired glands, the median reduced and empty, the posterior functional. We found two, sac-shaped, unpaired gland reservoirs directly beneath the ostioles. The reservoirs are distinct, quite small, the median smaller than the posterior. Thus we agree with Aldrich et al. (1990b). The reservoir of functional posterior gland is small, of the same size as the smallest gland reservoirs we found in *Liorhyssus hyalinus*, a much smaller bug than *B. trivittata*. We can assume, therefore, that at least one, but more probably two, dorso-abdominal scent glands are functional in adult Rhopalidae.

The existence of no more than two abdominal glands in larvae of all Rhopalidae represents an advanced condition; the possession of three glands, which occur in most heteropterans, is considered plesiomorphic (e.g., Aldrich et al., 1978). In Rhopalidae the anteriormost gland is completely reduced, including its ostiole. Two reservoirs of abdominal glands are developed in adults of all rhopalids studied. Sexual dimorphism occurs only in *Corizus hyoscyami*; the median reservoir is slightly larger in the male than in the female. The species is the only one studied with an aposematic colour pattern (see also below); it is questionable, however, if the sexual dimorphism is connected with this phenomenon. Sexual dimorphism of reservoirs of adult abdominal glands exists in several other heteropteran taxa (review Davidová-



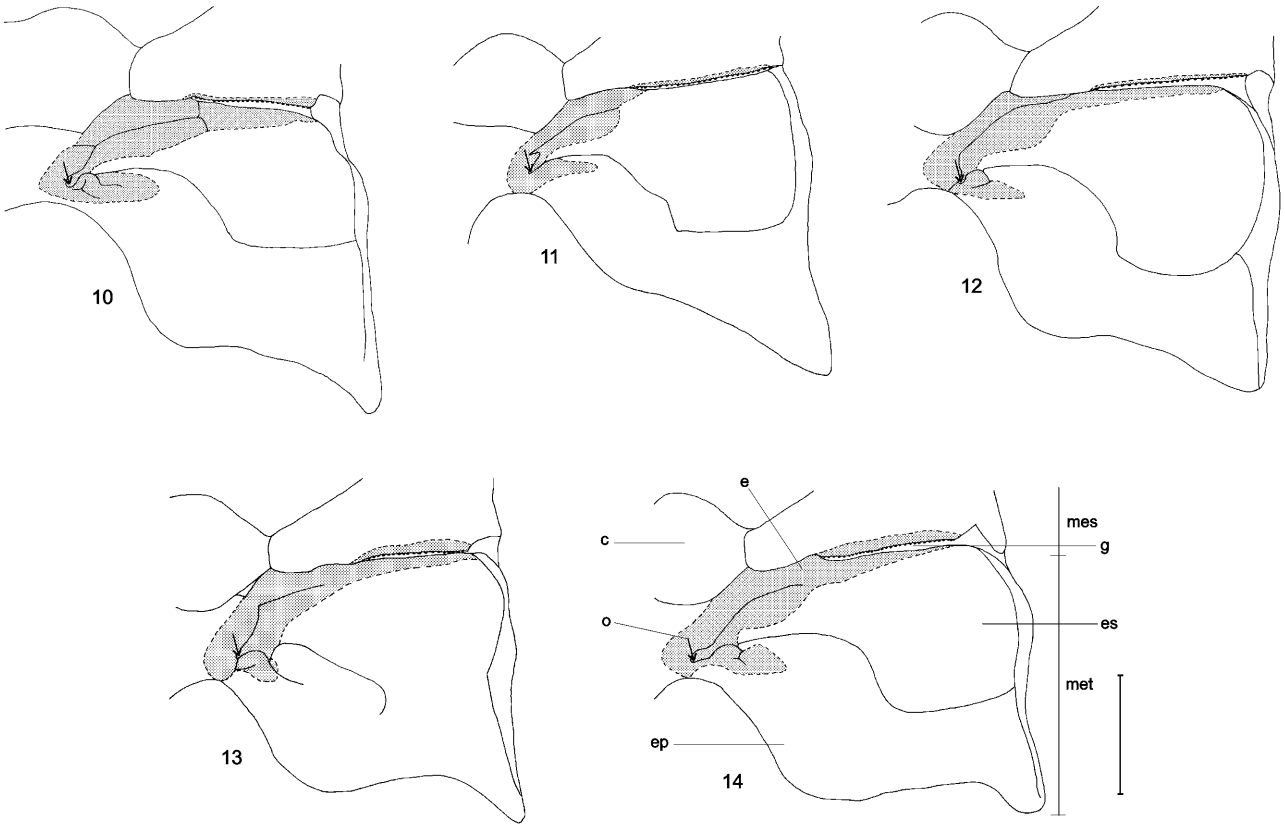
Figs 6–9: Dorsum of abdomen, ventral view, same in both sexes. 6 – *Chorosoma schillingii*, suture between segments V. and VI. not observed, probably not developed; 7 – *Myrmus miriformis miriformis*; 8 – *Maccevethus caucasicus*; 9 – *Stictopleurus abutilon*. o – ostiole; r – sclerotized ring; s – reservoir of scent gland; IV.–VI. – abdominal segment. Scale: 1 mm.

Vilímová, in prep.), but has not yet been described in Rhopalidae.

Three conditions of relative size were found in Rhopalidae: Median reservoir larger than posterior (*Corizus hyoscyami* male, *Rhopalus subrufus*, *Chorosoma schillingii*, *Myrmus miriformis*); posterior reservoir larger than median (*Rhopalus tigrinus*); median and posterior reservoirs of approximately the same size (*C. hyoscyami* female, *Liorhyssus hyalinus*, *Rhopalus maculatus*, *Maccevethus caucasicus*, *Stictopleurus abutilon*). Lacking histological data, we cannot determine if size differences reflect functional variation.

The tendency for reduction of MTG is considered advanced in Heteroptera. Also, the unusual chemical composition of gland secretion indicates an advanced phylogenetic position of Rhopalidae. The complete absence of secretional activity of MTG is known in Serinethinae. Gland secretion of only one rhopaline species, *Niesthrea louisianica*, was studied (Aldrich et al., 1979, 1990b). The pattern of MTG secretion fits that of the larval posterior DAG, which supports the presumption that the MTG functionally replaces the larval DAG. The possible groundplan of the adult Rhopalinae scent glands was proposed by Aldrich et al. (1990b) as follows: One repellent gland = MTG, one pheromonal gland = median DAG. The situation in Rhopalini (three genera and five species studied) agrees with the suggested Rhopalinae groundplan. MTGs are functional, two reservoirs of DAG were found, and the median gland could be functional at least in *Liorhyssus hyalinus*, *Rhopalus maculatus*, and *Rhopalus subrufus*; and almost surely it has a pheromonal function in *C. hyoscyami*, a species with sexual dimorphism (judging from the comparison with other Heteroptera, review in Davidová-Vilímová, in prep.). We can suppose that the posterior gland is reduced functionally, and its reservoir persists only structurally as a small membranous sac. Probably the posterior gland, or both glands, are functional in *R. tigrinus*, a species with a large, trilobate posterior reservoir, but a small, globular median reservoir. Published data about the occurrence of the MTG evaporatorium in the Rhopalini are listed in Table 2.

The situations in Chorosomatini and Maccevethini (two genera and two species studied of both tribes) do not fit the suggested Rhopalinae groundplan. MTGs in Chorosomatini are conspicuously reduced, and two elongated and sac-shaped reservoirs of DAG were found; the median gland is probably functional. Large differences were found in size; reservoirs are the largest in *Myrmus miriformis*, conspicuously larger than their ostioles, and very small in *Chorosoma schillingii,* of the same size as their



Figs 10–14: Left metathorax and posterior part of mesothorax, ventral view. 10 – *Corizus hyoscyami*; 11 – *Liorhyssus hyalinus*; 12 – *Rhopalus* (*Aeschyntelus*) *maculatus*; 13 – *Rhopalus* (*Brachycarenus*) *tigrinus*; 14 – *Rhopalus* (*Rhopalus*) *subrufus*. c – coxal cavity; e – evaporatorium (dotted); ep – epimeron; es – episternum; g – groove-like structure; mes – mesothorax; met – metathorax; o – ostiole; dashed line – outline of evaporatorium. Scale: 1 mm.

ostioles. MTGs are also reduced in Maccevethini, which have two reservoirs of DAG too; functionality of the glands is uncertain. The posterior reservoir is larger than the median in both species.

Aldrich et al. (1990b) supposed an evolution toward reduction of MTG in close connection with feeding specialization on toxic plants, and a consequent use of plant toxins in the form of blood toxins. The adult MTGs are then redundant. Serinethinae are, according to the authors, a typical example of such specialization (on Sapindaceae, see Schaefer & Chopra, 1982), accompanied by aposematic colouration. But the situation with reduced MTG is surely not so easily explained. *Corizus hyoscyami* possesses a typical aposematic colour pattern, but has both MTGs and two reservoirs of DAG developed. *Corizus hyoscyami* is widely polyphagous, not fixed on toxic plants (for a list of known host plants see Nejedlá, 1997). The explanation of complete reduction of MTG in some Rhopalidae, and some other Heteroptera, is probably more complicated.

Other unanswered questions remain. Why in Serinethinae is either the median (*Jadera*), or the posterior (*Boisea*) gland functional, when the adult DAG retains its repellent function? When the dorso-abdominal glands have a pheromonal function in adults, the anterior one is usually the functional one (review Davidová-Vilímová, in prep.; for information about Rhopalidae see Aldrich et al., 1979, 1990a). Then why has the posterior gland the pheromonal function in *Jadera*?

It is commonly accepted that Niesthreini and Rhopalini are closely related and the most generalized. MTGs are functional and all the associated structures are developed only in these two tribes. Only a single DAG (median) is functional in Niesthreini (Aldrich et al., 1979; Aldrich, 1988). Chemical properties of secretion and thus the functionality of DAGs have not yet been studied in Rhopalini. Two unpaired reservoirs of DAG structurally persist in the five species studied. The median gland reservoir is usually similar or larger than that of the posterior gland. The two unpaired glands in *Niesthrea louisianica* are structurally distinguishable; Aldrich et al. (1990a) recorded that only the anterior (= median) gland was functional, the posterior was inactive. We could assume that DAGs are morphologically homologous in the Niesthreini and Rhopalini. This result corroborates the hypothesis on close relationship of Rhopalini and Niesthreini.

The most advanced state of the MTG ostiole, occurring in Corizomorphini and Serinethinae, most probably evolved independently (Chopra, 1967). Corizomorphini, the most advanced tribe, has been studied only rarely, and the state of DAG is unknown. Most authors supposed this tribe to be closely related to Harmostini.

TABLE 2. The occurrence of MTG evaporatorium in the Rhopalidae: Rhopalinae: Rhopalini; + presence, – absence, n – not studied, nl – narrow, long.

Species	Author						
	R	S	H & Y	A & A	G–S	L & Z	pp
Corizus hyoscyami	n	+, nl	–	+, small	+	+	+
Liorhyssus hyalinus	n	+, nl	–	–	+	+	+
Rhopalus latus	n	n	n	n	n	+	n
Rhopalus maculatus	+	n	–	–	+	n	+
Rhopalus parumpunctatus	n	–	n	n	+	n	n
Rhopalus rufus	n	n	–	n	+	n	n
Rhopalus subrufus	n	n	–	n	+	n	+
Rhopalus tigrinus	n	n	n	–	+	n	+

A & A – Ahmad & Afzal (1978); G-S – Göllner-Scheiding (1978); H & Y – Hepburn & Yonke (1971); L & Z – Li & Zheng (1994); pp – present paper; R – Remold (1962, 1963); S – Schaefer (1965).

The taxon Serinethinae possesses the autapomorphic state of glands, the combination of the vestigial MTG with one or two functional DAGs. Unfortunately, this autapomorphy does not allow resolution of the relationship of the taxon. Several classifications are possible. Most authors classified the Serinethinae as sister group of all the other Rhopalidae (= subfamily Rhopalinae). Then the autapomorphic state of glands would have evolved independently, after the separation of Serinethinae from the main lineage. Serinethinae is considered sister group of Maccevethini by Schaefer & Chopra (1982). The advanced state of MTG and two reservoirs of DAG of the same size are found in Maccevethini. Both DAGs are very probably functional. However, Serinethinae is considered sister group of Chorosomatini by Li & Zheng (1994). The state of MTG is less advanced in Chorosomatini than in Maccevethini. Two small reservoirs of DAG occur in Chorosomatini, the median larger than the posterior, probably only the former gland functional. The gland pattern is quite different in Chorosomatini than in Serinethinae, and the relationship of Serinethinae with this tribe is less likely than with Maccevethini.

The relationship of Maccevethini represents the last confusion in the Rhopalidae classification. Putshkov (1986) synonymized Maccevethini with Rhopalini, and congruently Li & Zheng (1994) suggested combining Maccevethini and Rhopalini. The pattern of DAGs is similar in these two tribes: Two gland reservoirs are larger than their ostioles; but the character of MTG is quite different, because the plesiomorphic state was recorded in all species studied of Rhopalini and the highly advanced state in Maccevethini (see above). Maccevethini are prevailingly classified as related to the three tribes, Chorosomatini, Harmostini, and Corizomorphini. The scent gland pattern fits this view well because the reduction of MTG and associated structures, and the presence of two DAGs or at least of their reservoirs, occurs in all the tribes.

We have added new data to the knowledge about DAG reservoirs in Rhopalidae adults, which will partly help to clarify relationships within the family. The state of DAG reservoirs was so far unknown in any Rhopalini, and now also this character has confirmed expected relationship of Rhopalini with Niesthreini. The pattern of DAG reservoirs is described for the first time also in the representatives of Chorosomatini and Maccevethini. The pattern found here is closely similar in both tribes and also in the tribe Rhopalini. Therefore it does not help to resolve the tribal relationship without association with pattern of MTGs. Thus is evident a closer relationship of Maccevethini to Chorosomatini than to Rhopalini. Of the several published cladograms of rhopalid relationships (Chopra, 1967; Schaefer & Chopra, 1982; Putshkov, 1986; Li & Zheng, 1994), our data most closely agree with that of Schaefer & Chopra (1982) (Fig. 15).

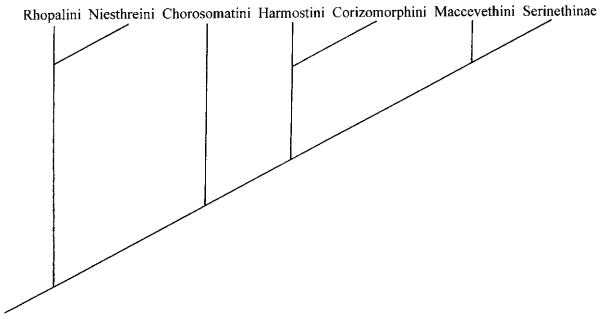


Fig. 15. Proposed cladogram of rhopalid higher taxa based on Schaefer & Chopra (1982, modified).

Only comprehensive histological and biochemical studies can resolve unclear questions of the functionality of DAGs in Rhopalini and other, not studied, tribes. Then adult scent gland patterns can contribute more to an understanding of relationships within the Rhopalidae taxa.

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