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Function of metathoracic scent glands in terrestrial Heteroptera

Funkce metathorakálních pachových žláz u terestrických ploštic

Bakalářská práce

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Praha 2009

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Abstract:

Defensive function is characteristic of the secretion of metathoracic glands of terrestrial Heteroptera; however, various other, mostly pheromonal functions are carried out by the secretion. Alkanes and aldehydes are effective in defence both against vertebrate and arthropod predators and as alarm pheromones, while esters usually act as attractive pheromones. However, the exact composition of the secretion is specific for individual families. The attractants from the secretion of the metathoracic glands have numerous functions, such as epigamic, aggregation, migratory and hibernation pheromones. The utilization of the secretion as kairomones by parasitoids is reported. Sequestration (storing chemicals obtained from food) occurs in many heteropteran families; the sequestered chemicals have mainly defensive function, though they could take part in intraspecific communication in some species as well.

Key words:

Heteroptera, metathoracic, glands, defence, allomones, pheromones, sequestration.

Funkce metathorakálních pachových žláz u terestrických ploštic

Abstrakt:

Obranná funkce je charakteristická pro sekreci metathorakálních žláz terestrických ploštic, i když touto sekrecí jsou vykonávány i různé další, většinou feromonální funkce. Alkany a aldehydy jsou účinné v obraně proti predátorům z řad obratlovců i bezobratlých a jako poplašné feromony, zatímco estery obvykle fungují jako atraktanty. Přesné složení sekrece je ale specifické pro jednotlivé čeledi. Atraktanty ze sekrece metathorakálních žláz mají mnoho funkcí, například jako epigamní, agregační, migrační a hibernační feromony. Je známo využívání sekrece parasitoidy jako kairomonu. Sekvestrace (ukládání látek získaných z potravy) se vyskytuje u mnoha čeledí ploštic; sekvestrované látky mají převážně obrannou funkci, ačkoliv se u některých druhů mohou účastnit i vnitrodruhové komunikace.

Klíčová slova:

Heteroptera, metathorakální, žlázy, obrana, allomony, feromony, sekvestrace.

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1 INTRODUCTION:

Heteroptera is one of the most successful groups of hemimetabolous insects. Their success is evident especially in their ecological diversity as no other major group of insects utilizes such an enormous array of different habitats as do the Heteroptera (Schuh and Slater 1995). One of the keys to this success is well-developed allomonal (inter-specific) and pheromonal (intra-specific) communication, provided by so-called scent gland system (Carayon 1971, Staddon 1979).

Of several types of heteropteran scent glands, the dorsoabdominal glands and the metathoracic glands are of the greatest importance, both often significant in defence (Remold 1963). As the dorsoabdominal glands are primarily developed in larvae, often persisting to adulthood, the metathoracic glands are exclusive for adults (Staddon 1979).

In this text I focus on terrestrial true bugs of the infra-orders Cimicomorpha, Aradomorpha and Pentatomomorpha. Object of my interest are the metathoracic glands (MTG in text). I hope both limitations contributed to better coherence of work. Besides, the work also refers to sequestration as a possible supplement to or replacement of antipredatory function of MTG or other glands.

When reviewing the functions of the MTG secretion, I especially focus on their variability, mechanisms, specifics in individual families, and ecological significance. I hope the text will provide a reader with a complex image of great variety of functions of the glands, and will offer some information useful in further research.

The classification of Heteroptera used in this text is taken over mostly from Schuh and Slater (1995), with exceptions of Aradomorpha, taken over from Sweet (1996), and Lygaeoidea ("Lygaeidae s.l."), taken over from Henry (1997).

2 MORPHOLOGY:

The morphology of MTG is reviewed briefly in this text, with focus on the mechanisms of their function. For more information on morphology of MTG, see Carayon (1971) and Staddon (1979).

MTG occupy a ventral position in the hind part of the metathorax (Staddon 1979). The gland itself does not usually extend over the edge of the metathorax but can reach second abdominal segment in well-fed bugs, as reported in Coreidae (Hepburn 1971).

Carayon (1971) classified heteropteran MTG two basic types: type omphalien, with one opening in metasternum, exceptionally two openings, close to each other; and type diastomien, with two openings in both metacoxal cavities; the omphalien type is probably primitive while the diastomien type is derived, occurring in terrestrial Heteroptera (Carayon 1971). However, as the glands are often reduced, often being secondary divided, and of various ontogenesis, the division of all MTG types actually seems to be much more complicated (Staddon 1979).

Typical diastomien MTG apparatus consists of paired lateral reservoirs with branching secretory tubules ("primary glands"), unpaired median reservoir with accessory gland, and paired excretory tubules (Staddon 1979) (fig. 1). However, morphology of MTG varies in different families. These specifics are mentioned in systematic part.

MTG are associated with a cuticle of complicated structure called evaporatorium (fig. 2). This cuticle is usually situated on metapleura but can completely cover lateral and ventral parts of thorax, as seen in some Plataspidae (Carayon 1971). Although some authors suggest that the main function of this structure is improving evaporation (Carayon 1971), it seems that it primarily prevents the secretion to overflowing to the rest of the body, especially to the tracheal openings (Remold 1963). For better effect, the evaporatorium is covered by mushroom-shaped sculptures, holding the fluid. These sculptures are complicated in structure, often being taxon-specific (Carayon 1971, Hepburn 1971) (fig. 3, 4).

It should be noted that the nomenclature of MTG structures is complicated and inconsistent; in this text the most established terms are used, mostly taken over from Staddon (1979).

The stored secretion differs in individual parts of the gland. Johansson (1957) noted that only the fluid from median reservoir had "bug-odour" while the fluid from lateral reservoir had pleasant smell for humans. This feature is caused by two stage synthesis of the metathoracic gland secretion: as the tubular glands mostly secrete esters, their derivatives are synthesised on the accessory gland; thus, the blend of lateral reservoirs contains mostly esters while aldehydes, alcohols etc. are the stored in the median reservoir blend (Games and Staddon 1973, Aldrich 1978).

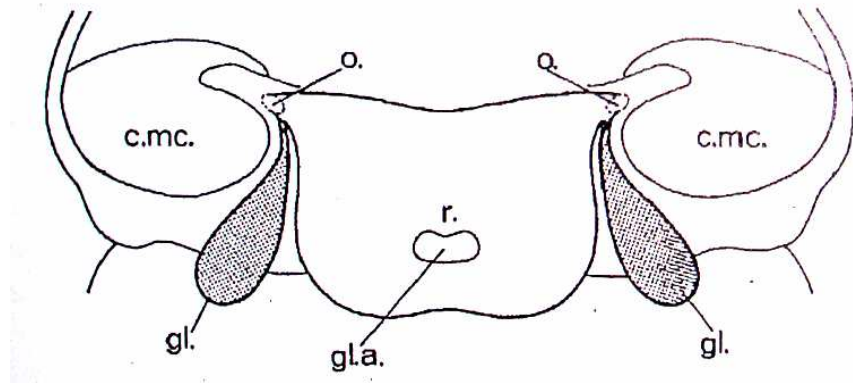


Fig. 1. Diastomien MTG with undivided median reservoir. C. mc., metacoxal comb; gl., lateral glandular reservoir; gl.a., accessory gland; r., median reservoir; o., orifice (after Carayon 1971).

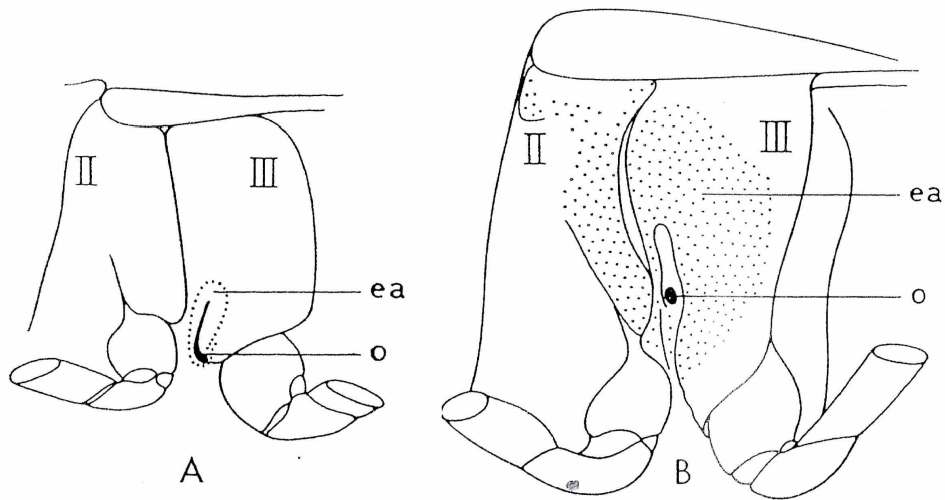


Fig. 2. The opening (o) and evaporative area (ea) of the metathoracic scent glands of *Oncopeltus fasciatus* (A) and *Dolycoris baccarum* (B). The dotted area is covered by the flaked (mushroom-shaped) cuticle. II: mesothorax. III: metathorax (Johansson 1970).

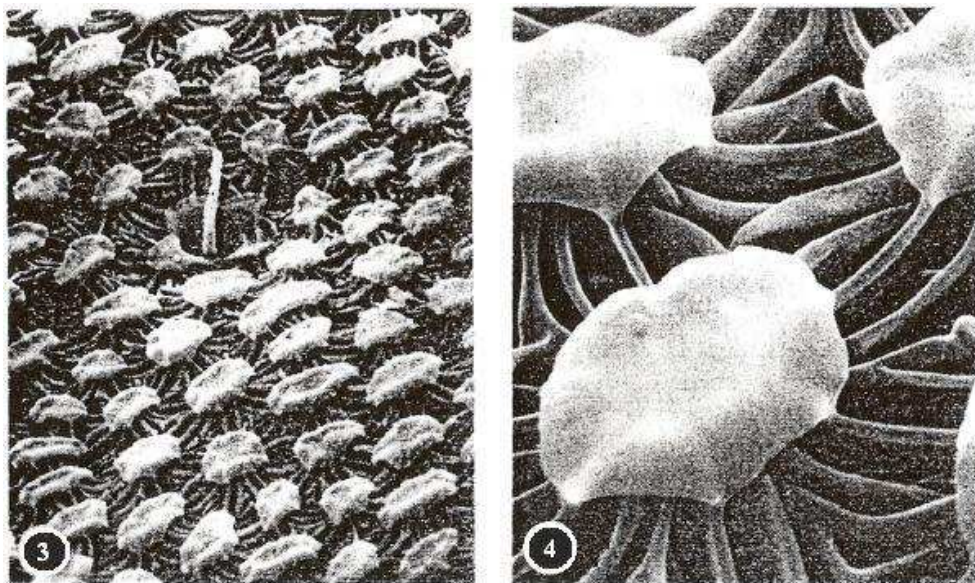


Fig. 3. *Dolycoris baccarum*. Flaked cuticle from the evaporative area, 1100:1.

Fig 4. *Pentatoma Rufipes*. Flaked cuticle from the evaporative area, 5600:1 (Johansson 1970).

Both blends can be used as final secretion of the gland (Games and Staddon 1973) and the size of lateral and median reservoirs, often sexually dimorphic, can themselves express the characteristics of the secretion (Staddon 1985).

The glandular apparatus is pigmentless, with an exception of median reservoir, which is pigmented an orange colour (e.g. Waterhouse and Gilby 1964, Staddon 1979). As the reservoir stores the most aggressive chemicals, it is presumed that the pigment prevents autotoxication (Waterhouse and Gilby 1964). However, the composition and the exact function of the pigment has not been investigated yet.

The reservoirs are not attached to any muscle; instead, their content is probably excreted by raising the haemolymph pressure by abdominal muscles (Staddon 1979). On the other hand, excretory tubules are articulated by dorsoventral muscle (Johansson 1957) and a chitine flap separating the reservoirs is attached to muscles as well (Remold 1963).

3 HETEROPTERAN FAMILIES

3.1 CIMICOMORPHA

3.1.1 Reduvidae

3.1.1.1 Reduviidae

Chemical ecology of the assassin bugs is characteristic for this group. They possess unique paired Brindley's and ventral scent glands, both located between metathorax and abdomen (Carayon 1971) (fig. 5). The morphology of reduviid MTG is also different from all other families. They are completely divided, with a small pigmentless reservoir, an unbranched secretory tubule and no accessory gland (Staddon 1979); moreover, MTG are often reduced or absent in some subfamilies of Reduviidae, such as Emesinae and Tribelocephalinae (Schofield and Upton 1978, Staddon 1979). Although possessing evaporatoria, Reduviidae also use long and stout setae, so-called metacoxal comb, to atomize the MTG secretion (Weirauch 2006).

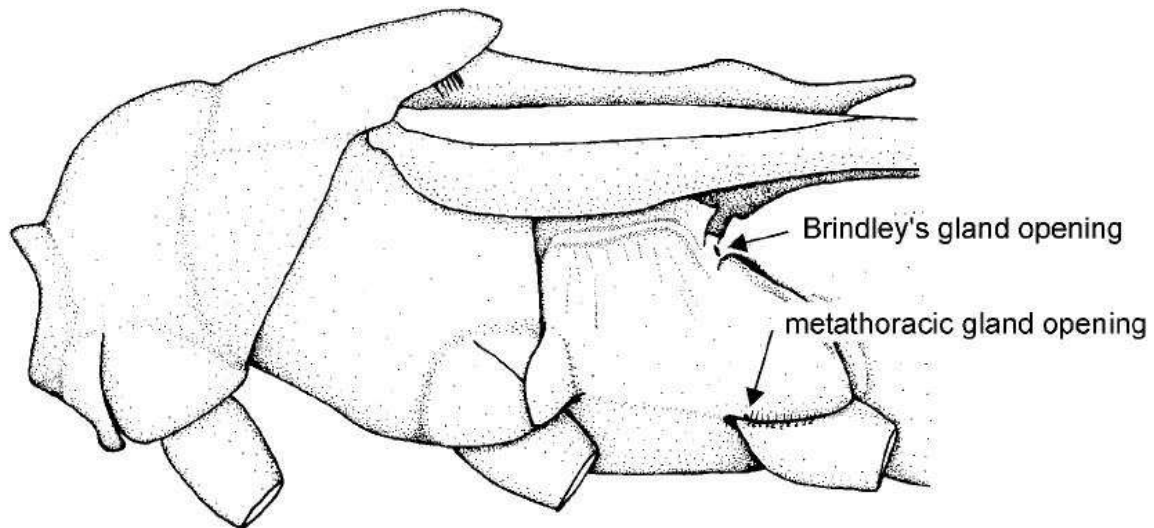


Fig. 5. Thorax of *Panstrongilus herreri* (Reduviidae: Triatominae) in lateral view (Weirauch 2006).

Chemical ecology of Triatominae, a subfamily including many human parasites and Chagas Disease vectors, is known relatively well, in contrast to other subfamilies. During a copulation, *Triatoma infestans* excretes 3-pentanone (which composes as much as 85% of MTG secretion), serving as an attractant. However, the function of this behaviour is not clear (Manrique 1995). When disturbed, the bugs release a secretion with the main components of isobutyric acid and 2- and 3-methyl-1-butanol, whereas 2-methyl-1-butanol composes only about 3% of MTG secretion and the other two chemicals do not occur in the secretion at all (Manrique 2006). Thus, MTG probably have a minor function in defence in this species.

In another triatomine species, *Dipetalogaster maximus*, 3-methyl-2-hexanone excreted from MTG probably acts as alarm and attractant pheromone, respectively, depending on its concentration (Rossiter and Staddon 1983).

3.1.2 Cimicoidea

3.1.2.1 Cimicidae

MTG of *Cimex lectularius* produce *trans*-2-hexenal, *trans*-2-octenal, acetaldehyde and 2-butanone. While unsaturated aldehydes have demonstrably served as an alarm pheromone in this species, a piece of paper saturated with female secretion triggered aggregation behaviour (Levinson and Bar Ilan 1971, Levinson *et al.* 1974). Individuals of *C. lectularius* were also

spat out by bats (natural hosts of bedbugs) when releasing their MTG secretion, showing its defence function (Levinson *et al.* 1974).

3.1.3 Miroidea

3.1.3.1 Miridae

The mirid MTG secretion has predominantly sexual function, with females as the main excretors of the pheromones (McBrien 1999). Moreover, the composition of the secretion differs in calm and disturbed bugs; however, experiments failed to prove an alarm function (Groot *et al.* 2001, Wardle *et al.* 2003). As mirid females are much more sensitive to plant volatiles than males (Groot *et al.* 1999), the pheromones also probably take part in the colonisation of new hosts.

The secretion of mirid MTG usually consists of a species-specific blend of various esters; however, species-specificity is not necessary in the reception- *Phytocoris relativus* was even attracted to a synthetic *Oncopeltus fasciatus* (Lygaeidae) pheromone as it contained esters analogous to those of the mirid (Zhang and Aldrich 2003a).

In *Campylomma verbasci*, the crucial chemicals for the attractive function are butyl butyrate and *trans*-2-butenyl acetate (Smith 1991, Drijfhout 2000). In *Lygus rugulipennis*, a mixture of hexyl butyrate and *trans*-2-hexenal serves as an attractant while other chemical, *trans*-2-hexenyl butyrate, is non-attractive, probably serving as a vaporization decelerator (Innocenzi *et al.* 2004, 2005). Similar situation occurs in *Phytocoris relativus*, where hexyl acetate and octenyl butyrate are essential (Millar 1997), and in *Phytocoris calii*, where a mixture of hexyl, *trans*-2-octenyl and *trans*-2-hexenyl/octyl acetate has a pheromonal function (Zhang and Aldrich 2008).

The function of non-attractive chemicals has been investigated extensively. One of their possible functions may be an inhibition of the reception of the attractants by related species, strengthening interspecific barrier. For example, a mixture of two chemicals from an attractant secreted from MTG of *Phytocoris difficilis* (hexyl and *trans*-2-octenyl acetates) also worked as an attractant for *Phytocoris brevisculus*. However, after addition of two remaining chemicals (*trans*-2-hexenyl and *trans*-2,4-hexadienyl acetates) the mixture lost its effect on this species (Zhang and Aldrich 2003a).

Such a function may be exploited in even more sophisticated way. Secretion of male *P. difficilis* contains 68% of hexyl butyrate. When added to an attractive blend, this chemical drastically inhibited male reaction to the blend, functioning as an anti-sex pheromone in *P. difficilis* (Zhang and Aldrich 2003b). Moreover, hexyl butyrate is excreted by disturbed female *Lygocoris pabulinus*, preventing females nearby from releasing their attractant (Groot *et al.* 2001).

An exception in Miridae is *Lopidea robiniae*, a large aposematic bug whose MTG have primarily defensive function. Thus, the MTG secretion differs from a typical mirid one, containing *trans*-2-octenal with *trans*-2-hexenal, *trans*-2-hexenol, *trans*-2-heptenal, *trans*-2-octenol and *cis*-2-octenol. This untypical defensive secretion was particularly effective against birds, the most significant predators of this species (Staples *et al.* 2002).

3.2 ARADOMORPHA:

MTG of Aradomorpha are well developed, with large evaporatoria (Usinger 1959). However, little is known about the chemical ecology of the group. It is for certain that flat bugs produce a volatile scent when disturbed (Långström *et al.* 2004) and there is a possibility of a pheromonal function as Aradomorpha can be found in aggregations of several hundred individuals (Usinger 1959).

3.3 PENTATOMOMORPHA

3.3.1 Pentatomoidea

3.3.1.1 Pentatomidae

Evaporatorium of Pentatomidae is much larger than those of other families, extending onto mesothorax (Johansson 1970). The accessory gland is long and wavy (Choudhuri 1970, Nagnan *et al.* 1994) (fig. 6), probably increasing its surface for more effective synthesis of secondary MTG products. The morphology of MTG of all Pentatomoidea has many specifics (Kment, unpublished), too numerous to be discussed in this text.

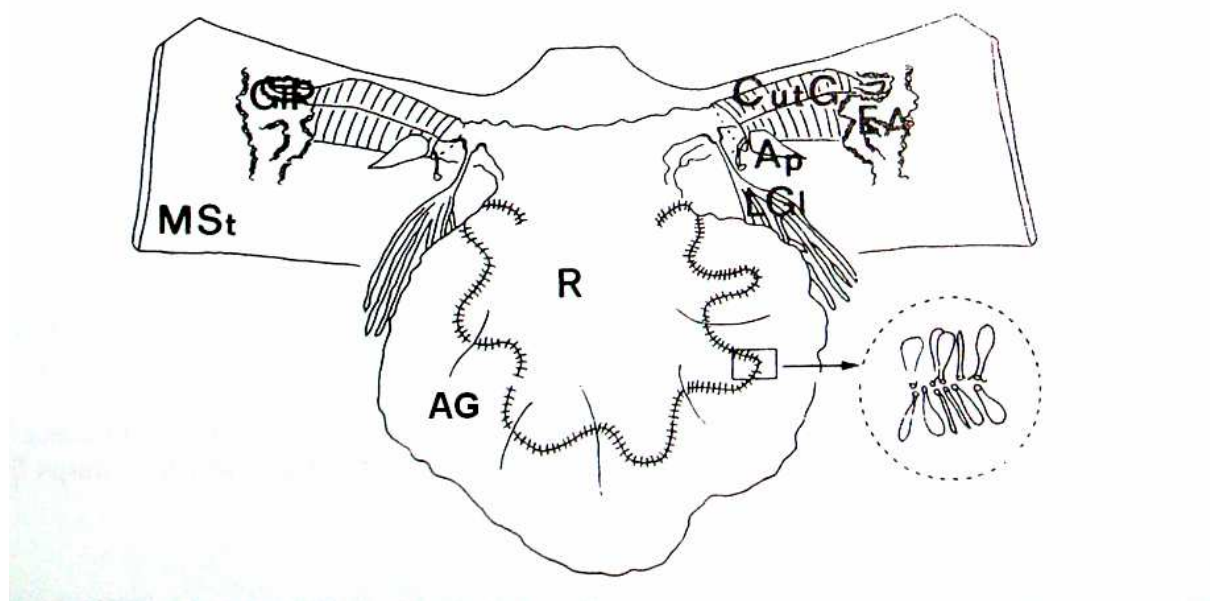


Fig. 6. Median reservoir (R) with a wavy accessory gland (AG) in *Lincus* sp. (after Nagnan *et al.* 1994).

In pentatomid MTG secretion, two phases were reported – clear fluid containing unpolar molecules, such as alkanes and long chain carbohydrates, and yellow fluid, with significant proportion of polar molecules, such as aldehydes (Gilby and Waterhouse 1965, MacLeod 1975). Its function, if any, remains unknown.

In *Nezara viridula*, cosmopolitan bug with scent gland chemistry characteristic for Pentatomidae, tridecane, *trans*-2-decenal, 4-oxo-*trans*-2-hexenal and minor components of *trans*-2-decenyl acetate, *trans*-2-hexenyl acetate, dodecan and *trans*-2-hexenal were present in MTG secretion (Waterhouse *et al.* 1961, Gilby and Waterhouse 1965). However, secretion of bugs from various populations differed dramatically – for example, American population did not secrete any *trans*-2-decenal (found in secretion of Australian and Hawaiian population), having 33% of the secretion composed of *trans*-2-heptenal instead (Gilby and Waterhouse 1965, 1967).

Comparison of many MTG secretions revealed uniformity of pentatomid MTG secretion as it is rarely composed of other chemicals than C₁₁-C₁₃ (sometimes C₁₅) alkanes, C₆, C₈ and C₁₀ unsaturated aldehydes and oxo-aldehydes, with minor amount of alkenyl acetates (Park 1962, Everton *et al.* 1974, Smith 1974, MacLeod 1975, Kou 1989, Nagnan *et al.* 1994, Aldrich 1997a, Stránský 1998, Krall 1999, Durak 2008).

Pentatomid MTG secretion is mostly defensive, with sophisticated mechanism of functioning. Unpolar alkanes are not toxic themselves, however, they disrupt the lipidic layer of the cuticle, enabling toxins to penetrate the cuticle and strengthening effectiveness of defensive secretion against arthropod predators (Remold 1963). Of various alkanes, tridecane showed to be the most effective in disrupting the lipidic layer, followed by undecane and dodecane (Gunawardena 1991). As these three chemicals are by far the most abundant alkanes in heteropteran secretion, this mechanism is obviously widely used in defence of Heteroptera.

The function of attractant for *N. viridula* was noted in tridecane (Lockwood 1986); however, as this alkane is also excreted by male dorsoabdominal glands (Aldrich *et al.* 1978), the attractive function of MTG is very uncertain in this case, being an insignificant side effect of the defensive secretion instead. On the other hand, MTG secretion of *Podisus* genus contains α -terpineol in addition to characteristic pentatomid chemicals (e.g. tridecane, *trans*-2-decenal, 4-oxo-*trans*-2-hexenal); therefore, MTG probably contributes to intraspecific communication in *Podisus* (Aldrich 1997a).

Secretion of MTG of sequestering Pentatomidae is unique among all Heteroptera and even insects. Secretion of *Murgantia histrionica* contains more than 85% of *trans*-2,6-octadienedial, while secretion of *Eurydema ventrale* is even more bizarre, being composed of *trans*-2-*trans*-6-octadienedial, 2,6-octadiene-1,8-diol diacetate a benzylalcohol. On the other hand, MTG secretion of *E. oleraceum* is quite usual among Heteroptera, with *trans*-2-octenal, pentadecane, *trans*-2-octenyl acetate and small quantity of α -pinene. As there are some indications that secretions of these species are sexually dimorphic, pheromonal function can be presumed for the blends (Aldrich 1996).

3.3.1.2 Tessaratomidae

This pentatomoid family has probably the most aggressive MTG secretion seen in Heteroptera. For example, the secretion of *TessarATOMA pappilosa*, which can be sprayed to the distance of 15-25 cm (Muir 1907), causes severe burns on human skin and even temporary blindness when sprayed into one's eyes (Falkenstein 1931). Secretion of *Musgraveia sulciventris* had similar effect (Cant 1996). However, the composition of the secretion of their MTG is surprisingly similar to that of Pentatomidae. *TessarATOMA aethiops* produces a

secretion composed of nearly an half of tridecane with support of *trans*-2-octenyl acetate, *trans*-2-octenal, *trans*-2-hexenal and *trans*-4-oxo-2-hexenal (Baggini 1966). This blend was highly lethal to ants (Janaiah 1979) and strong juvenoid-like effects of secretion of *Tessarotoma javanica* were also noted on late instar larvae of *Dysdercus* genus (Ashok *et al.* 1978, Rao *et al.* 1980). Effectiveness of defence against possible vertebrate predators needs not to be reiterated.

3.3.1.3 Scutelleridae

MTG secretion of Scutelleridae is very similar to that of Pentatomidae (Aldrich 1988), perhaps with minor occurrence of alkanes.

Small MTG (only 0.01% of body weight) of *Tectocoris diophthalmus* excrete mixture of *trans*-2-hexenal with *trans*-2-hexenyl and *trans*-2-octenyl acetates (Staddon 1987) while species with larger MTG, *Hotea gambiae*, excretes mixture of *trans*-2-hexenal with *trans*-2-octenal, 4-oxo-*trans*-2-hexenal, *trans*-2-decenal, limonene and β -pinene (Hamilton *et al.* 1985).

Pachycoris stalii secretes tridecane, *trans*-2-hexenal, *trans*-4-oxo-2-hexenal, *trans*-2-hexenyl acetate and dodecane. However, lateral reservoirs are filled with pure *trans*-2-hexenal in females and 99% tridecane in males, with the rest of the chemicals located in median reservoir (Williams 2001). These results disagree with established conception that aldehydes can be synthesised only in median reservoir (Games and Staddon 1973, Aldrich 1978).

3.3.1.4 Plataspidae

Squash bugs are one of the less investigated families among Heteroptera, yet their MTG secretion can be characterised as close to pentatomid (Aldrich 1988), composed of alkanes and unsaturated carbohydrates (Baggini 1966, Kitamura 1984). Unfortunately, origin of the volatiles is not specified in these works.

3.3.1.5 Cydnidae

MTG of burrowing bugs are sexually monomorphic, with composition of secretion matching that of Pentatomidae (Aldrich 1988)- for example, in secretion of various glandular

origin of *Macrostycus* sp., 4-oxo-*trans*-2-hexenal, tridecane, *trans*-2-decenyl acetate, dodecane and *trans*-2-octenyl acetate were identified (Baggini 1966).

An exception in Cydnidae is *Sehirus cinctus cinctus*, a species feeding on mint whose MTG secretion composed almost entirely of monoterpenoids- α - and β -pinene (about 90% of secretion), β -myrcene, limonene and α -terpinolene, effective against lizard (*Anolis carolinensis*) and bird (*Charadrius vociferus*, *Sturnus vulgaris*) predators (Krall 1997). The author also suggests that these chemicals, which do not occur in mint, may be synthesised by modifying those obtained from host plant.

3.3.2 Coreoidea

3.3.2.1 Coreidae

Secretion of Coreidae usually consists of saturated carbohydrates. Eight species of Coreidae investigated by Waterhouse and Gilby (1964) all secreted hexanal and hexyl acetate- about 90% of total amount, with supplement of 10% of hexanol and acetic acid. The "ester odour" of Coreidae also differed from the characteristic heteropteran smell. It must be mentioned that the composition of the secretion varied greatly (by 50% in some cases!), being affected by sex, treatment, season (with less ester and alcohol in autumn) etc. (Waterhouse and Gilby 1964). Similar results appeared in other coreid species, with a minor fraction of butyric acid and various C₈-C₁₂ even numbered saturated esters, with exception of heptyl acetate (McCulough 1971, 1973, 1974, 1974b, Kitamura 1984, Steinbauer and Bauer 1995, Blatt 1998, Prudic 2008).

Unlike larval secretion, consisting of unsaturated aldehydes and oxo-aldehydes, the secretion of adults, based on MTG, does not contain characteristic defensive chemicals; the secretion was also completely ineffective against *Stagmomantis californica* (Mantodea: Mantidae) predator (Prudic 2008). Its function is defensive, though, as it is active in alarm signalisation. However, the effect of the alarm pheromone in Coreidae is stage-specific since the adults' reaction to larval secretion is much weaker than that to their own and vice versa (Blatt 1998, Prudic 2008). When the alarm reaction to pure chemicals was tested, adults of *Thasus neocalifornicus* reacted to hexanal and hexyl acetate while hexanol was much less effective (Prudic 2008).

Coreid MTG pheromones may also work in hibernation behaviour as their function of alarm pheromone seems to shift to an attractant during autumn (Blatt 1998). On the other

hand, coreid MTG secretion seems to lack any epigamic function, which is generally provided by male dorsal and ventral abdominal glands with miscellaneous composition of the secretion (Aldrich 1976, 1988, 1993).

3.3.2.2 Hyocephalidae

The MTG secretion of *Hyocephalus* sp. contains only two components, both also common in Coreidae – 98% of hexanal with 2% of hexanol (Waterhouse and Gilby 1964). As the median reservoir of Hyocephalidae lacks any pigment, preventing autotoxication (Waterhouse and Gilby 1964), Hyocephalidae either possess unique protective mechanisms or their secretion is not aggressive enough to penetrate the wall of the reservoir.

3.3.2.3 Rhopalidae

Family Rhopalidae consists of two subfamilies: Serinethinae and Rhopalinae. Serinethinae, as one of the few groups of Heteroptera, have fully dysfunctional MTG (Carayon 1971). Instead, their defence is based on cyanolipides, sequestered from Sapindaceae plants. Furthermore, species of *Jadera* need to feed on Sapindaceae to produce lactone, 4-methyl-2(5H)-furanone, which serves as an attractant pheromone and enables the bugs to colonise host plants in great numbers (Aldrich 1990a).

On the other hand, members of the subfamily Rhopalinae have small but functional MTG (Aldrich 1979), which, as reported from *Niesthrea louisianica*, the only bug of this family whose MTG secretion have been analysed, contain monoterpenes – thymol, limonene, β -pinene and terpinolene in this case (Aldrich 1990b).

3.3.2.4 Alydidae

Pheromonal function of male secretion of many alydid species is often reflected by hypertrophied glandular tubules or lateral reservoirs of male MTG, modified for synthesis of esters (Aldrich 1993). In *Riptortus clavatus*, *trans*-2-hexenyl *trans*-2-hexenoate and *trans*-2-hexenyl *cis*-3-hexenoate work as epigamic and attractant pheromones in mixture with myristyl isobutyrate – although the natural ratio of the blend is 5:1:1, both hexenoates were almost equally effective in the mixture with miristyl isobutyrate, showing interchangeability of the pheromone components (Leal 1995, Endo 2005). Other alydid species, *Riptortus*

serripes and *Melanacanthus scutellaris*, have slightly different pheromone compounds – *trans*-2-hexenyl *cis*-3-hexenoate and *trans*-2-hexenyl *trans*-2-octenoate in *R. serripes* and *trans*-2-hexenyl butyrate in *M. scutellaris*; on the other hand, some species (e.g. *Alydus eurinus* and *Megalotomus quinquespinosus*) do not have sexually dimorphic MTG, suggesting their minor role in sexually attractive secretion (Aldrich 1993).

As secretions of both sexes generally contain significant fractions of *trans*-2-hexenal and *trans*-2-octenal, defensive function of MTG secretion is also likely in Alydidae (Aldrich 1993).

3.3.3 Pyrrhocoroidea

3.3.3.1 Pyrrhocoridae

According to results from investigation of four *Dysdercus* species and *Pyrrhocoris apterus*, *trans*-2-hexenal and *trans*-2-octenal are characteristic for pyrrhocorid MTG secretion, usually composing together about 90% of the secretion. In addition, small amounts of tridecane and various C₆ and C₈ carbohydrates are frequent in the secretions. Occurrence of linalool is also one of the very few characteristics for the *Dysdercus* spp. secretion (Daroogheh and Olagbemiro 1982, Farine *et al.* 1993). The pyrrhocorid secretion works simultaneously as a contact poison on ants and as an alarm pheromone (Farine 1988).

An exception in Pyrrhocoridae is *D. fasciatus* whose MTG secretion is expressively sexually dimorphic, with significant amount of 4-oxo-*trans*-2-hexenal in the secretion (50% in male one, 25% in female one) and 13% of esters (*trans*-2-hexenyl acetate and *trans*-2-octenyl acetate) in female secretion (Farine *et al.* 1993), probably of an epigamic function.

3.3.4 Lygaeoidea

3.3.4.1 Lygaeidae

As the seed bugs usually obtain defensive chemicals from food (especially from Asclepiadaceae, "milkweed"), their MTG secretion is often used in intraspecific communication (Aldrich 1988). In Lygaeidae it is males who produce attractive pheromones, *trans*-2-alkenyl and *trans*-2,n-alkadienyl acetates in this case (Games and Staddon 1973,

Aldrich 1999). As in Miridae, the composition of the pheromone is usually species-specific, with characteristic proportion of the chemicals, yet sometimes mistaken by related species (Aldrich 1997b) or even mirids (Zhang and Aldrich 2003a). In addition, C₆ and C₈ trans-2-alkenals and *trans*-2,4-alkadienals occur in both sexes (Staddon 1985, Aldrich 1997b), probably partly effective in defence against predators.

Pheromones are crucial in colonisation of new host plants in Lygaeidae as they serve as long-range attractant pheromones for adults of both sexes as well as larvae. Males of *Oncopeltus fasciatus*, who are also the main colonisators, excrete pheromones when finding a host plant, attracting more individuals, who, if males, also excrete the pheromone, strengthening the attraction effect (Aldrich 1999).

3.3.4.2 Oxycarenidae

MTG in Oxycarenidae are quite large, of about 1% of body weight, with large lateral reservoirs. In *Oxycarenus hyalinipennis*, the MTG secretion of freshly moulted adults composes of characteristic heteropteran C₆ and C₈ chemicals. However, in three days from the moult, its lateral reservoirs fill with mono- and sesquiterpenoids (α -farnesene with α -pinene, limonene, cineole and various unidentified terpenoids), composing 80% of the whole secretion in the end. Remaining 20% of the secretion, in which *trans*-2-octenal and *trans*-2-octenyl acetate are most abundant, is stored in median reservoir (Olagbemiro and Staddon 1983, Knight 1984).

This phenomenon, reported only in this species but probably much more frequent, is probably caused by gradual obtaining of terpenoids from the host plant (cotton and other Malvaceae) and their storage in MTG. As α -farnesene and limonene serve as ant alarm pheromones along with other terpenoids (Blum 1985), the function of MTG secretion as a mimic of these pheromones is likely in Oxycarenidae.

3.3.4.3 Geocoridae

In secretion of various glandular origin of undisturbed individuals of *Geocoris punctipes*, tridecane was the most abundant chemical, with minor fractions of *trans*-2-hexenyl acetate, *trans*-2-octenal and C₁₁-C₁₇ alkanes. In addition, female secretion contained much more *trans*-2-octenal and a significant amount of *trans*-2-octenyl acetate. This chemical and the whole

female secretion had attractive effect on males, proving sexual function of volatiles of *G. punctipes* (Marques *et al.* 2000).

3.3.4.4 Blissidae

Although these bugs are important pests in some regions, their chemical ecology is poorly understood. The sexually monomorphic secretion of various glandular origin of *Macchiademus diplopterus* consists of tridecane, *trans*-2-octenal and *trans*-2-hexenal (together 90% of the secretion) with minor components of *trans*-2-octenyl acetate, *trans*-2-hexenyl acetate and 4-oxo-*trans*-2-octenal (Oliver *et al.* 1996). The function of the secretion seems to be primarily defensive as the aldehydes are frequently used in defence in other families, yet pheromonal function should be investigated as numerous aggregations occur in some Blissidae (Kerr 1966).

4 FUNCTIONS

4.1 DEFENCE:

Carayon (1971) defined two groups of defensive chemicals: liquid poisons, applied by contact or spraying, and vapor poisons, mostly affecting respiratory system. Although this classification is relevant, because both mechanisms are present in heteropteran defence (e.g. Muir 1907, Hamilton 1985, Farine 1988), more exact classification was given by Brower (1984), who distinguished two new types of chemicals with respect to their function in antipredatory defence: type I, including toxic chemicals themselves, and type II, volatile, often repulsive chemicals signalling the toxicity of the bug. The type II chemicals are important on several levels- they can express the bug's unpalatability at long-range, protecting the bug from being attacked; they can be distasteful, causing the predator to drop the bug without killing it, and they can possibly enhance avoidance learning of predators.

So-called warning odour is only one way of expressing unpalatability (aposematism); mechanisms of this signalisation, often multimodal (including visual, chemical and acoustic signals), are a highly complex issue (e.g. Ruxton *et al.* 2004) and are not discussed in this work. It should be noted that aposematic species generally have smaller MTG than cryptic

ones (Staddon 1987) – the warning coloration possibly replaces semiochemicals in signaling unpalatability of the bug to visually orientating predators, especially birds and lizards.

The control of the defensive excretion is strikingly sophisticated. During detailed observation on *Cosmopepla bimaculata* (Pentatomidae), the secretion was excreted only on the side of body where the bug was disturbed. Also, the amount of the secretion corresponded to the intensity of disturbance. A drop of the secretion remained on evaporatorium and was pulled back into the gland when the threat passed (Krall 1999). Also, when a threat is close to the bug (*Coptosoma* sp. in this case), it can aim its spray to it (Remold 1963).

4.1.1 Vertebrates:

The chemicals used in defence against vertebrates are usually the same as that used against invertebrates- for example, tessaratomid secretion with characteristic anti-arthropod alkane and aldehyde composition causes severe damage of human skin (Falkenstein 1931). However, the mechanism of their functioning is different- as heteropteran defensive secretions are often lethal to other arthropods (e.g. Remold 1963, Prudic 2008), the effects on vertebrates are much weaker, causing nausea in worst cases (Staples 2002), being rather obnoxious to the predator, possibly enhancing avoidance learning.

Birds are the most frequent subjects in tests of heteropteran defence against predators. The unpalatability and/or toxicity of the secretion usually reflects clearly in bird's behaviour. When attacking the first bug offered, naive bird often dropped the bugs out of its bill, shook its head, wiped its bill, or even vomited, showing the bugs' unpalatability. After one or several more trials (depending on the predator species), the birds usually ignored the bugs but still consumed control insects (Krall 1997, 1999, Staples 2002, Exnerová *et al.* 2007, Svádová *et al.* 2009). As seen in comparison of wild-caught and naive birds, the birds remember unpalatability of the bug and its signals for a long time (Exnerová *et al.* 2007).

The reaction of birds to the unpalatable bugs differ greatly in various species. For example, when tested on pentatomid *Cosmopepla bimaculata*, starling (*Sturnus vulgaris*) and killdeer (*Charadrius vociferus*) both did not kill more than one bug while robin (*Turdus migratorius*) demonstrated only mild aversion (Krall 1999). Thus, the reactions of the birds depend both on

the bird's species and bug's species. Species-specific reaction of bird predators are discussed in detail by Exnerová *et al.* (2003, 2006, 2007).

In tests on aposematic *C. bimaculata* (with alkane and aldehyde-based defence) and a lizard predator *Anolis carolinensis*, each anolis consumed the first bug offered, then became hesitant in two or three bugs, eventually ingoring the fourth; alonis' aversive behaviour included spitting the bug out, backing away from the bug, wiping the head and mouth upon substrate, excessive mouthing before swallowing, and ignoring the bugs upon their introduction (Krall 1999). After few days, anoles refused to attack the bug either immediately or after consumption of the first bug (Krall 1999). Similar, even more striking results were reported in cryptic cydnid *Sehirus cinctus cinctus* (with terpenoid-based defence) and the same predator (Krall 1997).

A few taste tests on humans provided some information on the effects on vertebrate predators. For example, *Piezodorus teretipes* (Pentatomidae) tasted "unpleasantly peppery and oily," which was caused by *trans*-2-hexenal-based secretion (Gilchrist 1966). Another pentatomid bug, *Cosmopepla bimaculata*, with the secretion composed of alkanes with aldehydes and esters, caused "instantaneous burning sensation and chemical taste," which lasted for about 20 minutes and was followed by slight numbness of the tongue, lasting 1-2 hours (Krall 1999).

4.1.2 Arthropods:

Ants are an important threat especially to larvae and adults of small species. Undecane (Regnier 1968), *trans*-2-hexenal, hexanal, hexanol, hexanoic acid, 2-butyl-2-octenal, β -pinene, limonene and farnesenes are ant alarm or trail pheromones present in MTG secretion (Blum 1985, Aldrich 1988). However, this phenomenon has not been sufficiently investigated experimentally.

As alkanes help pentatomid secretion to penetrate the cuticle, it is no surprise that it showed to be both toxic and repellent against ants (Remold 1963, Surender 1990). However, the secretions of the other families proved to be effective as well. Secretion of *Dysdercus cingulatus* (Pyrrhocoridae) acts as a contact poison to ants (Farine 1988), being based on *trans*-2-hexenal (88%) with minor ingredients of *trans*-2-hexenyl acetate, *trans*-2-octenal and linalool (Farine *et al.* 1993).

When tested on other arthropods, pure *trans*-2-hexenal did not have any effect on *Stagmomantis californica* (Mantodea: Mantidae); however, mixture of *trans*-2-hexenal and 4-oxo-*trans*-2-hexenal and pure 4-oxo-*trans*-2-hexenal had a lethal effect on these predators (Prudic 2008). Also, the secretion of *Piezodorus teretipes* (Pentatomidae), dominated by *trans*-2-hexenal, repelled *Leiurus quinquestriatus* (Arachnida: Scorpiones) and *Galeodes granti* (Arachnida: Solifugae) predators (Gilchrist 1966). Blend of C₆-C₁₀ aldehydes had toxic effect on larvae of *Calliphora* sp. (Diptera) (Remold 1963). As *trans*-2-alkenals occur more frequently in larval secretion than in adults', it is likely that they primarily function in defence against small arthropods.

The significant difference of effectiveness between "almost pure" and pure *trans*-2-hexenal is striking in defence against arthropod predators. This phenomenon awaits explanation, yet suggestion can be made that *trans*-2-hexenal itself may be unable to penetrate the strong cuticle of a predator, requiring other chemicals (such as oxo-aldehydes and alkanes) to disrupt the cuticle first. On the other hand, the cuticle of a dipteran larva may not be resistant enough to prevent the aldehydes themselves to penetrate it.

4.2 PHEROMONES

4.2.1 Alarm function:

Alarm pheromones are developed very often in Heteroptera, especially in gregarious species (Blatt 1998). They usually cause the bugs to disperse from the source of the signal, with intensity correlating with concentration of the pheromone (Levinson and Bar Ilan 1971).

Many components of alarm pheromones are also effective in defence against predators-*trans*-2-hexenal and *trans*-2-octenal are the most evident examples of this double function (Levinson and Bar Ilan 1971, Ishiwatari 1974, 1976, Farine 1988, Blum 1996, Blatt 1998, Prudic 2008).

In *Cimex lectularius*, *trans*-2-hexenal was shown to affect the bugs immediately as an alarm pheromone while *trans*-2-octenal was slower (because of poorer evaporation), but more effective, showing bimodality of the signalisation (Levinson *et al.* 1974).

As MTG of many groups (Coreidae, for example) secrete chemicals different from the larval ones, they also have developed stage-specific system of warning. Due to different

predators and defensive behaviour of larvae and adults, the alarm pheromones have significant effects only on particular stage- larval alarm pheromones do not work on adults and vice versa (Blatt 1998, Prudic 2008). Esters are generally present in adult alarm pheromones, often supported by various, primarily defensive chemicals (MacLeod 1975, Kou 1989, Blatt 1998, Krall 1999, Prudic 2008).

4.2.2 Non-epigamic attraction:

Attractant pheromones are often mistaken for epigamic pheromones, especially because their secretion is often sexually dimorphic. These functions are often connected indeed, but have some major differences- for example, larvae are usually attracted to attractive pheromones as well as adults; attractant pheromones also do not necessarily trigger mating behaviour, as seen in some epigamic pheromones (Millar 2005).

As in all pheromonal functions, esters are the most important mediators of attractive (both non-epigamic and epigamic) communication. Their original position of highly volatile precursors of defensive chemicals was probably crucial for evolution of pheromonal function of MTG.

However, alarm pheromones have been repeatedly proved to serve as attractants as well- high concentration of a pheromone triggered dispersal behaviour while lower concentration were attractive to the bugs instead. This phenomenon has been reported in various families of Heteroptera, e.g. Cimicidae (Levinson and Bar Ilan 1971), Reduviidae- Triatominae (Rossiter and Staddon 1983), Pentatomidae (Ishiwatari 1974) and Pyrrhocoridae (Farine 1993).

Attractive behaviour is used in defence of aposematic species, such as many Pyrrhocoridae, and in advertising a food source (Triatominae) or a hideout (Cimicidae). Moreover, some functions have been modified to serve in migration and hibernation behaviour.

As reported in systematic part, Lygaeidae use males as colonisators who, if successful, signalize proper conditions by pheromones. This mechanism is based on long-range effect of attractive pheromones and as such they attract adults and larvae of both sexes (Aldrich *et al.* 1997b, 1999). This phenomenon is known in Lygaeidae but probably occurs in many other groups such as pyrrhocorid *Dysdercus* spp. and mirid *Harporocera thoracica*, where one sex is always capable of flight, lives longer than other sex, and migrates to new hosts (Aldrich 1988, 1999).

Functioning of hibernation pheromones is similar to that of migration as they are basically long-range attractant pheromones effective on both sexes. However, the pheromones are usually not specific to hibernation; instead, the reaction to pheromones of various functions shifts as the bugs are about to hibernate (McBrien 1999). For example, individuals of *Leptoglossus occidentalis* (Coreidae) collected in autumn did not disperse when exposed to the alarm pheromone, being rather attracted to it instead (Blatt 1998). Not surprisingly, aggregation pheromones are effective in hibernation behaviour as well (Toyama 2006).

4.2.3 Epigamic function:

As in other insect orders, pheromones play a crucial role in mating of true bugs. In most terrestrial Heteroptera males excrete sexual pheromones, with significant exception of Miridae (McBrien 1999). Attractiveness of males rather than females corresponds with exposure to parasitoids (Aldrich 1988)- if a female attracted parasitoids, her eggs could be parasitised as well. Field tests support this theory, since males of *Nezara viridula* are more parasitised than females (Salles 1991).

Sexual pheromones, as defined, trigger mating behaviour, thereby they differ from non-epigamic attractant pheromones. This fact could be seen in field tests- mirid males were even observed trying to copulate with pheromone lures (Millar 2005).

The epigamic function of MTG is of minor importance, with respect to occurrence of various sexually specific glands in Heteroptera (Staddon 1979). Moreover, when dorsoabdominal glands persist in adults, they are often connected with sexual functions (Aldrich 1988). However, in groups where defensive function of MTG has been reduced (e.g. Lygaeidae and Miridae), MTG secretion has acquired a significant role in pheromonal signalisation (Aldrich 1988).

Unlike the secretion of dorsoabdominal and other glands, sexually active secretion of MTG is quite uniform in Heteroptera. It usually consists of even-numbered esters of C₄-C₁₀ saturated and unsaturated alcohols and C₂- C₆ acids. Because of this, the pheromone blends cannot be fully species-specific, causing misunderstandings in communication (Zhang and Aldrich 2003a). Characteristic pheromone blends for individual families, as well as specifics of their function are discussed sufficiently in the systematic part.

On the other hand, secretion of mirid MTG may effectively disrupt sexual communication. The function of this secretion may be defensive, such as when attacked female inhibits attractant secretion in other females (Groot *et al.* 2001), or purely competitive, such as when males inhibit pheromone receptors of other males (Zhang and Aldrich 2003b).

4.3 OTHER FUNCTIONS

4.3.1 Antimicrobial and fungistatic functions:

Of chemicals isolated from MTG secretion, *trans*-2-heptenal was the most effective in killing fungal spores. More interestingly, frequently occurring chemicals – hexanol, *trans*-2-hexenal, *trans*-2-octenal, *trans*-2-hexenyl acetate and undecane proved to be quite effective as well, hexyl acetate were mediumly effective and tridecane, pentadecane, octyl acetate, butyl butyrate and *trans*-2-hexenyl butyrate had poor effect on the spores; dodecane was not effective at all (Surender 1987, Ravinder 1992). As the most effective antifungal agent occurs rarely in Heteroptera and undecane as the most effective alkane is much less abundant than tridecane in the secretion, antifungal function probably plays a very small role in scent gland biology.

In similar research, *trans*-2-hexenyl acetate, *trans*-2-hexenal a *trans*-2-heptenal had lethal effect on both gram-positive and gram-negative bacterial cultures, *trans*-2-octenal had effect only on gram negative bacteria and other chemicals, such as C₁₁-C₁₃ alkanes and *trans*-2-hexenyl butyrate were ineffective on bacteria; octyl acetate even stimulated growth of the cultures (Surender 1988). Antimicrobial function also seems to be of lesser importance in terrestrial Heteroptera.

As antimicrobial function is one of the most important function of MTG secretion in water bugs (Maschwitz 1971, Staddon 1979), its significance in terrestrial Heteroptera is only secondary.

4.3.2 Kairomonal function:

As a side effect of pheromone-baited traps, dipteran and hymenopteran parasitoids of Heteroptera are sometimes attracted to the pheromones, showing their kairomonal effect.

Lygaeid pheromones, conservative in composition, proved to be especially attractive to the parasitoid *Leucostoma gravipes* (Diptera: Tachinidae) (Aldrich 1999).

Parasitoid specialisation is well reflected in fact that some parasitoids are even more sensitive to pheromone quality than the bugs themselves- for example, *Podisus maculiventris* (Pentatomidae) was attracted to synthetic isomere of its pheromone while two of four tachinid parasitoids did not respond at all (Aldrich 1984).

Some defensive chemicals may have kairomonal function as well – for example, *trans*-2-decenal, a toxin from defensive secretion of *Nezara viridula*, attracted parasitoid *Trissolcus basalis* (Hymenoptera: Scelionidae) (Mattiacci 1993).

Components of defensive MTG secretion of Miridae also showed to be attractive to females of kleptoparasitic flies (Diptera: Chloropidae, Milichiidae). The benefit of the attraction for a fly is evident- when the bug is attacked, it might be killed, giving an opportunity of feeding to the scavenging fly (Zhang and Aldrich 2004).

5 SEQUESTRATION:

The most frequently used context of sequestration is that "some phytophages, unscathed, imbue their bodies with foreign 'toxins' as basis of chemical defence against foes" (Duffey 1980). However, sequestered chemicals often function in an intraspecific communication, mostly in the context of colonisation or epigamic behaviour. The term "sequestration" is also used for obtaining various substances functioning in metabolism such as ions, amino acids, sugars, lipids etc. (Duffey 1980), which I would prefer to call sequestration *sensu lato*.

Duffey (1980) also reports a phenomenon of so-called Potentiator Sequestration. This term characterizes a situation in which a sequestered chemical serves as an initiator or a precursor of biosynthetic reactions. A typical example is a diet-dependent synthesis of lactone in *Jareda* genus (Aldrich 1990a). However, in most heteropteran researches this phenomenon is missed out.

In Heteroptera, sequestration mostly occurs in families Miridae, Lygaeidae, Rhopalidae and Pentatomidae. The evolution of the sequestration is linked either with a reduction of MTG (as seen in Serinethinae, and in minor degree in all sequestering species) or with a change of their function (such as the pheromonal function in Lygaeidae (Aldrich 1988)).

Most common defensive chemicals sequestered by Heteroptera are cyanolipids (Aldrich 1990a), glycosides (Aldrich 1990b, Aliabadi 2002) and cardiac glycosides (e.g. Scudder and Duffey 1972, Evans 1986, Aldrich 1999), and pyrrolizidine alkaloids (McLain 1984, Aldrich 1999, Klitzke 2000). Types of sequestered chemicals are often taxonomically specific both in sequestrators (e.g. sequestration of cardiac glycosides characteristic for subfamily Lygaeinae (Aldrich 1988)) and in host plants (e.g. *Senecio* spp. as a source plant of most sequestered pyrrolizidine alkaloids (Duffey 1980, McLain 1984, Aldrich 1999, Klitzke 2000)).

Sequestered defensive chemicals, as reported in *Oncopeltus fasciatus*, are stored mostly a vacuolated epidermal cell layer, located in integument of thorax and abdomen (fig. 7), with minor fraction in MTG and haemolymph (Duffey and Scudder 1974). External pressure causes a rupture of the epidermal layer in restricted areas and a passive excretion of a toxic fluid onto the surface of the bug (Scudder and Meredith 1982, Scudder *et al.* 1986). However, the mechanisms of storage are much less known in other bugs.

Semiochemistry of sequestering bugs is sometimes based on excretion of alkylmethoxypyrazines (Aldrich 1996, 1997b, Aliabadi 2002). These chemicals have not been proven to be sequestered; instead, they seem to carry out the function of a secondary warning odour as MTG are often reduced in sequestering Heteroptera (Aldrich 1988) and alkylmethoxypyrazines are common defensive chemicals in various insect orders (Moore 1990). These chemicals, occurring in many insect orders, have not been proven to be sequestered, probably acquiring their function rather due to their high effectivity in deterring vertebrate predators (Moore 1990).

Moreover, *Murgantia histrionica* and *Eurydema* spp. (Pentatomidae) possess unique excretory glands, allowing them to excrete a fluid containing alkylmethoxypyrazines from prothorax (fig. 8); the mechanism of this excretion is unknown, possibly connected with the tracheal system as bubbles occur in the secretion (Aldrich 1996).

As shown in *Coturnix coturnix coturnix* predator, cardiac glycosides stored by *Caenocoris neri* (Lygaeidae) are highly effective against bird predators as the bugs fed cardiac glycoside-rich seeds were much more likely to survive the quail's attack (Evans 1986). Similar results were reported in other chemicals. *Sturnus vulgaris* and *Passer domesticus* consumed only 5% of individuals of *Murgantia histrionica*, a species sequestering glycosides and excreting pyrazine-rich fluid from prothorax (Aliabadi 2002). Also, *Neacoryphus bicrucis* (Lygaeidae) and *Lopidea instabile* (Miridae), both sequestering pyrrolizidine alkaloids, were distasteful to *Anolis carolinensis* (McLain 1974).

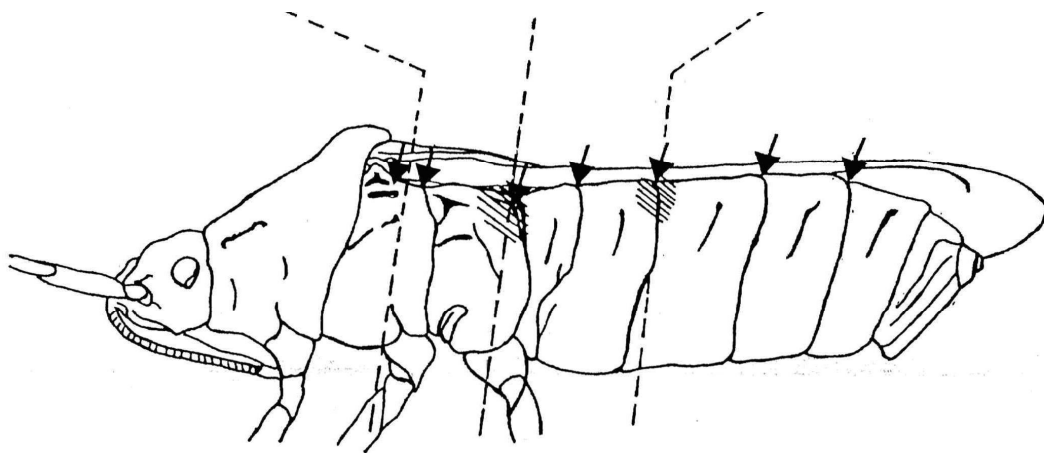


Fig. 7. A diagram of *O. Fasciatus* adult indicating points at which glycoside-rich fluid droplets form (solid arrows) as well as location and extent of glycoside compartment (stripped areas) (after Scudder and Meredith 1982).

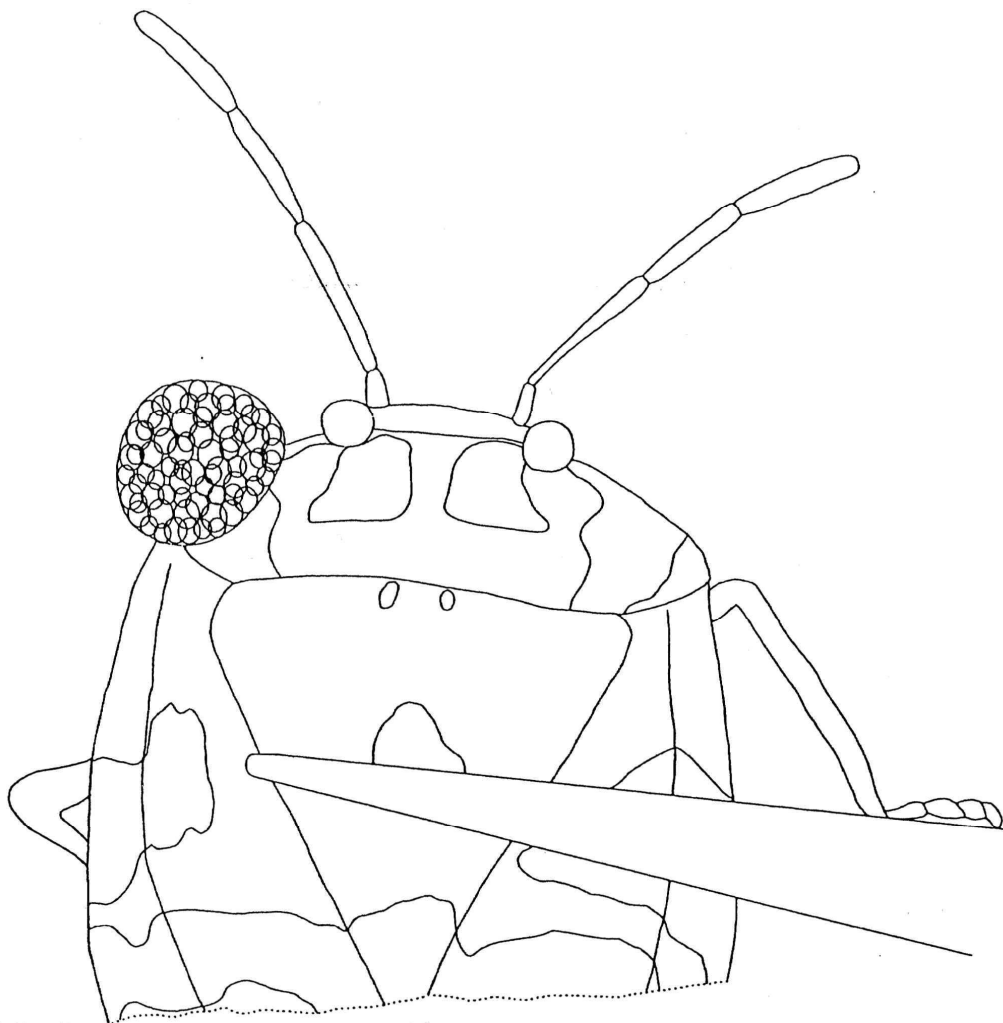


Fig. 8. Dorsal view of a *Murgantia histrionica* adult showing the position of fluid froth emitted from the left prothoracic margin when the bug was squeezed with foreceps (Aldrich 1996).

Effects of sequestered chemicals on arthropod predators have been studied extensively. When fed seeds containing cardiac glycosides, *Oncopeltus fasciatus* was toxic to *Tenodera aridifolia* (Mantodea: Mantidae), which even refused to eat the bugs after several trials (Berenbaum and Miliczky 1984). In studies of Lepidoptera, pyrrolizidine alkaloids have shown to be effective against spider predator *Nephila clavipes*, causing the spider to cut out a field-caught ithomiine butterfly from its net but eating a freshly emerged one (Brown 1984). Also, DHPB phorbol ester in *Pachycoris klugii* (Scutelleridae), one of the less common chemicals sequestered, is highly toxic to both invertebrates and vertebrates (Wink *et al.* 2000). Thus, sequestration seems to be a potent mechanism of defence against both vertebrate and arthropod predators.

Terpenoids obtained from host plants are often present in MTG secretion. This trend is especially frequent in secretion of bugs feeding on Malvaceae, e.g. Lygaeidae, Alydidae, Pyrrhocoridae and Scutelleridae (Gough 1985). However, the terpenoids found in heteropteran exocrine secretion often differ from those found in host plants (Olagbemi and Staddon 1983, Gough 1985, Aldrich 1990b, Krall 1997), reflecting high complexity of their synthesis.

These chemicals, often involved in intraspecific communication (e.g. Aldrich 1997a), may also work in defence as their toxicity has been proved on beetles (Phillips *et al.* 1995).

6 CONCLUSIONS:

Alkanes, aldehydes, esters, alcohols and terpenoids are the most common chemicals found in MTG secretion. Less common chemicals are lactones, ketones, alkenes and miscellaneous compounds (Farine 1993). Proteins seem to occur frequently in MTG reservoirs, possibly helping in secretion metabolism (Nagnan *et al.* 1994); however, they still await chemical and functional analysis.

Steroids have been also found in MTG secretion (Durak and Kalender 2007a, 2007b, 2009); however, these findings are so much inconsistent with findings of other authors that they should be further inspected.

C₆, C₈ and C₁₀ aldehydes, alcohols and esters are much more abundant in heteropteran secretion than other chemicals of these types, reflecting connected syntheses of these chemicals (Aldrich 1978). These chemicals also mostly occur as *trans* isomers (Staddon

1979); as *cis* isomers are usually very unstable, they are rarely found in more than trace amounts in MTG secretion, with exceptions found in Miridae (Staples 2002) and Alydidae (Leal 1995).

Alkanes and aldehydes are commonly used in defence against all kinds of predators, however, they have acquired pheromonal function in some cases. Esters have proven to generally serve as MTG pheromones of various functions. Significance of alcohols in the MTG secretion is less clear, probably effective as long-range allomones, especially in Coreidae (Blatt 1998), along with function of precursor of the final secretion.

Among heteropteran exocrine glands, MTG are of greatest importance in defence. Pheromonal functions, on the other hand, are more frequently provided by other glands, often present only in one sex. As seen in text, many chemicals found in the MTG secretion have more than one function. A duality of defensive and alarm functions or alarm and attractant functions of the secretion is very common in terrestrial Heteroptera.

The functions of MTG are unknown in many families, often including important pests (Aradidae, Blissidae) or pest predators (Anthocoridae, Geocoridae). Many studies also ignore the origin of the secretion, preventing their use in analyses of functions of MTG. Thus, the future research should focus on secretion in less investigated groups, with respect to its functions in ecology and ethology, chemistry and glandular origin.

Acknowledgements:

I am honored to thank my supervisor, dr. Alice Exnerová, and my consultant, prof. Pavel Štys, for their kindness, tolerance and numerous constructive comments during reviewing this text. I am also indebted to Petr Kment for providing me with valuable literature. Last but not least, I thank my family for a great support during whole studies.

Literature cited:

1. Aldrich, J.R., et al., *Male Specific Natural-Products in Bug, Leptoglossus-Phyllopus - Chemistry and Possible Function*. Journal of Insect Physiology, 1976. **22**(9): p. 1201-1206.
2. Aldrich, J.R., et al., *Pentatomid Natural-Products - Chemistry and Morphology of Iii-Iv Dorsal Abdominal Glands of Adults*. Journal of Chemical Ecology, 1978. **4**(2): p. 161-172.
3. Aldrich, J.R., et al., *Novel Exocrine Secretions from 2 Species of Scentless Plant Bugs (Hemiptera, Rhopalidae)*. Entomologia Experimentalis Et Applicata, 1979. **26**(3): p. 323-331.
4. Aldrich, J.R., J.P. Kochansky, and C.B. Abrams, *Attractant for a Beneficial Insect and Its Parasitoids, Pheromone of the Predatory Spined Soldier Bug, Podisus-Maculiventris (Hemiptera, Pentatomidae)*. Environmental Entomology, 1984. **13**(4): p. 1031-1036.
5. Aldrich, J.R., *Chemical Ecology of the Heteroptera*. Annual Review of Entomology, 1988. **33**: p. 211-238.
6. Aldrich, J.R., et al., *Sapindaceae, Cyanolipids, and Bugs*. Journal of Chemical Ecology, 1990. **16**(1): p. 199-210.
7. Aldrich, J.R., et al., *Exocrine Secretions of Scentless Plant Bugs - Jadera, Boisea and Niesthrea Species (Hemiptera, Heteroptera, Rhopalidae)*. Biochemical Systematics and Ecology, 1990. **18**(5): p. 369-376.
8. Aldrich, J.R., et al., *Male-Specific Volatiles from Nearctic and Australasian True Bugs (Heteroptera, Coreidae and Alydidae)*. Journal of Chemical Ecology, 1993. **19**(12): p. 2767-2781.
9. Aldrich, J.R., et al., *Semiochemistry of cabbage bugs (Heteroptera: Pentatomidae: Eurydema and Murgantia)*. Journal of Entomological Science, 1996. **31**(2): p. 172-182.
10. Aldrich, J.R., et al., *Semiochemistry of aposematic seed bugs*. Entomologia Experimentalis Et Applicata, 1997. **84**(2): p. 127-135.
11. Aldrich, J.R., et al., *Field tests of predaceous pentatomid pheromones and semiochemistry of Podisus and Supputius species (Heteroptera: Pentatomidae: Asopinae)*. Anais da Sociedade Entomológica do Brasil, 1997. **26**(1): p. 1-14.
12. Aldrich, J.R., et al., *Pheromones and colonization: reassessment of the milkweed bug migration model (Heteroptera: Lygaeidae: Lygaeinae)*. Chemoecology, 1999. **9**(2): p. 63-71.
13. Aliabadi, A., J.A.A. Renwick, and D.W. Whitman, *Sequestration of glucosinolates by harlequin bug Murgantia histrionica*. Journal of Chemical Ecology, 2002. **28**(9): p. 1749-1762.
14. Ashok, S., et al., *Defensive Secretion of Soap-Nut Bug, Tessaratoma-Javanica (Thunberg) (Heteroptera, Pentatomidae) as a Juvenile Hormone Mimic*. Zoologische Jahrbucher-Abteilung Fur Allgemeine Zoologie Und Physiologie Der Tiere, 1978. **82**(4): p. 383-394.
15. Baggini, A., et al., *Ricerche sulle secrezioni difensive di Insetti Emitteri Eterotteri*. Revista Espanola de Entomologia, 1966. **42**: p. 7-26+1 table.
16. Berenbaum, M.R. and E. Miliczky, *Mantids and Milkweed Bugs - Efficacy of Aposematic Coloration against Invertebrate Predators*. American Midland Naturalist, 1984. **111**(1): p. 64-68.
17. Blatt, S.E., et al., *Alarm pheromone system of the western conifer seed bug, Leptoglossus occidentalis*. Journal of Chemical Ecology, 1998. **24**(6): p. 1013-1031.
18. Blum, M.S., *Alarm pheromones*. In *Comprehensive Insect Physiology, Biochemistry and Pharmacology, Vol. 9, ed. Kerkut, G. A., Gilbert, L. I.* Oxford: Pergamon, 1985: p. 193-224.
19. Blum, M.S., *Semiochemical parsimony in the Arthropoda*. Annual Review of Entomology, 1996. **41**: p. 353-374.

20. Brower, L.P., *Chemical defence in butterflies*. In *The biology of butterflies*, ed. Ackery, P., Vane-Wright, R. I. London: Academic Press, 1984: p. 109-134.
21. Brown, K.S., *Adult-Obtained Pyrrolizidine Alkaloids Defend Ithomiine Butterflies against a Spider Predator*. *Nature*, 1984. **309**(5970): p. 707-709.
22. Cant, R.G., et al., *The Biology and ecology of the bronze orange bug, Musgraveia sulciventris, (Stal) - a literature review. Part II - Feeding, control, defensive secretions, pheromones, reproduction and aggregation*. *General and Applied Entomology*, 1996. **27**: p. 30-42.
23. Carayon, J., *Notes et documents sur l'appareil odorant métathoracique des Hémiptères*. *Annales De La Societe Entomologique De France*, 1971. **7**(4): p. 737-&.
24. Choudhuri, D.K. and K.K. Das, *The stink apparatus of the pentatomid bug, Halys dentata Fabricius, and its stink components*. *Proceedings of the Zoological Society (Calcutta)*, 1970. **23**: p. 213-221.
25. Daroogheh, H. and T.O. Olagbemiro, *Linalool from the Cotton Stainer Dysdercus-Superstitiosus (F) (Heteroptera, Pyrrhocoridae)*. *Experientia*, 1982. **38**(4): p. 421-423.
26. Drijfhout, F.P., et al., *On-line thermal desorption-gas chromatography of intact insects for pheromone analysis*. *Journal of Chemical Ecology*, 2000. **26**(6): p. 1383-1392.
27. Duffey, S.S. and G.G.E. Scudder, *Cardiac-Glycosides in Oncopeltus-Fasciatus (Dallas) (Hemiptera-Lygaeidae) .1. Uptake and Distribution of Natural Cardenolides in Body*. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, 1974. **52**(2): p. 283-290.
28. Duffey, S.S., *Sequestration of plant natural products by insects*. *Annual Review of Entomology*, 1980. **25**: p. 447-477.
29. Durak, D. and Y. Kalender, *Fine structure and chemical analysis of the metathoracic scent gland of Eurygaster maura (Linnaeus, 1758) (Heteroptera : Scutelleridae)*. *Folia Biologica-Krakow*, 2007. **55**(3-4): p. 133-141.
30. Durak, D. and Y. Kalender, *Morphology and chemical analysis of the metathoracic scent glands of Coreus marginatus (Linnaeus, 1758) (Heteroptera : Coreidae) from Turkey*. *Entomological News*, 2007. **118**(3): p. 227-234.
31. Durak, D., *Morphology and chemical composition of metathoracic scent glands in Dolycoris baccarum (Linnaeus, 1758) (Heteroptera : Pentatomidae)*. *Acta Zoologica*, 2008. **89**(3): p. 193-199.
32. Durak, D. and Y. Kalender, *Fine structure and chemical analysis of the metathoracic scent gland secretion in Graphosoma lineatum (Linnaeus, 1758) (Heteroptera, Pentatomidae)*. *Comptes Rendus Biologies*, 2009. **332**(1): p. 34-42.
33. Endo, N., et al., *Ambiguous response of Riptortus clavatus (Heteroptera : Alydidae) to different blends of its aggregation pheromone components*. *Applied Entomology and Zoology*, 2005. **40**(1): p. 41-45.
34. Evans, D.L., N. Castoriades, and H. Badruddine, *Cardenolides in the Defense of Caenocoris-Nerii (Hemiptera)*. *Oikos*, 1986. **46**(3): p. 325-329.
35. Everton, I.J., D.E. Games, and B.W. Staddon, *Composition of Scents from Apodiphus-Amygdali*. *Annals of the Entomological Society of America*, 1974. **67**(5): p. 815-816.
36. Exnerova, A., et al., *Reactions of passerine birds to aposematic and nonaposematic firebugs (Pyrrhocoris apterus; Heteroptera)*. *Biological Journal of the Linnean Society*, 2003. **78**(4): p. 517-525.
37. Exnerova, A., et al., *Importance of colour in the reaction of passerine predators to aposematic prey: experiments with mutants of Pyrrhocoris apterus (Heteroptera)*. *Biological Journal of the Linnean Society*, 2006. **88**(1): p. 143-153.
38. Exnerova, A., et al., *Avoidance of aposematic prey in European tits (Paridae): learned or innate?* *Behavioral Ecology*, 2007. **18**(1): p. 148-156.
39. Falkenstein, R.B., *A general biological study of the lychee stink bug, Tessaratoma Papillosa Drur. (Heteroptera, Pentatomidae)*. *Lingnan Science Journal*, 1931. **10**(1): p. 29-82.

40. Farine, J.P., *The Exocrine Glands of Dysdercus-Cingulatus F (Heteroptera, Pyrrhocoridae) - Morphology and Function of Adults Glands*. Annales De La Societe Entomologique De France, 1988. **24**(3): p. 241-256.
41. Farine, J.P., et al., *Defensive Secretions of Nymphs and Adults of 5 Species of Pyrrhocoridae (Insecta, Heteroptera)*. Biochemical Systematics and Ecology, 1993. **21**(3): p. 363-371.
42. Games, D.E. and B.W. Staddon, *Chemical Expression of a Sexual Dimorphism in Tubular Scent Glands of Milkweed Bug Oncopeltus-Fasciatus (Dallas) (Heteroptera-Lygaeidae)*. Experientia, 1973. **29**(5): p. 532-533.
43. Gilby, A.R. and D.F. Waterhouse, *Composition of Scent of Green Vegetable Bug Nezara Viridula*. Proceedings of the Royal Society of London Series B-Biological Sciences, 1965. **162**(986): p. 105-&.
44. Gilby, A.R. and D.F. Waterhouse, *Secretions from Lateral Scent Glands of Green Vegetable Bug Nezara Viridula*. Nature, 1967. **216**(5110): p. 90-&.
45. Gilchrist, T.L., F. Stansfield, and J.L. Cloudsley-Thompson, *The odoriferous principle of Piezodorus teretipes (Stal) (Hemiptera: Pentatomoidea)*. Proceedings of the Royal Entomological Society of London, 1966. **41**(4-6): p. 55-56.
46. Gough, A.J.E., et al., *Multichemical Defense of Plant Bug Hotea-Gambiae (Westwood) (Heteroptera, Scutelleridae) - Sesquiterpenoids from Abdominal Gland in Larvae*. Journal of Chemical Ecology, 1985. **11**(3): p. 343-352.
47. Groot, A.T., et al., *Sex-related perception of insect and plant volatiles in Lygocoris pabulinus*. Journal of Chemical Ecology, 1999. **25**(10): p. 2357-2371.
48. Groot, A.T., et al., *Disruption of sexual communication in the mirid bug Lygocoris pabulinus by hexyl butanoate*. Agricultural and Forest Entomology, 2001. **3**: p. 49-55.
49. Gunawardena, N.E. and H. Herath, *Significance of Medium Chain Normal-Alkanes as Accompanying Compounds in Hemipteran Defensive Secretions - an Investigation Based on the Defensive Secretion of Coridius-Janus*. Journal of Chemical Ecology, 1991. **17**(12): p. 2449-2458.
50. Hamilton, J.G.C., et al., *Multichemical Defense of Plant Bug Hotea-Gambiae (Westwood) (Heteroptera, Scutelleridae) - (E)-2-Hexenol from Abdominal Gland in Adults*. Journal of Chemical Ecology, 1985. **11**(10): p. 1399-1409.
51. Henry, T.J., *Phylogenic Analysis of the Family Groups within the Infraorder Pentatomomorpha (Hemiptera: Heteroptera), with Emphasis on the Lygaeoidea*. Annals of the Entomological Society of America, 1997. **90**(3): p. 275-301.
52. Hepburn, H.R. and T.R. Yonke, *The Metathoracic Scent Glands of Coreoid Heteroptera*. Journal of the Kansas Entomological Society, 1971. **44**(2): p. 187-210.
53. Innocenzi, P.J., et al., *Investigation of long-range female sex pheromone of the European tarnished plant bug, Lygus rugulipennis: Chemical, electrophysiological, and field studies*. Journal of Chemical Ecology, 2004. **30**(8): p. 1509-1529.
54. Innocenzi, P.J., et al., *Attraction of male European tarnished plant bug, Lygus rugulipennis to components of the female sex pheromone in the field*. Journal of Chemical Ecology, 2005. **31**(6): p. 1401-1413.
55. Ishiwatari, T., *Studies on the scent of stink bugs (Hemiptera: Pentatomidae), I: Alarm pheromone activity*. Applied Entomology and Zoology, 1974. **9**(3): p. 153-158.
56. Ishiwatari, T., *Studies on the Scent of Stink Bugs (Hemiptera: Pentatomidae) II. Aggregation Pheromone Activity*. Applied Entomology and Zoology, 1976. **11**(1): p. 38-44.
57. Janaiah, C., et al., *Chemical Composition of the Scent Glands of Adults and Nymphs of the Bug Tessaratoma-Javanica Thunberg*. Indian Journal of Experimental Biology, 1979. **17**(11): p. 1233-1235.
58. Johansson, A.S., *The functional anatomy of the metathoracic scent glands of the milkweed bug, Oncopeltus fasciatus (Dallas) (Heteroptera: Lygaeidae)*. Norsk Entomologisk

- Tidsskrift, 1957. **10**: p. 95-109.
59. Johansson, A.S. and T. Braten, *Cuticular Morphology of the Scent Gland Areas of some Heteropterans*. Entomologica Scandinavica, 1970. **1**: p. 158-162.
 60. Kerr, S.H., *Biology of the lawn chinch bug, Blissus insularis*. The Florida Entomologist, 1966. **49**: p. 9-18.
 61. Kitamura, C., S. Wakamura, and S. Takahashi, *Identification and functions of ventral glands secretion of some Heteroptera*. Applied Entomology and Zoology, 1984. **19**: p. 33-41.
 62. Klitzke, C.F. and J.R. Trigo, *New records of pyrrolizidine alkaloid-feeding insects. Hemiptera and Coleoptera on Senecio brasiliensis*. Biochemical Systematics and Ecology, 2000. **28**(4): p. 313-318.
 63. Knight, D.W., M. Rossiter, and B.W. Staddon, *(Z,E)-Alpha-Farnesene - Major Component of Secretion from Metathoracic Scent Gland of Cotton Seed Bug, Oxycarenus Hyalinipennis (Costa) (Heteroptera, Lygaeidae)*. Journal of Chemical Ecology, 1984. **10**(4): p. 641-649.
 64. Kou, R., D.S. Tang, and Y.S. Chow, *Alarm Pheromone of Pentatomid Bug, Erthesina-Fullo Thunberg (Hemiptera, Pentatomidae)*. Journal of Chemical Ecology, 1989. **15**(12): p. 2695-2702.
 65. Krall, B.S., et al., *Chemistry and defensive efficacy of secretion of burrowing bug (Sehirus cinctus cinctus)*. Journal of Chemical Ecology, 1997. **23**(8): p. 1951-1962.
 66. Krall, B.S., et al., *Chemical defense in the stink bug Cosmopepla bimaculata*. Journal of Chemical Ecology, 1999. **25**(11): p. 2477-2494.
 67. Langstrom, B., et al., *"Non-coleopteran insects"*. Bark and Wood Boring Insects in Living Trees in Europe, a Synthesis, 2004: p. 501-538.
 68. Leal, W.S., et al., *Multifunctional Communication in Riptortus-Clavatus (Heteroptera, Alydidae) - Conspecific Nymphs and Egg Parasitoid Ooencyrtus-Nezarae Use the Same Adult Attractant Pheromone as Chemical Cue*. Journal of Chemical Ecology, 1995. **21**(7): p. 973-985.
 69. Levinson, H.Z. and A.R. Barilan, *Assembling and Alerting Scents Produced by Bedbug Cimex-Lectularius L*. Experientia, 1971. **27**(1): p. 102-&.
 70. Levinson, H.Z., A.R. Levinson, and U. Maschwitz, *Action and Composition of Alarm Pheromone of Bedbug Cimex-Lectularius L*. Naturwissenschaften, 1974. **61**(12): p. 684-685.
 71. Lockwood, J.A. and R.N. Story, *Adaptive Functions of Nymphal Aggregation in the Southern Green Stink Bug, Nezara-Viridula (L) (Hemiptera, Pentatomidae)*. Environmental Entomology, 1986. **15**(3): p. 739-749.
 72. MacLeod, J.K., et al., *Volatile scent gland components of some tropical Heteroptera*. Journal of Insect Physiology, 1975. **21**: p. 1219-1224.
 73. Manrique, G. and C.R. Lazzari, *Existence of a sex pheromone in Triatoma infestans (Hemiptera: Reduviidae): I. Behavioural evidence*. Memórias do Instituto Oswaldo Cruz, 1995. **90**(5): p. 645-648.
 74. Manrique, G., et al., *Chemical Communication in Chagas Disease Vectors. Source, Identity, and Potential Function of Volatiles Released by the Metasternal and Brindley's Glands of Triatoma infestans Adults*. Journal of Chemical Ecology, 2006. **32**: p. 2035-2052.
 75. Maschwitz, U., *Wasserstoffperoxid als Antiseptikum bei einer Wasserwanze*. Naturwissenschaften, 1971. **58**: p. 572.
 76. Mattiacci, L., et al., *A Long-Range Attractant Kairomone for Egg Parasitoid Trissolcus-Basalis, Isolated from Defensive Secretion of Its Host, Nezara-Viridula*. Journal of Chemical Ecology, 1993. **19**(6): p. 1167-1181.
 77. McBrien, H.L. and J.G. Millar, *Phytophagous bugs*. Pheromones of Non-Lepidopteran Insects Associated with Agricultural Plants, 1999: p. 277-304.

78. McCulough, T., *Chemical Analysis of the Defensive Scent Fluid Released by Hypselonotus punctiventris (Hemiptera: Coreidae)*. Annals of the Entomological Society of America, 1971. **64**(3): p. 749.
79. McCulough, T., *Chemical Analysis of the Defensive Scent Fluid from the Bug Mozena Obtusa (Hemiptera: Coreidae)*. Annals of the Entomological Society of America, 1973. **66**(1): p. 231-232.
80. McCulough, T., *Chemical Analysis of the Defensive Scent Fluid from the Cactus Bug, Chelinidea vittiger*. Annals of the Entomological Society of America, 1974. **67**(2): p. 300.
81. McCulough, T., *Chemical Analysis of the Defensive Scent Fluid Produced by Mozena Lunata (Hemiptera: Coreidae)*. Annals of the Entomological Society of America, 1974. **67**(2): p. 298.
82. McLain, D.K., *Coevolution - Mullerian Mimicry between a Plant Bug (Miridae) and a Seed Bug (Lygaeidae) and the Relationship between Host Plant Choice and Unpalatability*. Oikos, 1984. **43**(2): p. 143-148.
83. Millar, J.G., R.E. Rice, and Q. Wang, *Sex pheromone of the mirid bug Phytocoris relativus*. Journal of Chemical Ecology, 1997. **23**(7): p. 1743-1754.
84. Millar, J.G., *Pheromones of true bugs*. Chemistry of Pheromones and Other Semiochemicals Ii, 2005. **240**: p. 37-84.
85. Moore, B.P., W.V. Brown, and M. Rotschild, *Methylalkylpyrazines in aposematic insects, their hostplants and mimics*. Chemoecology, 1990. **1**(2): p. 43-51.
86. Muir, F., *Notes on the stridulating organ and stink-glands of Tessaratoma papillosa, Thunb.* The Transactions of the Royal Entomological Society of London, 1907(2): p. 256-258.
87. Nagnan, P., et al., *Fine-Structure and Physicochemical Analysis of the Metathoracic Scent Glands of Lincus-Malevolus (Rolston) and L-Spurcus (Rolston) (Heteroptera, Pentatomidae)*. International Journal of Insect Morphology & Embryology, 1994. **23**(4): p. 355-370.
88. Olagbemiro, T.O. and B.W. Staddon, *Isoprenoids from Metathoracic Scent Gland of Cotton Seed Bug, Oxycarenus-Hyalinipennis (Costa) (Heteroptera, Lygaeidae)*. Journal of Chemical Ecology, 1983. **9**(10): p. 1397-1412.
89. Oliver, J.E., A.J. Reinecke, and S.A. Reinecke, *Verdedigingsekresies van die graanstinkluis Macchiademus diplopterus (Heteroptera: Lygaeidae)*. Suid-Afrikaanse Tydskrif vir Natuurwetenskap en Tegnologie, 1996. **15**(4): p. 172-174.
90. Park, R.J. and M.D. Sutherland, *Volatile components of the bronze orange bug, Rhoecocoris sulciventris*. Australian Journal of Chemistry, 1962. **15**(2): p. 172-174.
91. Phillips, T.W., M.N. Parajulee, and D.K. Weaver, *Toxicity of Terpenes Secreted by the Predator Xylocoris-Flavipes (Reuter) to Tribolium-Castaneum (Herbst) and Oryzaephilus-Surinamensis (L)*. Journal of Stored Products Research, 1995. **31**(2): p. 131-138.
92. Prudic, K.L., K. Noge, and J.X. Becerra, *Adults and nymphs do not smell the same: The different defensive compounds of the giant mesquite bug (Thasus neocalifornicus : Coreidae)*. Journal of Chemical Ecology, 2008. **34**(6): p. 734-741.
93. Rao, B.K., et al., *Insect Ectohormones and Natural Pest Control*. Proceedings of the Indian Academy of Parasitology, 1980. **1**(1): p. 35-40.
94. Ravinder, K., C. Janaiah, and S.M. Reddy, *Fungicidal Activity of Scent Secretions of Certain Heteropteran Bugs*. National Academy Science Letters-India, 1992. **15**(4): p. 103-105.
95. Regnier, F.E. and E.O. Wilson, *Alarm-Defence System of Ant Acanthomyops Claviger*. Journal of Insect Physiology, 1968. **14**(7): p. 955-&.
96. Remold, H., *Scent-Glands of Land-Bugs, Their Physiology and Biological Function*. Nature, 1963. **198**(488): p. 764-&.
97. Rossiter, M. and B.W. Staddon, *3-Methyl-2-Hexanone from the Triatomine Bug*

- Dipetalogaster-Maximus (Uhler) (Heteroptera, Reduviidae)*. *Experientia*, 1983. **39**(4): p. 380-381.
98. Ruxton, G.D., T.N. Sherratt, and M.P. Speed, *Avoiding attack*. New York: Oxford University Press, 2004: p. 249.
 99. Salles, L.A.B., *Aspects of Trichopoda-Pennipes (Fabricius) (Diptera, Tachinidae) Oviposition and Its Relation to Parasitization on the Adults of Nezara-Viridula (Linnaeus) (Heteroptera, Pentatomidae)*. *Pesquisa Agropecuaria Brasileira*, 1991. **26**(1): p. 39-44.
 100. Schofield, C.J. and C.P. Upton, *Brindley's scent-glands and the metasternal scent-glands of Panstrongylus megistus (Hemiptera, Reduviidae, Triatominae)*. *Revista Brasileira de Biologia*, 1978. **38**: p. 665-678.
 101. Schuh, R.T. and J.A. Slater, *True Bugs of the World (Hemiptera: Heteroptera): Classification and Natural History*. Ithaca, NY: Comstock Publisher Associates, 1995: p. 336.
 102. Scudder, G.G.E. and S.S. Duffey, *Cardiac-Glycosides in Lygaeinae (Hemiptera-Lygaeidae)*. *Canadian Journal of Zoology*, 1972. **50**(1): p. 35-&.
 103. Scudder, G.G.E. and J. Meredith, *Morphological Basis of Cardiac Glycoside Sequestration by Oncopeltus-Fasciatus (Dallas) (Hemiptera, Lygaeidae)*. *Zoomorphology*, 1982. **99**(2): p. 87-101.
 104. Scudder, G.G.E., *Sequestration of cardenolides in Oncopeltus fasciatus: Morphological and physiological adaptations*. *Journal of Chemical Ecology*, 1986. **12**(5): p. 1171-1187.
 105. Smith, R.M., *The defensive secretion of Vitellus insularis (Heteroptera: Pentatomidae)*. *New Zealand Journal of Zoology*, 1974. **1**(3): p. 375-376.
 106. Smith, R.F., H.D. Pierce, and J.H. Borden, *Sex-Pheromone of the Mullein Bug, Campylomma-Verbasco (Meyer) (Heteroptera, Miridae)*. *Journal of Chemical Ecology*, 1991. **17**(7): p. 1437-1447.
 107. Staddon, B.W., *The scent glands of Heteroptera*. *Advances in Insect Physiology*, 1979. **14**: p. 351-418.
 108. Staddon, B.W., et al., *Sex Dimorphism for Ester Production in the Metathoracic Scent Gland of the Lygaeid Bug Spilostethus-Rivularis (Germar) (Heteroptera)*. *Comparative Biochemistry and Physiology B-Biochemistry & Molecular Biology*, 1985. **80**(2): p. 235-239.
 109. Staddon, B.W., M.J. Thorne, and D.W. Knight, *The Scent Glands and Their Chemicals in the Aposematic Cotton Harlequin Bug, Tectocoris-Diophthalmus (Heteroptera, Scutelleridae)*. *Australian Journal of Zoology*, 1987. **35**(3): p. 227-234.
 110. Staples, J.K., et al., *Chemical defense in the plant bug Lopidea robiniae (Uhler)*. *Journal of Chemical Ecology*, 2002. **28**(3): p. UNSP 0098-0331/02/0300-0601/0.
 111. Steinbauer, M.J. and N.W. Davies, *Defensive Secretions of Amorbus-Obscuricornis (Westwood), a-Rubiginosus (Guerin-Meneville) and Gelonus-Tasmanicus (Leguillou) (Hemiptera, Coreidae)*. *Journal of the Australian Entomological Society*, 1995. **34**: p. 75-78.
 112. Stransky, K., et al., *Volatiles from stink bug, Graphosoma lineatum (L.), and from green shield bug, Palomena prasina (L.), (Heteroptera : Pentatomidae)*. *Hrc-Journal of High Resolution Chromatography*, 1998. **21**(8): p. 475-476.
 113. Surender, P., et al., *Antifungal Activity of Secretions of Scent Glands from Heteropteran Bugs*. *Indian Journal of Experimental Biology*, 1987. **25**(4): p. 233-234.
 114. Surender, P., et al., *Bactericidal Activity of Certain Volatile Scent Components of Heteropteran Bugs*. *Proceedings of the Indian National Science Academy. Part A. Biological Sciences*, 1988. **54**(5): p. 315-316.
 115. Svadova, K., et al., *Role of different colours of aposematic insects in learning, memory and generalization of naive bird predators*. *Animal Behaviour*, 2009. **77**(2): p. 327-336.
 116. Sweet, M.H., *The Comparative External Morphology of the Pregenital Abdomen of Hemiptera*. In *Studies on Hemipteran Phylogeny*, ed. Schaefer, C. W. Lanham, MD:

- Entomological Society of America, 1996: p. 119-158.
117. Toyama, M., F. Ihara, and K. Yaginuma, *Formation of aggregations in adults of the brown marmorated stink bug, Halyomorpha halys (Stal) (Heteroptera : Pentatomidae): The role of antennae in short-range locations*. Applied Entomology and Zoology, 2006. **41**(2): p. 309-315.
 118. Usinger, R.L. and R. Matsuda, *Classification of the Aradidae (Hemiptera-Heteroptera)*. London: British Museum, 1959: p. 410.
 119. Wardle, A.R., et al., *Volatile compounds released by disturbed and calm adults of the tarnished plant bug, Lygus lineolaris*. Journal of Chemical Ecology, 2003. **29**(4): p. 931-944.
 120. Waterhouse, D.F., D.A. Forss, and R.H. Hackman, *Characteristic odour components of the scent of stink bugs*. Journal of Insect Physiology, 1961. **6**: p. 113-121.
 121. Waterhouse, D.F. and A.R. Gilby, *The Adult Scent Glands and Scent of Nine Bugs of the Superfamily Coreoidea*. Journal of Insect Physiology, 1964. **10**(6): p. 977-987.
 122. Weirauch, C., *Metathoracic glands and associated evaporatory structures in Reduvioidea (Heteroptera : Cimicomorpha), with observation on the mode of function of the metacoxal comb*. European Journal of Entomology, 2006. **103**(1): p. 97-108.
 123. Williams, L., P.E. Evans, and W.S. Bowers, *Defensive chemistry of an aposematic bug, Pachycoris stallii uhler and volatile compounds of its host plant Croton californicus Muell.-Arg*. Journal of Chemical Ecology, 2001. **27**(2): p. 203-216.
 124. Wink, M., et al., *Sequestration of phorbol esters by the aposematically coloured bug Pachycoris klugii (Heteroptera : Scutelleridae) feeding on Jatropha curcas (Euphorbiaceae)*. Chemocology, 2000. **10**(4): p. 179-184.
 125. Zhang, Q.H. and J.R. Aldrich, *Male-produced anti-sex pheromone in a plant bug*. Naturwissenschaften, 2003. **90**(11): p. 505-508.
 126. Zhang, Q.H. and J.R. Aldrich, *Pheromones of milkweed bugs (Heteroptera : Lygaeidae) attract wayward plant bugs: Phytocoris mirid sex pheromone*. Journal of Chemical Ecology, 2003. **29**(8): p. 1835-1851.
 127. Zhang, Q.H. and J.R. Aldrich, *Sex pheromone of the plant bug, Phytocoris calli knight*. Journal of Chemical Ecology, 2008. **34**(6): p. 719-724.

Appendix: Classification of species named in text*

Heteroptera:

<i>Alydus eurinus</i>	(Say 1825)	Alydidae: Alydinae
<i>Campylomma verbasci</i>	(Meier-Dür 1843)	Miridae: Phylinae
<i>Cimex lectularius</i>	(L. 1758)	Cimicidae: Cimicinae
<i>Cosmopepla bimaculata</i>	(Thomas 1865)	Pentatomidae: Pentatominae
<i>Dipetalogaster maximus</i>	(Uhler 1894)	Reduviidae: Triatominae
<i>Dysdercus cingulatus</i>	(Fabricius 1775)	Pyrrhocoridae
<i>Dysdercus fasciatus</i>	(Signoret 1860)	Pyrrhocoridae
<i>Eurydema oleacrum</i>	(L. 1758)	Pentatomidae: Pentatominae
<i>Eurydema ventrale</i>	(Kolenati 1846)	Pentatomidae: Pentatominae
<i>Geocoris punctipes</i>	(Say 1832)	Geocoridae
<i>Harpocera thoracica</i>	(Fallén 1807)	Miridae: Phylinae
<i>Hotea gambiae</i>	(Westwood 1837)	Scutelleridae
<i>Leptoglossus occidentalis</i>	(Heidemann 1910)	Coreidae: Coreinae
<i>Lopidea robiniae</i>	(Uhler 1861)	Miridae: Orthotylinae
<i>Lygocoris pabulinus</i>	(L. 1761)	Miridae: Mirinae
<i>Lygus rugulipennis</i>	(Poppius 1911)	Miridae: Mirinae
<i>Macchiademus diplopterus</i>	(Distant 1904)	Blissidae
<i>Megalotomus quinquespinosus</i>	(Say 1825)	Alydidae: Alydinae
<i>Melanacanthus scutellaris</i>	(Dallas 1852)	Alydidae: Alydinae
<i>Murgantia histrionica</i>	(Hahn 1834)	Pentatomidae: Pentatominae
<i>Nezara viridula</i>	(L. 1758)	Pentatomidae: Pentatominae
<i>Niestheria louisianica</i>	(Sailer 1961)	Rhopalidae: Rhopalinae
<i>Oncopeltus fasciatus</i>	(Dallas 1852)	Lygaeidae: Lygaeinae
<i>Oxycarenus hyalinipennis</i>	(A. Costa 1843)	Oxycarenidae
<i>Pachycoris klugii</i>	(Burmeister 1835)	Scutelleridae
<i>Pachycoris stalii</i>	(Uhler 1863)	Scutelleridae
<i>Phytocoris brevisculus</i>	(Reuter 1876)	Miridae: Mirinae
<i>Phytocoris calii</i>	(Knight 1934)	Miridae: Mirinae
<i>Phytocoris difficilis</i>	(Knight 1927)	Miridae: Mirinae
<i>Phytocoris relativus</i>	(Knight 1968)	Miridae: Mirinae
<i>Piezodorus teretipes</i>	(Stål 1865)	Pentatomidae: Pentatominae
<i>Podisus maculiventris</i>	(Say 1832)	Pentatomidae: Asopinae
<i>Pyrrhocoris apterus</i>	(L. 1758)	Pyrrhocoridae
<i>Riptortus clavatus</i>	(Thunberg 1783)	Alydidae: Alydinae
<i>Riptortus serripes</i>	(Fabricius 1775)	Alydidae: Alydinae

* the brackets are used incorrectly in this chapter due to the author's mistake

<i>Sehirus cinctus cinctus</i>	(Palisot 1811)	Cydnidae: Sehirinae
<i>Tectocoris diophthalmus</i>	(Thunberg 1783)	Scutelleridae
<i>Tessaratoma aethiops</i>	(Distant 1877)	Tessaratomidae
<i>Tessaratoma javanica</i>	(Thunberg 1783)	Tessaratomidae
<i>Tessaratoma pappilosa</i>	(Drury 1770)	Tessaratomidae
<i>Thasus neocalifornicus</i>	(Brailovsky & Barrera 1995)	Coreidae: Coreinae
<i>Triatoma infestans</i>	(Klug 1834)	Reduviidae: Triatominae

Other:

<i>Anolis carolinensis</i>	(Voigt 1832)	Reptilia: Squamata: Polychrotidae
<i>Charadrius vociferus</i>	(L. 1758)	Aves: Charadriiformes: Charadriidae
<i>Coturnix coturnix coturnix</i>	(L. 1758)	Aves: Galliformes: Phasianidae
<i>Galeodes granti</i>	(Pocock 1903)	Sulifugae: Galeodidae
<i>Leiurus quinquestriatus</i>	(Ehrenberg, 1828)	Scorpionida: Buthidae
<i>Leucostoma gravipes</i>	(Wulp 1890)	Diptera: Tachinidae: Phasiinae
<i>Nephila clavipes</i>	(L. 1767)	Araneae: Araneidae
<i>Passer domesticus</i>	(L. 1758)	Aves: Passeriformes: Passeridae
<i>Stagmomantis californica</i>	(Rehn and Hebard 1909)	Mantodea: Mantidae: Mantinae
<i>Sturnus vulgaris</i>	(L. 1758)	Aves: Passeriformes: Sturnidae
<i>Tenodera aridifolia</i>	(Stoll 1813)	Mantodea: Mantidae: Mantinae
<i>Trissolcus basalis</i>	(Wollaston 1858)	Hymenoptera: Scelionidae: Teleoniminae
<i>Turdus migratorius</i>	(L. 1766)	Aves: Passeriformes: Turdidae