A pair of basi-abdominal sex pheromone glands
in the male of some burrower bugs
(Hemiptera: Heteroptera: Cydnidae)

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Abstract. Paired pleural basi-abdominal glands (PBA glands) were found in males of some burrower bugs (Pentatomoidea: Cydnidae). So far, they seem to be restricted to the subfamily Cydninae, tribes Cydnini (except *Cydnus aterrimus* (Forster, 1771) and Geotomini, and are absent in examined representatives of the subfamilies Amaurocorinae, Cephalocteinae, and Sehirinae. PBA glands are laterally and symmetrically situated underneath the mediotergite 3. They are simple sac-like formations covered by several hundreds of secretory units. Each gland opens to the exterior in the posterior part of the membranous pleural area of the fused first and second mediotergites, just in front of the connective line linking laterotergite and sternite 3. The slit-shaped minute ostioles are hidden by the wing in the resting insect and are located adjacent to the stridulatory structures. The secretory activity of the PBA glands is clearly correlated with sexual activity and mating period; therefore the glands might be the source of an attractant sex pheromone for the female. PBA glands are possibly functionally associated with stridulation-vibration during courtship and mating. Unlike the Sehirinae (lacking the paired PBA glands), the Cydninae exhibit an unusual copulatory position, the male being positioned underneath the female, similar to the condition found in the Aradidae and Ceratocombidae.

Key words. Heteroptera, Cydnidae, Cydninae, Cydnini, Geotomini, pleural basi-abdominal glands, sex pheromones, mating, copulatory position, stridulatory structures

Introduction

Means for communication between sexes in Heteroptera include acoustic signals and semiochemical substances. There is also recent evidence to suggest that vibrational signals

and pheromone emission interact during mate location in some pentatomid species (MIKLAS 2002, MIKLAS et al. 2003, BAGWELL et al. 2008).

Stridulation and vibratory signals have been extensively studied in Cydnidae – see the excellent review given by GOGALA (2006) – but pheromones are less well known. In Heteroptera, pheromones may be derived from the widespread defensive scent glands (metathoracic and dorso-abdominal glands) or from other epidermal glands (small isolated scattered secretory units, glandular areas, or complex glands) variously distributed depending on the taxa (STADDON 1979, 1986, 1999; ALDRICH 1988, 1996; MILLAR 2005).

Except a brief statement that the anterior paired dorso-abdominal glands are slightly smaller in males than in females of *Sehirus luctuosus* Mulsant & Rey,1866 (DAVIDOVÁ-VILÍMOVÁ & PODOUBSKÝ 1999), sexually dimorphic exocrine glands have not been described in Cydnidae until now; but data on glandular system still remain incomplete. Epidermal glands other than the scent glands (metathoracic and dorso-abdominal glands) were not investigated in Cydnidae except by STADDON (1999).

Like other Pentatomoidea, burrower bugs possess well developed metathoracic glands. Their internal structures were studied by ROTH (1961) and AHMAD & MOIZUDDIN (1977) and the very variable external elements by several authors, in particular FROESCHNER (1960), SCHAEFER (1972), DETHIER (1974), LINNAVUORI (1993), and LIS (1994).

Larval and adult dorso-abdominal glands have been investigated in Cydninae and Sehirinae by DAVIDOVÁ-VILÍMOVÁ & PODOUBSKÝ (1999), who confirmed the persistence of the anterior paired glands in adults of many cydnids and other Pentatomoidea and by LIS & HOHOL-KILIN-KIEWICZ (2002). No morphological differences were found between the sexes in any species studied, even when counting and comparing the small efferent ductules of the secretory units as did STADDON (1999) in six cydnid species.

The presence of glandular areas on the pregenital abdomen was also investigated in several cydnid representatives by STADDON (1999); but, unlike other Pentatomoidea, the cydnid integument was found practically devoid of secretory units except in males of *Legnotus* Schiødte, 1848 and *Tritomegas* Amyot & Serville, 1843, where Staddon observed very few secretory units scattered on sternites and laterotergites.

The present paper describes paired glands found laterally in the male abdomen of some burrower bug species, in close proximity of the stridulatory structures. It mainly documents the gross morphology of the glands based on cuticular elements (intima lining the gland reservoir and efferent ductules of the secretory units); it also includes limited information on the secretory activity period, and comprises some observations on mating and copulatory position in three cydnid species. The possible functions of the paired glands during mating and a possible interaction between glands and stridulatory structures are briefly discussed.

Most of the observations were made many years ago when dissecting series of live specimens during several stays in Senegal. I am very pleased for the opportunity to now present these data and to dedicate this paper to Pavel Štys, in recognition of his important contribution to the morphology, biology, systematics, and higher classification of true bugs.

Material and methods

Male and female cydnid specimens were examined in the following taxa.

Cephalocteinae: Cephalocteini – *Cephalocteus scarabaeoides* (Fabricius, 1803); Scaptocorini – *Stibaropus pseudominor* Lis, 1991; **Cydninae**: Cydnini – *Chilocoris somalicus* Mancini, 1939; *Chilocoris* sp., *Cydnus aterrimus* (Forster, 1771); Geotomini – *Byrsinus pseudosyriacus* (Linnavuori, 1977), *Endotylus brevicornis* Horváth, 1919, *Fromundus glaber* (Signoret, 1858), *Geotomus* sp., *Lactistes vericulatus* Schiødte, 1848, *Macroscytus brunneus* (Fabricius, 1803), *Paraethus capicola* (Westwood, 1837). **Sehirinae** – *Canthophorus dubius* (Scopoli, 1763), *Legnotus limbosus* (Geoffroy, 1785), *Tritomegas bicolor* (Linnaeus, 1758), *Sehirus morio* (Linnaeus, 1761), *Ochetostethus* sp. **Amaurocorinae** – *Amaurocoris curtus* (Brullé, 1838).

The cydnid classification is that of Froeschner (1960) and Lis (1994), except for the amaurocorine species group now upgraded to a separate subfamily (see Pluot-Sigwalt & Lis 2008).

Morphological study was carried out mainly using dry or alcohol preserved specimens. Glands were examined after the following steps: 10% KOH treatment of the abdomen, washing and cleaning, clearing in glycerol or lactophenol, staining with chlorazol black. Examinations were made under the microscope in provisory (lactophenol) or definitive (canada basalm) whole mounts. Descriptions were made from cuticular structures remaining after the glands were cleared: reservoir and cuticular ductules of the secretory units.

Live specimens were examined in all the above-mentioned geotomine species and in *Chilocoris somalicus* Mancini, 1939 (Cydnini). Specimens were collected in the field (Senegal) or obtained from laboratory cultures. Many geotomine species may be easily reared for several generations. The plastic rearing cages contained a thick layer of soil (sand + peat; half moist, half dry) and were provisioned with various seeds (Gramineae) and *Ficus* seeds (Moraceae).

After dissection of anesthetized adult specimens, glands were dissected out and observed as a fresh whole mount in insect saline or fixed with carnoy and stained by the Feulgen technique and Fast green. The male physiological condition, immature or mature, was also noted from the aspect of the different parts of the reproductive system (testes, efferent lateral ducts, accessory glands).

Mating behaviour was observed using a stereomicroscope, under low light conditions. Males and females were kept separately after the imaginal molt and combined later in pairs in small Petri dishes.

Gland terminology is that of Noirot & Quennedey (1991). The paired glands described here are complex glands of class III. Secretory units are multicellular (the secretory cell is associated with a saccule cell and a duct cell) and they possess an efferent cuticular ductule.

Results

Location of the glands. The pleural basi-abdominal glands (PBA glands) are dorso-laterally situated in the base of the abdomen (Figs. 1-3). Glands appear as a pair of sacs more or less voluminous lying under the lateral parts of the mediotergite 3. The external openings are located on the membranous pleural area of the fused terga 1 and 2, the slit-like ostioles being

just in front of the anterior margin of the abdominal segment 3, at the level of the sulcus linking the laterotergite and sternite 3 (Fig. 4). The origin of the glands is clearly abdominal and intersegmentary.

Because the paired glands are located in a modified abdominal region, mainly affected by the basi-abdominal vibratory and stridulatory structures, the abdominal area surrounding the gland openings will be described in detail.

Specialized features of the surrounding area. In resting insects, the gland openings are hidden, covered by the wings; moreover, they seem also to be hidden underneath the posterior lateral angles of the metathorax projecting backwards onto the abdomen as a spur (this process connects the posterodorsal part of the epimeron and the lateral part of the pseudonotum).

Around the external openings of the PBA glands, Figures 1 and 3 show the close proximity of three structures: the metathoracic glands, the anterior paired dorso-abdominal glands still functioning in cydnid adults as small paired sacs (DAVIDOVÁ-VILÍMOVÁ & PODOUBSKÝ 1999), and the stridulatory apparatus (plectrum and stridulitrum).

The cydnid-sound producing structures are now well known (DUPUIS 1953, LESTON 1954, DRAŠLAR & GOGALA 1976, SCHAEFER 1980, LIS & HEYNA 2001; ČOKL et al. 2006). The plectrum (lima) is a small striated area; the stridulitrum or strigil (a row of teeth situated on the undersurface of the hind wing) is located on the first anal vein as shown by LIS & HEYNA (2001), not on the postcubital or first vannal vein as usually stated by most authors. The fused mediotergal plate 1 and 2 functions as a tymbal (GOGALA 1969, DRAŠLAR & GOGALA 1976). There are specialized muscles which can move the plate to produce tymbal sounds (GOGALA 1984). On the mediotergal plate, longitudinal muscles are attached to a pair of apodemes located along the intersegmental sulcus 1-2. The paired apodemes appear considerably larger in the males than in the females in all species examined within Cydninae.

Distribution within the cydnid family. Among the cydnid representatives investigated, the PBA glands were only found in Cydninae. Within this subfamily, glands are present in both tribes: Cydnini – with the notable exception of *Cydnus aterrimus* which is devoid of these glands – and Geotomini. No glands were found in the other subfamilies studied: Amaurocorinae, Cephalocteinae, and Sehirinae. Location and gross morphology of the PBA glands were the same in all species examined. Only some variation was noticed in the form of the reservoir: elongated in Geotomini, more globular in Cydnini.

Gland morphology. The description is of the *Paraethus capicola* glands.

PBA glands are simple membranous sac-like structures (each ca. 1.2-2 mm × 0.2-0.5 mm); a short efferent canal connects the sac to the external opening; a cuticular thickening (soft endocuticule) is present around the base of the canal (Figs. 3, 5).The ostiole is a narrow slit hidden in folds of the round membranous area. No cuticular specialization surrounds the ostiole. A group of minute setae (also present in females) can be seen just above the ostiole (Fig. 4).

The membranous reservoir is covered by several hundred cuticular efferent ductules; these ductules represent a connection between the gland cells and the lumen. Each ductule is composed of: (1) a very fine long and coiled conducting canal; (2) a spherical dilatation
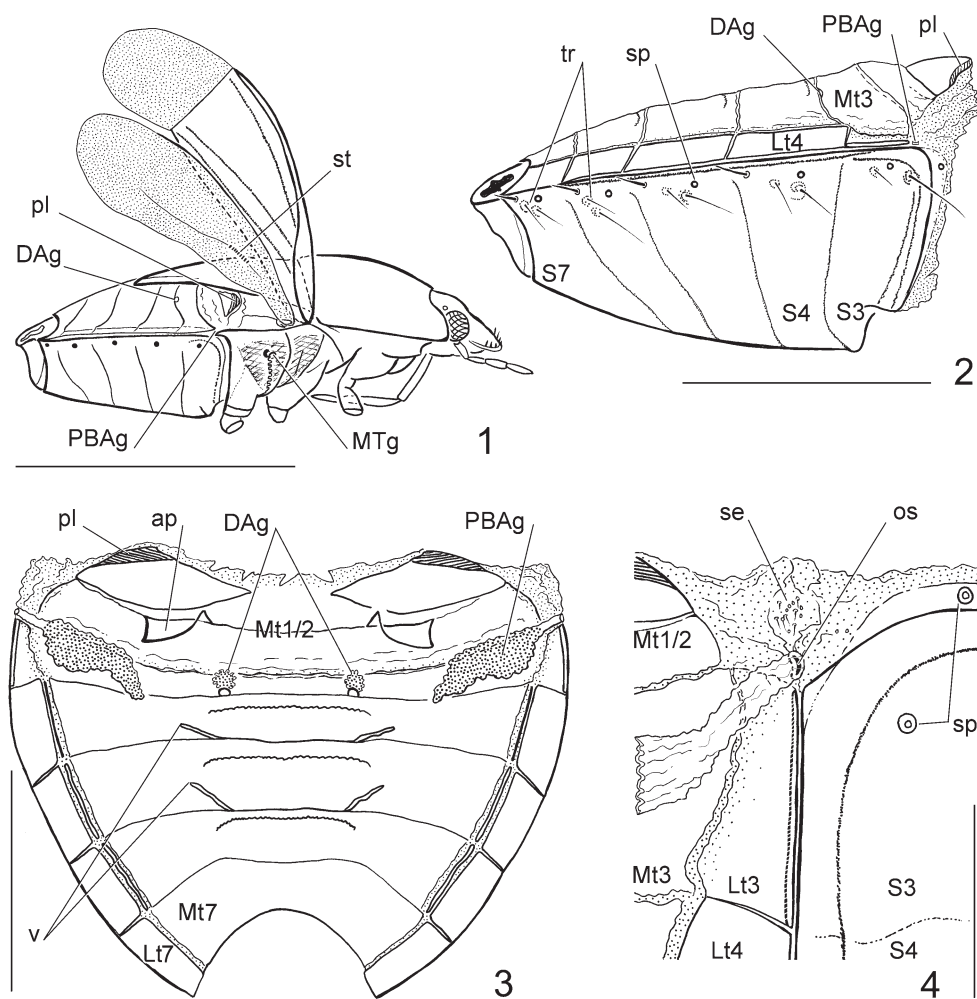
Figs. 1-4. *Paraethus capicola* (Westwood, 1837) (Geotomini), location of the male basi-abdominal glands. 1 – male adult in lateral view showing the site of the external opening of the glands and surrounding structures: stridulatory apparatus (plectrum and stridulitrum), anterior dorso-abdominal glands and metathoracic glands; scale bar: 5 mm. 2 – detail of the abdomen and location of the PBA gland ostiole; scale bar: 2 mm. 3 – internal view of the abdominal tergum, showing place of PBA glands and surrounding structures; scale bar: 2 mm. 4 – detail of the external opening on the pleural area in front of the sternite 3 and laterotergite 3, internal view; scale bar: 0.2 mm. Abbreviations: ap – apodeme; DAg – anterior dorso-abdominal gland; Lt – laterotergite; Mt – mediotergite; MTg – metathoracic gland; PBAg – pleuro basi-abdominal gland (ostiole); os – ostiole; pl – plectrum; S – sternite; sp – spiracle; se – setae; st – stridulitrum; tr – trichobothries; v – vestiges of the median and posterior dorso-abdominal glands.

(saccule); (3) a short bulbous receiving canal with fibrillae (Fig. 6). Such ductules exhibit the typical tripartite structure belonging to the three-cells secretory units often encountered in various hemipteran glands and comprising a spherical dilatation; see for instance the ductules illustrated in different glands and different taxa: the type B in Brindley's glands (BARRET et al. (1979) in *Rhodnius* Stål, 1859); the glandular units along tracheae (STADDON & EDMUNDS (1991) in *Aelia* Fabricius, 1803); the anterior dorso-abdominal glands (FARINE (1987) in *Dysdercus* Guérin Méneville, 1831).

The efferent canal of the reservoir is devoid of ductules. The membranous intima shows numerous regularly scattered pore-like holes which actually represent bases of small internal cone-shaped invaginations as shown in Fig. 7. I have never encountered such structures in other glands or in the literature and have no suggestion for their function.

In vivo observations. In live specimens, PBA glands appeared as more or less inflated white sacs embedded and anchored by the main tracheal branches. The gland reservoir was filled with a colourless substance. The produced material was relatively clear and watery, without perceptible odour.

The presence of muscles has not been ascertained. There is no muscle surrounding the gland reservoir and no distinct muscle fibers around the ostiole. The release of scent may be performed by some small indistinct muscles, but more probably also – at least partly – by the strong muscles relating to the adjacent stridulatory apparatus: i. e., lateral dorso-ventral muscles and longitudinal muscles (DRAŠLAR & GOGALA 1976). The mediotergal plate 1-2 can shift backward and forward extensively. The movement is allowed by the very large intersegmental membrane between mediotergites 1-2 and 3 (DUPUIS 1953) and the strong longitudinal muscles.

Emission of the secretion could not be studied. Nevertheless, secretory activity of the gland could be deduced from the appearance of the secretory cells, their variation in size, and from the content of the gland reservoir. Full secretory activity coincided with sexual activity.

In newly emerged male adults and all sexually immature males (with small testes, empty efferent lateral ducts and accessory glands), the gland reservoir was flat, small and seemingly empty. In sexually mature males (with large testes, efferent lateral ducts compactly filled with spermatozoa, accessory glands filled with secretion), the gland reservoir was larger and greatly distended with secretion.

Mating and copulatory position. Courtship behaviour and mating were observed several times in three species (*Macroscytus brunneus*, *Fromundus glaber*, *Chilocoris somalicus*) under experimental conditions. In addition, pairs in copula were often observed, discovered by surprise during cage cleaning in different species.

Our data confirm the observations already made by SCHORR (1957) for *Cydnus aterrimus* and by BERTINI (1978) for *Chilocoris somalicus*. The copulatory position is unusual for Heteroptera, the male being positioned underneath the female, never in the upper position or in the end-to-end position (or tail-to-tail position).

When sexually isolated males and females were placed together in the same container, mating took place usually within 10-20 minutes. Courtship behaviour is initiated by the male. The male approaches the female; there is a period of close body contact. When they make
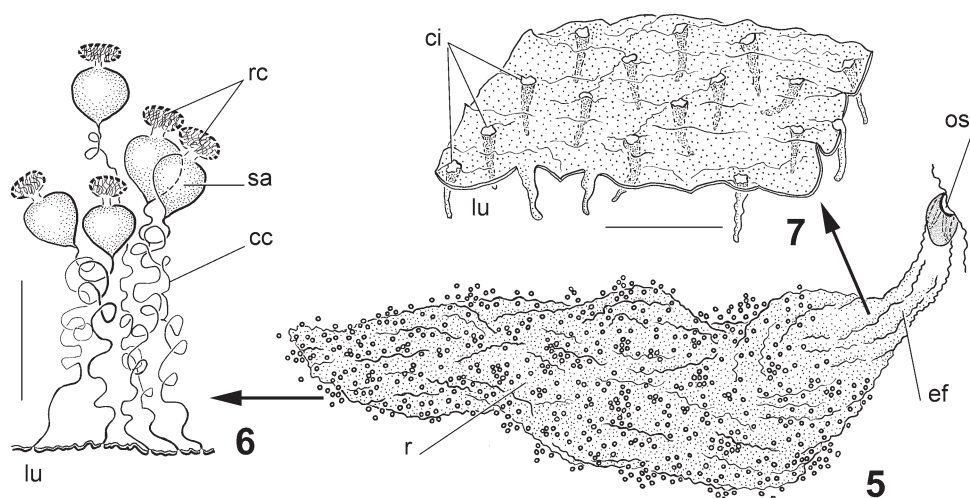
Figs. 5-7. *Paraethus capicola* (Westwood, 1837) (Geotomini), cuticular structure of the male basi-abdominal glands. 5 – general view of the glands; scale bar: 0.5 mm. 6 – detail of the tripartite ductules of the secretory units; scale bar: 0.02 mm. 7 – detail of the intima at the level of the efferent canal connecting the reservoir to the external opening; scale bar: 0.02 mm. Abbreviations: cc – conducting canal; ci – cone-shaped invagination; du – ductule; ef – efferent canal; lu – lumen; os – ostiole; r – reservoir; rc – receiving canal; sa – saccule.

contact the female becomes motionless. The male slips underneath the female, then extends its genitalia outwards and upwards to one side of the posterior tip of the female's abdomen. The female remains motionless. Copulation follows. The pair remains in copula, usually motionless, for several hours. A sudden direct lighting causes the separation of the pair. If disturbed, the female begins to walk, carrying the male with her; the male turned then upside down, lying on its back as illustrated by SCHORR (1957: Fig. 16).

Discussion

The paired pleural basi-abdominal glands are confined to the male adult burrower bugs. Within the Cydnidae, they seem restricted to the most speciose subfamily with a worldwide distribution, the Cydninae which contains two tribes, Cydnini and Geotomini. Their presence in both tribes – and absence in other subfamilies and other Pentatomoidea – suggests that the PBA glands could be considered a synapomorphic character of the subfamily Cydninae. They appear to be absent in Amaurocorinae, Cephalocteinae, and Sehirinae. Representatives of the other cydnid subfamilies, Amnestinae and Garsauriinae, were not examined, as well as other taxa formerly included within Cydnidae (i.e., *Dismegistus* Amyot & Serville, 1843, *Parastrachia* Distant, 1883, *Thaumastella* Horváth, 1896, *Thyreocoris* Schrank, 1801) and now placed in their own families (except *Dismegistus*). All these taxa should be examined. According to COBBEN (1968: 369), undescribed paired basi-abdominal glands exist in Thaumastellidae, but the author did not determine if these glands are present in both sexes.

Within Cydninae: Cydnini, the case of *Cydnus aterrimus* which is devoid of PBA glands is at first sight rather surprising – confirmation were made on several specimens – and cannot be currently explained; absence of glands might be a secondary loss.

In Heteroptera, the thoraco-abdominal junction is a body part rich in various glands, a region in which gland differentiation seems favoured. The cydnid PBA glands should not be confused with more or less similar paired glands known in this area in other heteropteran families. Omitting from discussion the widespread fundamental metathoracic glands (according Carayon (1962, 1971), they have an intersegmental unpaired ventral origin at the junction of thorax and abdomen), these glands are restricted in their distribution to particular species-groups. The Brindley's glands, considered as defensive, are known in most Reduviidae (Brindley 1930, Kälin & Barret 1975, Barret et al. 1979) and in the Pachynomidae (Carayon & Villiers 1968). Paired ventral glands – also known as 'Carayon's glands' as proposed by Staddon (1979) – are described in Phymatinae and some other Reduviidae (Carayon et al. 1958). Dorsolateral glands are present in all Tingidae on the thoraco-abdominal junction (Carayon 1962, Lis 2008) and were considered as homologous of the Brindley's glands (Carayon 1962), but this might be a convergence as confirmed by Schuh & Štys (1991). These glands are present in both sexes and sex dimorphism has never been encountered until now.

Sexual dimorphism in glandular systems may be observed in several heteropteran taxa at the level of the scent glands (metathoracic and dorso-abdominal glands) (see the reviews of Staddon 1979 and Aldrich 1988, 1996; see also Davidová-Vilímová & Podoubský 1999, Ho et al. 2003, Weirauch 2006). Sexual dimorphism may also be observed in the pregenital abdomen, where various glands are present in the male, but not in the female or are smaller in the latter. Nevertheless, in male land bugs, complex glands similar to the cydnid PBA glands, seem very rare: as far I am aware, only the paired sac-like sternal glands restricted to the male in some Anthocoridae (Carayon 1954) may be directly compared. In contrast, glandular sternal areas are rather common, particularly in pentatomomorphan bugs (Staddon 1979; Staddon & Edmunds 1991; Aldrich 1988, 1996). Glandular areas or setal patches in the sternites and laterotergites of male adults seems widespread within Pentatomoidea, where they are a likely source of sex pheromones: Carayon (1981: Pentatomoidea, 1984: Scutelleridae), Staddon (1990: Acanthosomatidae, 1999: Pentatomoidea), Staddon & Edmunds (1991: Pentatomoidea), Cassis & Vanags (2006: Scutelleridae). In Pentatomoidea, it seems the rule that the males emit pheromones that are attractive to females (Staddon 1990, Millar 2005; Zahn et al. 2008). According to Aldrich (1996), pheromones are produced by males in taxa characterized by large individuals.

The cydnid PBA glands are probably involved in pair formation, courtship, or mating. The secretory activity of the glands is correlated with sexual activity, for they become maximally active during the mating period. Therefore these glands might be the source of a sex pheromone attractive to the female.

In Cydnidae: Cydninae, the male mates slipping under the female and, if not disturbed, remains in this position during copulation. The dorsolateral position of the PBA glands could be efficient in diffusion of pheromones or an aphrodisiac substance for the female during courtship and mating. This copulatory position (the male underneath the female) is very unu-

sual in Heteroptera (SCHUH & SLATER 1995, SWEET 2006), but not as unique as these authors state. SCHORR (1957) already indicated that among the Heteroptera, aradids exhibit such an unusual copulatory position. Cydnidae: Cydninae exhibit the same position as the Aradidae (SCHORR 1957, present paper) and also Ceratocombidae as shown by MELBER & KÖHLER (1992) in *Ceratocombus coleoptratus* (Zetterstedt, 1819). SWEET (2006) considered that the aradid mating behavior (also male underneath female) is plesiomorphic compared to the side-to-side position of the Leptopodomorpha and Cimicomorpha, or to the end-to-end position of the Pentatomomorpha. But one may also consider that the male position underneath the female in both taxa may be a convergence due to relatively similar modes of life in tight spaces: subcorticolous in Aradidae, underground in soil or litter in Cydnidae: Cydninae, under moist moss in Ceratocombidae.

Within Cydnidae, this unusual copulatory position seems up to now restricted to the Cydninae. In Sehirinae devoid of PBA glands and living on plants, courtship is also initiated by the male but the copulatory position is end-to-end, as observed by SOUTHWOOD & HINE (1950: in *Tritomegas bicolor* (Linnaeus, 1758) (as *Sehirus*)) and by SITES & MCPHERSON (1982: in *Sehirus cinctus cinctus* (Palisot, 1811)).

The close proximity of the PBA glands and the sound-producing structures suggests a possible interaction between both organs. The PBA glands are necessarily affected by the movements of the tergal plate (fused terga 1 and 2) during stridulation or vibration. Specialized muscles can move the plates as a whole dorsoventrally, forward and backward, or deform it to produce tymbal sounds (DRAŠLAR & GOGALA 1976, GOGALA 1984). It is tempting to regard emission of the PBA glands as perhaps involved in the courtship behaviour and mating of Cydninae, acting in conjunction with stridulation. Data obtained in *Nezara viridula* (Linnaeus, 1758) suggest that pheromone emission might be modulated by acoustic signals from conspecifics in the mate recognition system (MIKLAS et al. 2003).

According to GOGALA (1984, 2006), acoustic communication is complex in Cydnidae. There is a combination of stridulation and abdominal low frequency vibration (DRAŠLAR & GOGALA 1976). Stridulation occurs in particular during mating, usually with two courtship songs (GOGALA 1969, 1970). However, acoustic communication in Cydnidae was mainly studied in sehirine species, and rarely in cydnine species: only two species have been investigated (*Cydnus aterrimus* and *Macroscytus brunneus*). GOGALA (1978) observed differences in the two subfamilies: in contrast to most Sehirinae, Cydninae do not show rivalry alternation but a kind of chorusing. There are also acoustic emissions of unclear function, probably aggregation signals, and possibly others.

These differences in sound emission between Sehirinae and Cydninae may be related to environmental factors, i.e., to the different ways of life of the two subfamilies: Sehirinae are plant-feeders and live on the above-ground parts of plants; Cydninae (Geotomini and Cydnini) are litter-inhabiting bugs, feeding on seeds or underground parts of plants. In such different environments, communication systems between sexes and individuals and the various signals (visual, chemical, vibrational, acoustic) are necessarily different. For instance, stridulatory signals are attenuated when transmitted through the soil (ČOKL et al. 2006). Cydninae are highly specialized for burrowing and the paired PBA glands could be an adaptive feature for

the underground environment. SCHAEFER (1972) found some correlations between habitat and importance of the metathoracic glands in land bugs: evaporative areas are well developed in ground living species; less developed in plant dwelling species.

Glandular systems have to be recorded and analyzed in Cydnidae. I am convinced that a careful comparison of both sexes in representatives of both subfamilies (Cydninae and Sehirinae) may reveal significant differences between the burrower cydnines and the plant dwelling sehirines. Possible correlations could be detected between glands, stridulatory structures, and ways of life.

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