

SHORT COMMUNICATION

Presence of uradenia in male adults of the genus *Dismegistus* (Hemiptera: Heteroptera: Parastrachiidae)

Dominique PLUOT-SIGWALT¹⁾ & Jerzy A. LIS²⁾

¹⁾ Museum national d'Histoire naturelle, Département Adaptation du Vivant, UMR 7179 MECADEV (mécanisme adaptatif et évolution), 57 rue Cuvier, CP 50 (Entomologie), F-75231 Paris, France; e-mail: dps@mnhn.fr

²⁾ Department of Biosystematics, Opole University, Oleska 22, PL-45-052 Opole, Poland; e-mail: cydnus@uni.opole.pl

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Abstract. Uradenia, often referred to as paragenital glands, are usually voluminous paired exocrine glands located ventrally in the abdomen mostly on the intersegmental membrane between abdominal segments (= urites) VII–VIII or VIII–IX, depending on sex or the taxon. They have been previously recorded from eight pentatomomorph families belonging to Coreoidea, Lygaeoidea and Pyrrhocoroidea (Hemiptera: Heteroptera), found either in males, females or both sexes, and were thought to be absent in Pentatomoidea. We report here the first instance of uradenia in a pentatomoid genus, the African *Dismegistus* Amyot & Serville, 1843 (Parastrachiidae). Only the male adult possesses uradenia located on the intersegmental membrane of segments VIII–IX. The only other genus of the family, *Parastrachia* Distant, 1883, as well as other examined genera belonging to pentatomoid families possibly related to Parastrachiidae (Cydnidae, Thyreocoridae), do not possess uradenia. The uradenia of *Dismegistus* exhibit the same fundamental structure as in other trichophoran families but differ by their dorso-lateral position (instead of ventral), and also by the paired orifices (instead of unpaired and median). The implications of the presence of uradenia within member of a pentatomoid genus are briefly discussed.

Key words. Hemiptera, Heteroptera, Pentatomoidea, Parastrachiidae, *Dismegistus*, *Parastrachia*, morphology, abdominal segment VIII, ectodermal gland, uradenia

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Introduction

The term “uradenia” – from the Greek, *ourà* and *adên* meaning: “posterior part” and “gland” – has been proposed by THOUVENIN (1965) to name paired ventral abdominal glands which are present on the last abdominal segments (= urites) in several representatives of Lygaeoidea, Pyrrhocoroidea and Coreoidea. Previously, these glands were variously referred to as “Oeldrüsen” in *Pyrrhocoris* Fallén, 1814 (MAYER 1874, 1875), “Drüsenschlauch” in *Lygaeus* Fabricius, 1794 (LUDWIG 1926), “paired accessory glands” in *Dysdercus* Guérin-Méneville, 1831 (GUPTA 1951), “paragenital glands” in females and “subgenital glands” in males of *Oncopeltus* Stål, 1868 (BONHAG & WICK 1953), “paragenital glands” in *Trichophora* (ŠTYS 1962), “sac-like structures” in males of *Dicranocephalus* Hahn, 1826 (LANSBURY 1965), “glande à huile” in *Pyrrhocoris* (MERLE

1965), “ventral uradenial scent glands” in Coreidae (STAD-
DON 1986), and finally “Uradenien” (KALLENBORN 2005).

In her well-documented comparative study, THOUVENIN (1965) showed that the paired uradenia are present in eight trichophoran families (Coreoidea: Alydidae, Coreidae, Stenocephalidae; Pyrrhocoroidea: Largidae, Pyrrhocoridae; Lygaeoidea: Lygaeidae, Rhyparochromidae), either in male, or in female, or in both sexes. Glands open directly to the exterior through the intersegmental membrane between abdominal segments VII–VIII or VIII–IX, or on abdominal segment IX (see Table 1), usually laterally in the female, in the mid-ventral line in the male through a single orifice, both glands being united just before the outlet into a short common efferent duct. In addition to detailed morphological data, THOUVENIN (1965) gave some information on the histological structures of the glands in



Table 1. Taxonomic distribution of the male and female uradenia in the main trichophoran families according to THOUVENIN (1965) and this study.

Superfamily	Taxon	Female uradenia	Male uradenia	Genera or tribes explicitly examined
Coreoidea	Alydidae	absent	VII–VIII, lobate, single median orifice	
	Coreidae	VIII–IX, bi- or multilobate, paired lateral orifices	VII–VIII, tubular or lobate, single median orifice	<i>Puppeia</i> , <i>Dalader</i> , <i>Holopterna</i>
	Coreidae: Petascelini (partim)	VII–VIII, branched, paired lateral orifices	VII–VIII, multibranching, paired orifices + lateral gl. IX on each side of the phallus	<i>Petascelis</i> , <i>Oxypristis</i>
	Coreidae: Petascelini (partim)	VIII–IX	[no data]	<i>Petascelisca</i>
	Rhopalidae	absent	VII–VIII, lobate, single median orifice	
	Stenocephalidae	absent	VII–VIII, sac-like, paired median orifices in a wide inter-segmental fold	<i>Dicranocephalus</i>
Pyrrhocoroidea	Pyrrhocoridae	IX, branched with basal reservoir, paired lateral orifices	absent	<i>Pyrrhocoris</i> , <i>Dysdercus</i> , <i>Dermatinus</i> , <i>Callibaphus</i>
	Largidae: Larginae	IX, reservoir + many diverticula, paired lateral orifices	absent	<i>Largus</i> , <i>Stenomacra</i>
	Largidae: Physopeltinae	absent	absent	
Lygaeoidea	Lygaeidae	VIII–IX near IX, tubular apically swollen, paired lateral orifices	VIII–IX, tubular or clavate, single median orifice	<i>Lygaeus</i> , <i>Oncopeltus</i> , <i>Lygaeosoma</i> , <i>Nysius</i>
	Rhyparochromidae (mentioned as Lygaeidae)	IX, paired orifices (save unpaired in Cleradini), tubular, apically globose	[no data]	<i>Beosus</i> , <i>Megalonotini</i> , <i>Myodochini</i>
Pentatomoidea	Parastrachiidae	absent	VIII–IX, branched with basal reservoir, paired orifices	<i>Dismegistus</i>
		absent	absent	<i>Parastrachia</i>
	remaining taxa	absent	absent	

Remarks. In her study, THOUVENIN (1965), unfortunately, did not provide a list of the species she examined. She only mentioned in the text some names of species or genera having glands and certainly not all the taxa (apparently numerous) she examined; the genera or tribes mentioned in her paper are included in the table.

both sexes. Histological and histochemical aspects of the female uradenia were also reported by CHEVAILLIER (1965) and FARINE (1988) in female *Dysdercus*. For the sake of completeness, we must add that CARAYON (1954) also described paired ventro-abdominal glands in the males of Anthocoridae (Scolopini), on sternite IV, rarely V; these glands were later recognized as uradenia by him. CARAYON (1972) considered that they were serially homologous of the uradenia described by THOUVENIN (1965) in trichophoran families.

Very little is known about the function of these glands. *In vivo*, the secretion has an oily and yellowish aspect at least in Coreidae and Pyrrhocoridae (MAYER 1874, 1875; MERLE 1965; DPS pers. observations) and also in Anthocoridae (CARAYON 1954). Only male uradenia in coreid bugs (species of *Pachylis* Le Pelletier & Serville, 1825, *Euthochtha* Mayr, 1865, and mainly *Leptoglossus* Guérin-Méneville, 1831 were studied (as “ventral abdominal gland”) and evidence for male-produced sex pheromones has been demonstrated (ALDRICH & YONKE 1975; ALDRICH et al. 1976, 1979, 1982; GOUGH et al. 1985; ALDRICH 1988; WANG & MILLAR 2000). The secretion of the male uradenia releases species-specific volatile compounds that may act as long-range attractants for the female; it may have the odour of cherries, vanilla, cinnamon and rose (ALDRICH 1988).

Uradenia are considered as lacking within the Pentatomoidea (THOUVENIN 1965, STADDON 1979, PAVIS 1987).

Therefore, the discovery in adult males of the genus *Dismegistus* Amyot & Serville, 1843, of a paired abdominal gland exhibiting morphological characteristics of the uradenia previously described within other trichophoran subfamilies, was unexpected. It is interesting especially because the phylogenetic position of *Dismegistus* within Pentatomoidea has been a matter of debate for a long time and still remains somewhat enigmatic (LIS et al. 2017).

The African genus *Dismegistus* includes six described aposematic species, and was originally placed in Cydnidae Sehirinae by AMYOT & SERVILLE (1843). Later, on the basis of morphological characters, it was transferred to Pentatomidae Pentatominae Strachiini (SIGNORET 1881), to Pentatomidae Asopinae (BERGROTH 1923) jointly with the Asiatic genus *Parastrachia* Distant, 1883, including only two aposematic species and having been placed into various pentatomid groups (Asopinae, Pentatominae, Tessaratomidae, Cydnidae) (see SCHAEFER et al. 1988 and SWEET & SCHAEFER 2002) until LESTON (1956), after a large comparative study of morphological characters including male and female genitalia, proposed the placement of *Dismegistus* among the Cydnidae Sehirinae. After having rectified several of Leston’s misinterpretations, DOLLING (1981) concluded that *Dismegistus* cannot belong to Cydnidae. More recently, PLUOT-SIGWALT & LIS (2008) showed the great similarity in the structure of the spermatheca in *Dismegistus* and *Parastrachia*, suggesting close relation-

ships between these genera. In a phylogenetic analysis of the Pentatomoidea based on morphological and molecular characters, GRAZIA et al. (2008) recognized the group of *Parastrachia* + *Dismegistus* as monophyletic and suggested that the family Parastrachiidae is apparently related to the Cydnidae and Thyreocoridae. MATESCO et al. (2012) following GRAZIA et al. (2008) included the Parastrachiidae (as Parastrachiinae) in the Thyreocoridae in the broadest sense, but a recent molecular analysis (LIS et al. 2017) proved it was unjustified. In the same paper (LIS et al. 2017) the monophyly of *Parastrachia* + *Dismegistus* suggested previously by GRAZIA et al. (2008) was also questioned.

The purpose of this paper is to describe the main structural features of the uradenia in *Dismegistus* spp. and to compare them with those described in male Coreoidea and Lygaeoidea. We also investigated *Parastrachia*, the second genus of the family to verify whether it has uradenia similar to the condition found in *Dismegistus*.

In order to facilitate the comparison of the male uradenia of *Dismegistus* with those known in other trichophoran families, we firstly summarise the main features of the male and female uradenia in Coreoidea, Lygaeoidea, Pyrrhocoroidea as described by THOUVENIN (1965). Table 1 reviews the main conditions of the glands (presence-absence, shape, location, number of orifices) given by THOUVENIN (1965) in both sexes of representatives of eight trichophoran families. Female uradenia are lacking in Alydidae, Rhopalidae and Stenocephalidae; male uradenia in Pyrrhocoridae and Largidae Larginae, while Physopeltinae lack uradenia in both sexes. To date, only Coreidae and Rhyparochromidae are known to possess uradenia in both sexes.

Uradenia are variously shaped compound ectodermal glands: sac-like, tubular, clavate, branched or lobate. They are characterized by several common features: ventral location on posterior abdominal segments, paired condition with unpaired orifice (usually in males) or paired orifices (usually in females), opening directly to the exterior, sexual dimorphism frequent, size moderate to large. THOUVENIN (1965) gave the following definition (in French) for the uradenia: “Ectodermal glands, serially homologous, derived from the abdominal segments VII to X, having paired or unpaired ventral orifice”.

Material and methods

Species examined. Male and female dried specimens of *Dismegistus sanguineus* (De Geer, 1778) (Kenya), *D. fimbriatus* (Thunberg, 1783) (South Africa), and *Parastrachia japonensis* (Scott, 1880) (Japan) were examined.

Methods. The entire abdomen was separated from the body and cleared (24 hours) in cold 10% KOH solution. It was then washed in water and stored in glycerol. After careful dissection, the abdomen was placed in an alcoholic solution of chlorazol black for staining of the membranous components, and then placed in glycerol for observation, gland localisation, and further dissection, if necessary. Small pieces of tegument bearing glands were observed using a microscope at 100–200× magnifications.

Terminology. We follow the terminology proposed by THOUVENIN (1965) naming the uradenia according the seg-

mental or intersegmental origin of the glands, i.e., uradenia VII–VIII or VIII–IX open on intersegmental membrane delimited by abdominal segments VII–VIII or VIII–IX respectively; uradenia IX open on abdominal segment IX. Gland terminology follows NOIROT & QUENNEDEY (1991).

Results

Among the species examined only males of *Dismegistus sanguineus* and *D. fimbriatus* possess uradenia. *Dismegistus* females and both sexes in *Parastrachia* are devoid of any ventral abdominal glands at the level of the last abdominal segments.

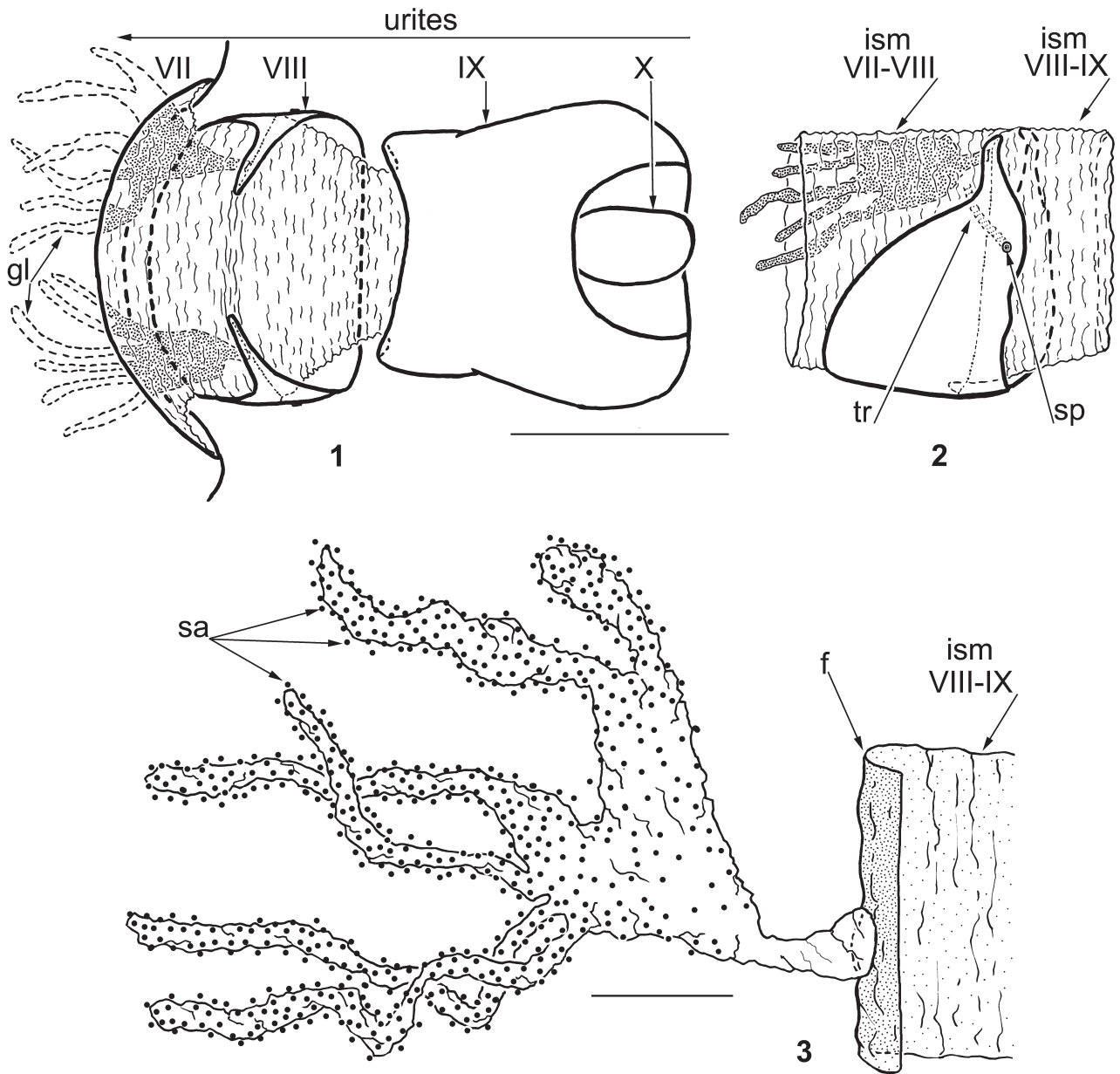
The male uradenia VIII–IX in *Dismegistus*. In *Dismegistus*, the male uradenia are partially lying in abdominal segment VIII and open to the exterior dorso-laterally through the intersegmental membrane between abdominal segments VIII–IX. The abdominal segment VIII succinctly illustrated by LESTON (1956) in *D. sanguineus* (as *D. binotatus*) is described first in *D. sanguineus*, prior to the gland description.

The abdominal segment VIII (Figs 1, 2, 4). At rest, abdominal segment VIII is almost totally telescoped within segment VII. It is not distinct as it is the rule in most Pentatomoidea, the segment is reduced and poorly sclerotized; there is no distinction between tergum and sternum; the venter and lateral margins are large, the dorsum is short and mostly membranous, only two lateral sclerotized stripes remain from the progressively reduced margins (Figs 1, 2, 4). We agree with BAKER (1931) regarding the condition of abdominal segment VIII in Pentatomidae: “it is probable that the eighth segment is largely, if not entirely, made up from the eighth sternum with the resultant atrophy of the eighth tergum”. The spiracles are placed in lateral position, close to the posterior margins, and are relatively well developed compared to the remaining abdominal spiracles and also functional, provided with tracheae and a closing valve. As in other Pentatomoidea, the intersegmental membrane VIII–IX arises far from the posterior margin of abdominal segment VIII (LESTON 1953c).

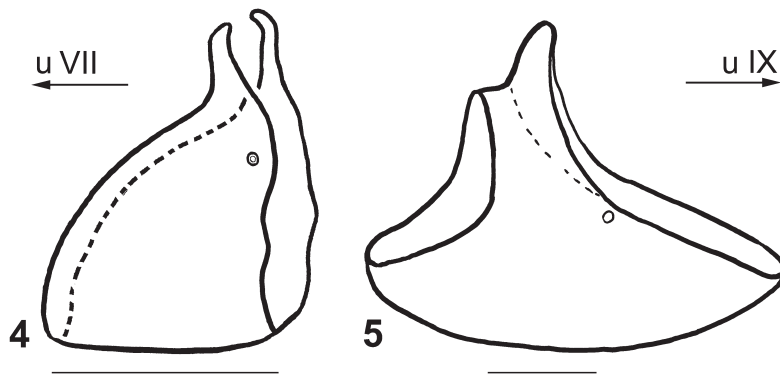
Surprisingly, segment VIII in *Parastrachia* is quite different from that of *Dismegistus*. The former was described in detail and illustrated by SCHAEFER et al. (1988) in *P. nagaensis* (Distant, 1908) and *P. japonensis*. We provide the illustration which allows comparison of *P. japonensis* with *D. sanguineus* (Figs 4, 5). In contrast to *Dismegistus*, the segment VIII in *Parastrachia* is largely exposed (not concealed within segment VII), ventrally produced anteriorly and posteriorly, the short dorsum is sclerotized (not membranous) and the spiracle is vestigial and non-functional.

Gross morphology of the glands (Fig. 3). In both examined species of the genus *Dismegistus*, uradenia constitute voluminous paired glands that lie inside abdominal segment VIII and extend anteriorly at least into abdominal segment VII.

Each gland consists of a basal sac-like reservoir extending distally into five to six long and tubular digitations (Fig. 3). They are much longer and thinner in *D. fimbriatus* than in *D. sanguineus*, and extend along the abdomen



Figs 1–3. Male uradenia in *Dismegistus sanguineus* (De Geer, 1778). 1 – dorsal view of the last abdominal segments (VII to X) showing location of the paired uradenia (scale bar = 1 mm). 2 – abdominal segment VIII and uradenia in lateral view (scale bar = 1 mm). 3 – detail of a gland and of its opening into the fold of the intersegmental membrane VIII–IX (scale bar = 0.5 mm). Abbreviations: f – fold; gl – glands; ism – intersegmental membrane; sa – saccule of a ductule); sp – spiracle; tr – trachea.



Figs 4–5. Male abdominal segment VIII, lateral view. 4 – *Dismegistus sanguineus* (De Geer, 1778); 5 – *Parastrachia japonensis* (Scott, 1880). Scale bar = 1 mm.

nearly to the thorax in the former, while only along abdominal segment VII in the latter species (Fig. 1). Numerous tracheoles are intertwined to form an inextricable network with the digitations. Glands open separately dorsolaterally via a short efferent canal and a pore located – just under the sclerotized stripes of abdominal segment VIII – in a transverse fold of intersegmental membrane VIII–IX which is apparently permanent. No particular structure (such as muscular apodeme, sclerotization or thickening) is associated with the orifice which therefore is hard to locate.

The thin membranous cuticular intima of the gland is strongly wrinkled; it is entirely covered with hundreds of short cuticular ductules which open into the lumen and represent the efferent duct of the glandular units covering the intima in living specimens. Ductules are denser along the digitations than on the sac itself. The structure of the efferent ductules is the same as that already described in the female uradenia of *Dysdercus* (FARINE 1988), i.e. it is characterized by a minute apical spherical dilation called a “sacculle”.

Discussion

The male *Dismegistus* is the first representative of Pentatomoidea known to possess male uradenia similar to representatives of eight families belonging to Coreoidea, Pyrrhocoroidea and Lygaeoidea. The female of *Dismegistus* as well as both sexes of *Parastrachia*, the second genus of Parastrachiidae, do not possess these glands. We are also confident that the majority of the pentatomoid families do not possess uradenia, in particular the Cydnidae and Thyreocoridae, considered to be related to Parastrachiidae (GRAZIA et al. 2008, LIS et al. 2017). This opinion is based on the results of previous studies, where numerous species of Cydnidae and Thyreocoridae were examined (PLUOT-SIGWALT & LIS 2008, PLUOT-SIGWALT 2008), as well as results of an unpublished survey devoted to a novel exocrine gland specific to most Pentatomoidea and absent in *Dismegistus* (PLUOT-SIGWALT, in preparation).

Particularities of the uradenia VIII–IX in *Dismegistus*.

Although the paired glands in the male of *Dismegistus* and the male uradenia in other trichophoran families share the same fundamental structure, they also exhibit three peculiarities.

(1) *Dismegistus* shares only with the Lygaeidae a location of the orifice between abdominal segments VIII and IX, almost adjoining to abdominal segment VIII in *Dismegistus*, to abdominal segment IX in Lygaeidae. In other families (Table 1) orifices of male uradenia are located on intersegmental membrane VII–VIII.

(2) *Dismegistus* is the only genus having a pair of orifices of the uradenia in dorsolateral position; in the other trichophoran families male uradenia usually open with a single median orifice ventrally, with the exception of several representatives of Coreidae Petascelini (members of the genera *Petascelis* Signoret, 1847 and *Oxypritis* Signoret, 1861) in which their efferent ducts are not united and have paired medioventral orifices on intersegmental membrane VII–VIII.

(3) The glove-like, digitate shape of the gland is particular to *Dismegistus*, but it is similar to multi-digitate or lobate glands observed in male Coreidae, and the indented uradenia found in female Pyrrhocoridae.

The definition given by THOUVENIN (1965) for the uradenia can be applied to the uradenia of *Dismegistus*, except for the location of the orifices. The fact that abdominal segment VIII undergoes considerable modification in the adult stage may explain this particular location. However, it should be noted that male uradenia VIII–IX in the Lygaeidae have a single ventromedian orifice.

Therefore, at present, it is unclear whether these structures in *Dismegistus* and in other trichophoran families are homologous or not.

On some morphological differences between *Dismegistus* and *Parastrachia*. Though *Dismegistus* and *Parastrachia* were suggested by GRAZIA et al. (2008) as a monophyletic group, and a close relationship between the two genera was also suggested by PLUOT-SIGWALT & LIS (2008), on the basis of similarities in the structure of the spermatheca, their monophyletic origin was not confirmed recently in results of studies on the 18S+28S rDNA of pentatomoid bugs (LIS et al. 2017).

However, there are several shared morphological characters by *Dismegistus* and *Parastrachia* besides those accepted by GRAZIA et al. (2008), e.g., the coxal combs (LIS 2010a), pretarsal structures (LIS 2010b); the presence of a median groove accompanied with dense setae on the tarsal margins (J. A. Lis, unpublished data), and metathoracic wing venation (LIS & HEYNA 2001). Moreover, these morphological characters are same as in species of the subfamily Sehirinae (LIS & HEYNA 2001; LIS 2010a,b). A similarity of *Dismegistus* and *Parastrachia* to the species of Sehirinae was confirmed also in the molecular study based on the nuclear ribosomal DNA sequences (LIS et al. 2017).

Nevertheless, both genera of Parastrachiidae exhibit autapomorphies (LIS & SCHAEFER 2005) found in the tibial combs, i.e., their two outer setae are a slightly longer (in *Parastrachia*) and clearly longer (in *Dismegistus*) than the remaining ones, and the median concavity of tibial fossula bears long setae in *Parastrachia*, and very short setae in *Dismegistus*.

Moreover, in addition to the presence of uradenia, the present study shows that several characters of the abdominal segment VIII separate *Dismegistus* and *Parastrachia*. These characters were not mentioned in the analysis of GRAZIA et al. (2008) who attributed characters found in *Parastrachia* to *Dismegistus* as well.

In *Dismegistus*, segment VIII is not exposed posteriorly as in *Parastrachia*, but it is entirely telescoped into the abdominal segment VII as in most Pentatomidae. Except of *Parastrachia*, within Pentatomoidea, the male abdominal segment VIII is exposed ventrally only in Acanthosomatidae (KUMAR 1974), Urostylididae (GAPUD 1991), Lestoniidae, and Tessaratomidae (Tessaratominae: Platytatini and Sepinini) (GRAZIA et al. 2008).

In *Dismegistus*, the dorsum of abdominal segment VIII is not sclerotized as in *Parastrachia*. It is membranous in a similar way as in many pentatomoid representatives

(Pentatomidae, Acanthosomatidae, Tessaratomidae, Dinidoridae) (LESTON 1953a,b,c, 1954a,b). The general shape of the abdominal segment VIII in *Dismegistus* is somewhat similar to that illustrated by LESTON (1954b) for *Coridius* Illiger, 1807 (Dinidoridae) and *Elisabetha* Schouteden, 1916 (Tessaratomidae).

GRAZIA et al. (2008) indicated that spiracles of segment VIII were absent in Parastrachiidae, in particular in *D. sanguineus*. This contradicts our findings, which document non-functional and atrophied spiracles in *Parastrachia* (DPS, pers. observations). In *Dismegistus*, the presence of functional spiracles is not surprising given that glandular organs require oxygen for their activity and are always associated with a network of tracheae. Within Pentatomoidea, functional spiracles on segment VIII are known in some Phloeidae (LESTON 1953c) and in Tessaratomidae (LESTON 1954b). RIBAUT (1923) described also the spiracles of the pentatomid *Rhaphigaster nebulosa* (Poda, 1761) as functional, while in other pentatomids they are completely lacking.

Taxonomic and phylogenetic significance of uradenia.

THOUVENIN (1965) and CARAYON (1972) claimed that uradenia have a taxonomic value mainly at higher taxonomic levels. The general shape of the gland is consistent within a given family: female Pyrrhocoridae possess highly indented uradenia, male and female Lygaeidae tubular glands, male Stenocephalidae sac-like uradenia (THOUVENIN 1965; MERLE 1969; FARINE 1988; DPS, pers. observations). Presence or absence of the uradenia may be also informative for classification; in Largidae, female uradenia are present in Larginae, but not in Physopeltinae. THOUVENIN (1965) considered the distribution of the uradenia within the Coreidae as somewhat “capricious”; the glands are indeed often lacking in females (DPS, personal observations) and may be lacking in males.

Are the uradenia in *Dismegistus* phylogenetically informative? At present, we cannot answer this question, given that we cannot determine whether the uradenia of *Dismegistus* are homologous to those of other pentatomomorphans or evolved independently.

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References

ALDRICH J. R. 1988: Chemical ecology of the Heteroptera. *Annual Review of Entomology* **33**: 211–238.
 ALDRICH J. R., BLUM M. S., DUFFEYS S. S. & FALES H. M. 1976: Male specific natural product in the bug, *Leptoglossus phyllopus*: Chemistry and possible function. *Journal of Insect Physiology* **22**: 1201–1206.

ALDRICH J. R., BLUM M. S. & FALES H. M. 1979: Species-specific natural products of adult male leaf-footed bugs (Hemiptera: Heteroptera). *Journal of Chemical Ecology* **5**: 53–62.
 ALDRICH J. R., KOCHANSKY J. P., LUSBY W. R. & DUTKY S. R. 1982: Volatile male-specific natural products of a coreid bug (Hemiptera: Heteroptera). *Journal of Chemical Ecology* **8**: 1369–1376.
 ALDRICH J. R. & YONKE T. R. 1975: Natural products of abdominal gland and metathoracic glands of coreid bugs. *Annals of the Entomological Society of America* **68**: 955–960.
 AMYOT C. J. B. & [AUDINET-]SERVILLE J. G. 1843: *Histoire naturelle des Insectes. Hémiptères*. Librairie encyclopédique de Roret, Paris, lxxvi + 675 + 6 pp.
 BAKERA. D. 1931: A study of the male genitalia of Canadian species of Pentatomidae. *Canadian Journal of Research* **4**: 148–220.
 BERGROTH E. 1923: On the systematic position of the genera *Dismegistus* A. & S. and *Parastrachia* Dist. *Annales de la Société Entomologique de Belgique* **63**: 70–72.
 BONHAG P. F. & WICK J. R. 1953: A functional anatomy of the milkweed bug, *Oncopeltus fasciatus* (Dallas) (Heteroptera: Lygaeidae). *Journal of Morphology* **93**: 177–284.
 DOLLING W. R. 1981: A rationalized classification of the burrower bugs (Cydnidae). *Systematic Entomology* **6**: 61–76.
 CARAYON J. 1954: Un type nouveau d'appareil glandulaire propre aux mâles de certains Hémiptères Anthocoridae. *Bulletin du Muséum National d'Histoire Naturelle, 2 Série* **26**: 602–606.
 CARAYON J. 1972: Caractères systématiques et classification des Anthocoridae (Hemipt.). *Annales de la Société Entomologique de France, Nouvelle Série* **8**: 309–349.
 CHEVAILLIER P. 1965: Etude des phénomènes sécrétoires dans les uradénies des femelles de *Dysdercus fasciatus* Sign. (Hemiptera, Pyrrhocoridae). *Annales de la Société Entomologique de France, Nouvelle Série* **1**: 989–994.
 FARINE J. P. 1988: The exocrine glands of *Dysdercus cingulatus* F. (Heteroptera: Pyrrhocoridae): morphology and function of adults' glands. *Annales de la Société Entomologique de France, Nouvelle Série* **24**: 241–256.
 GAPUD V. P. 1991: A generic revision of the subfamily Asopinae, with consideration of its phylogenetic position in the family Pentatomidae and superfamily Pentatomoidea (Hemiptera-Heteroptera). *Philippine Entomologist* **8**: 865–961.
 GOUGH A. J. E., GAMES D. E., STADDON B. W. & OLAGBEMIRO T. O. 1985: Male produced volatiles from coreid bug *Leptoglossus australis* (Heteroptera). *Zeitschrift für Naturforschung* **40c**: 142–144.
 GRAZIA J., SCHUH R. T. & WHEELER W. C. 2008: Phylogenetic relationships of family groups in Pentatomoidea based on morphology and DNA sequences (Insecta: Heteroptera). *Cladistics* **24**: 932–976.
 GUPTA P. D. 1951: On the structure, development and homology of female reproductive organs of *Dysdercus cingulatus* (Fabr.) (Heteroptera). *Indian Journal of Entomology* **11** [1949–1951]: 131–142.
 KALLENBORN H. G. 2005: Was wissen wir über die Uradenien (ventralen Abdominaldrüsen) der Wanzen? *Heteropteron* **21**: 17–19.
 KUMAR R. 1974: A revision of World Acanthosomatidae (Heteroptera: Pentatomoidea): keys to and descriptions of subfamilies, tribes and genera with designation of types. *Australian Journal of Zoology, Supplementary Series* **34**: 1–60.
 LANSBURY I. 1965: New organ in Stenocephalidae (Hemiptera-Heteroptera). *Nature* **205**: 106.
 LESTON D. 1953a: Notes on the Ethiopian Pentatomoidea (Hem.). XVI, An Acanthosomatid from Angola, with remarks upon the status and morphology of Acanthosomatidae Stål. *Publicações Culturais de Companhia de Diamantes de Angola* **16**: 123–132.
 LESTON D. 1953b: On the wing-venation, male genitalia and spermatheca of *Podops inucta* (F.), with a note on the diagnosis of the subfamily Podopinae Dallas (Hem., Pentatomidae). *Journal of the Society for British Entomology* **4**: 129–135.
 LESTON D. 1953c: Phloeidae Dallas (Hem. Pentatomoidea): systematics and morphology, with remarks on the phylogeny of Pentatomoidea Leach and upon the position of *Serbana* Distant. *Revista Brasileira de Biologia* **13**: 121–140.
 LESTON D. 1954a: Notes on the Ethiopian Pentatomoidea (Hem.). XII, On some specimens from Southern Rhodesia, with an investigation of certain features in the morphology of *Afrius figuratus* (Germar) and

- remarks upon the male genitalia in Amyotinae. *Occasional Papers of the National Museum of Southern Rhodesia* **19**: 678–686.
- LESTON D. 1954b: Wing venation and male genitalia of Tessaratoma Berthold, with remarks on Tessaratominae Stål (Hemiptera: Pentatomidae). *Proceedings of the Royal Entomological Society of London, Series A* **29**: 9–16.
- LESTON D. 1956: The Ethiopian Pentatomoidea (Hemiptera). XXII, On Dismegistus Amyot & Serville (Cydnidae). *Proceedings of the Royal Entomological Society of London, A* **31**: 87–94.
- LIS J. A. 2010a: Coxal combs in the Cydnidae sensu lato and three other related “cydnoid” families – Parastrachiidae, Thaumastellidae, Thyreocoridae (Hemiptera: Heteroptera): functional, taxonomic, and phylogenetic significance. *Zootaxa* **2476**: 53–64.
- LIS J. A. 2010b: Pretarsal structures in the family Parastrachiidae (Hemiptera: Heteroptera: Pentatomoidea). *Zootaxa* **2693**: 60–62.
- LIS J. A. & HEYNA J. 2001: Metathoracic wings venation in Cydnidae (Hemiptera: Heteroptera) and its bearing on the classification of the family. *Annales Zoologici* (Warszawa) **51**: 429–465.
- LIS J. A. & SCHAEFER C. W. 2005: Tibial combs in the Cydnidae (Hemiptera: Heteroptera) and their functional, taxonomic and phylogenetic significance. *Journal of Zoological Systematics and Evolutionary Research* **43**: 277–283.
- LIS J. A., ZIAJA D., LIS B. & GRADOWSKA P. A. 2017: Non-monophyly of the “cydnoid” complex within Pentatomoidea (Hemiptera: Heteroptera) revealed by Bayesian phylogenetic analysis of nuclear rDNA sequences. *Arthropod Systematics and Phylogeny* **75**: 481–496.
- LUDWIG W. 1926: Untersuchungen über den Copulationsapparat der Baumwanzen. *Zeitschrift für Ökologie und Morphologie der Tiere* **5**: 291–380.
- MATESCO V. C., BIANCHI F. M., CAMPOS L. A. & GRAZIA J. 2012: Egg ultrastructure of two species of Galgupha Amyot & Serville, with a discussion of the eggs and oviposition patterns of thyreocorid and allied groups (Hemiptera: Heteroptera: Pentatomoidea: Thyreocoridae). *Zootaxa* **3247**: 43–51.
- MAYER P. 1874: Anatomie von Pyrrhocoris apterus. I. *Archiv für Anatomie, Physiology und Wissenschaftliche Medicin* **7**: 313–347 + pls. vii–ix.
- MAYER P. 1875: Anatomie von Pyrrhocoris apterus. II. *Archiv für Anatomie, Physiology und Wissenschaftliche Medicin* **8**: 309–355 + 341–344 bis, pls. ix–x.
- MERLE J. 1969: Anatomie des appareils génitaux mâle et femelle et fonctionnement ovarien de Pyrrhocoris apterus (L.) (Hemiptera, Pyrrhocoridae). *Acta Entomologica Bohemoslovaca* **66**: 275–288.
- NOIROT C. & QUENNEDEY A. 1991: Glands, gland cells, glandular units: some comments on terminology and classification. *Annales de la Société Entomologique de France, Nouvelle Série* **27**: 123–128.
- PAVIS C. 1987: Les sécrétions exocrines des Héteroïptères (allomones et phéromones). Une mise au point bibliographique. *Agronomie* **7**: 547–561.
- PLUOT-SIGWALT D. 2008: A pair of basi-abdominal sex pheromone glands in the male of some burrower bugs (Hemiptera: Heteroptera: Cydnidae). *Acta Entomologica Musei Nationalis Pragae* **48**: 511–522.
- PLUOT-SIGWALT D. & LIS J. A. 2008: Morphology of the spermatheca in the Cydnidae (Hemiptera: Heteroptera): bearing of its diversity on classification and phylogeny. *European Journal of Entomology* **105**: 279–312.
- RIBAUT H. 1923: L'urite IX des mâles chez les Pentatomides. *Bulletin de la Société d'Histoire Naturelle de Toulouse* **51**: 183–184.
- SCHAEFER C. W., DOLLING W. R. & TACHIKAWA S. 1988: The shieldbug genus Parastrachia and its position within the Pentatomoidea (Insecta: Hemiptera). *Zoological Journal of the Linnean Society* **93**: 283–311.
- SIGNORET V. 1881: Révision du groupe des Cydnides, I. *Annales de la Société Entomologique de France, 6^e Série* **1**: 25–52.
- STADDON B. W. 1979: The scent glands of Heteroptera. *Advances in Insect Physiology* **14**: 351–418.
- STADDON B. W. 1986: Biology of scent glands in the Hemiptera-Heteroptera. *Annales de la Société Entomologique de France, Nouvelle Série* **22**: 183–190.
- ŠTYS P. 1962: Morphology of the abdomen and female ectodermal genitalia of the trichophorous Heteroptera and bearing on their classification. Pp. 37–43. In: STROUHAL H. & BEIER M. (eds.): *XI. Internationaler Kongress für Entomologie. Wien, 17. bis 25. August 1960. Verhandlungen. Band I (Sektion I bis VI)*. Organisationskomitee des XI. Internationalen Kongresses für Entomologie, Wien, xlv + 803 pp. + xx pls.
- SWEET M. H. & SCHAEFER C. W. 2002: Parastrachiinae (Hemiptera: Cydnidae) raised to family level. *Annals of the Entomological Society of America* **95**: 441–448.
- THOUVENIN M. 1965: Etude préliminaire des “uradénies” chez certains Hémiptères Pentatomomorphes. *Annales de la Société Entomologique de France, Nouvelle Série* **1**: 973–988.
- WANG Q. & MILLAR J. G. 2000: Mating behavior and evidence for male-produced sex pheromones in *Leptoglossus clypealis* (Heteroptera: Coreidae). *Annals of the Entomological Society of America* **93**: 972–976.

