

Dorsal abdominal glands in *Aradus betulae* (Heteroptera, Aradidae)¹

J. DAVIDOVÁ-VILÍMOVÁ

Abstract: Dorsal abdominal scent glands (= DAGs) develop as three unpaired structures in the nymphs of *Aradus betulae* (LINNAEUS 1758). The reservoirs of all three DAGs persist in the adults, are distinctly larger in males than in females, and are responsible for slight sexual dimorphism. The possible function of the adult DAGs in the Aradidae is discussed in relation to specific aradid biology.

Key words: Adult dorsal abdominal glands, function, ostiole, persistence in adults, reservoir.

Introduction

Combined development of the larval dorso-abdominal and the adult metapleural scent glands represents an apomorphy of the Heteroptera. The scent glands were first described in adult Heteroptera by DUFOUR (1833) and in the nymphs by KÜNKELE (1866). The larval dorso-abdominal scent glands (= DAG/DAGs) develop as serially metameric invaginations of the epidermis, up to a maximum of five (STADDON 1979). VERHOEFF (1893) first mentioned the persistence of the DAGs in heteropteran adults, HENRICI (1939) confirmed this phenomenon in subsequent morphological studies. DUPUIS (1947) presented a brief summary of the literature, based on his own results and published data. Consequently, he has been incorrectly referred to by other authors as the first individual who described the DAGs' persistence in adults. The recent literature concerning the DAGs' persistence in the adults has been reviewed by COBBEN (1978), STADDON (1979, 1986), and ALDRICH (1988a, 1988b, 1996).

Previously, the complete reduction of DAGs in adults and the total substitution of these structures by metapleural scent glands (= MTG/MTGs) often has been uncritically accepted. The wings, because they pre-

vent evaporation from the DAGs, have been suggested as the main cause of the DAGs' reduction (e.g., GUPTA 1964). However, many recent studies have confirmed the adult DAGs' persistence in the Heteroptera (e.g., GOUGH et al. 1985; JAMES & WARREN 1989; STADDON 1990, 1999). Representatives of nine higher taxa, five of them classified within the Pentatomoidea, possess functional DAGs as adults. Even sexual dimorphism of adult DAGs have been found to vary in several taxa (e.g., DUPUIS 1949; GOUGH et al. 1985).

VERHOEFF (1893) mentioned the presence of ostioles of DAGs in the adults of *Aradus* species. USINGER & MATSUDA (1959) referred to the more or less persistent DAGs' openings in representatives of all aradid subfamilies. They employed this character in a diagnostic key and phylogenetic discussion. LESTON (1955) provided the sole examination of DAGs' reservoirs in the adults of *Aradus cinnamomeus* PANZER 1806. Several studies have described the DAGs' ostioles in adults of the Aradidae, conspicuously more distinct in apterous taxa (e.g., MONTEITH 1966, 1997; VÁSÁRHELYI 1982; JACOBS 1986; HEISS 1988, 2004). The DAGs' reservoirs and the secretory units have not been described in detail so far in the adults of any aradid taxon.

¹It is great pleasure to dedicate this paper to Ernst Heiss, who is not only a famous heteropterist but also a wonderful person. This paper represents actually only an insignificant event in comparison with Ernst's whole-life excellent contributions to the knowledge of the family Aradidae.

Figs 1-3. *Aradus betulae* (LINNAEUS 1758), 2nd instar (1) whole body, dorsal view (2) detail of DAGs' ostioles and reservoirs visible through cuticle, dorsal view (3) detail of dissected DAGs' ostioles, ventral view. 3, 4, 5, 6 - abdominal terga; o - DAG's ostiole.



The family Aradidae is accepted as the closest relative of the Pentatomoidea by most authors (e.g., SCHAEFER 1993). The aradids have developed a cryptic way of life, either beneath bark on trees or in crevices on the underside of dead wood in rainforests (USINGER & MATSUDA 1959; MONTEITH 1969). Knowledge on their scent glands is still minimal. The purpose of this paper is a description of the DAGs in the nymphs and the adults of *Aradus betulae* (LINNAEUS 1758), the nominotypical species of the Aradidae. The state of adult DAGs indicates their possible functionality. The situation is discussed in regard to MTGs and the specific aradid biology.

Material and methods

Material examined: The number reported after the locality name represents the grid mapping square code used for faunistic research in the Czech Republic (PRUNER & MÍKA 1996).

Aradidae: Aradinae: *Aradus betulae* (LINNAEUS 1758): Bohemia occ., Krušné hory Mts., Klíny (5347) env., nr. Litvínov, June 2004, October 2004, June 2005, October 2005, beneath bark of beech (*Fagus sylvatica*), 2nd to 5th nymphal instars, males, females, altogether 98 specimens, J. Vilímová and J. Zima lgt., J. Vilímová det. and coll.

Methods

A standard method was used for all developmental stages studied: Fresh specimens were dissected in distilled water. Abdominal sterna were cut off and all soft tissues dissected from the ventral side. Photographs were made by using a stereomicroscope Olympus SZX9 with camera Olympus Camedia C-5060WZ and software PhotoMicro 2.0 and PhotoShop 7.0.

Results

The shape, size, colour, structure and level of sclerotization of DAGs' ostioles, area of cuticle with specific structure surrounding ostioles and DAGs' reservoirs were studied in the 2nd to 5th instars and in adults of both sexes in *Aradus betulae*.

Abdominal dorsum

Nymphs (Figs 1, 4, 8, 11)

Dorsal abdominal cuticle transparent, orange-beige abdominal tissues visible through cuticle, including DAGs reservoirs. Cuticle with distinct brown, pigmented, sclerotized, circle-shaped, glabrous areas.



Figs 4-7. *Aradus betulae* (LINNAEUS 1758), 3rd instar (4) whole body, dorsal view (5) detail of DAGs' ostioles, dorsal view (6) detail of dissected DAGs' ostioles, ventral view (7) detail of dissected DAGs' reservoirs, ventral view. 3, 4, 5, 6 - abdominal terga; o - DAG's ostiole; r - DAG's reservoir.

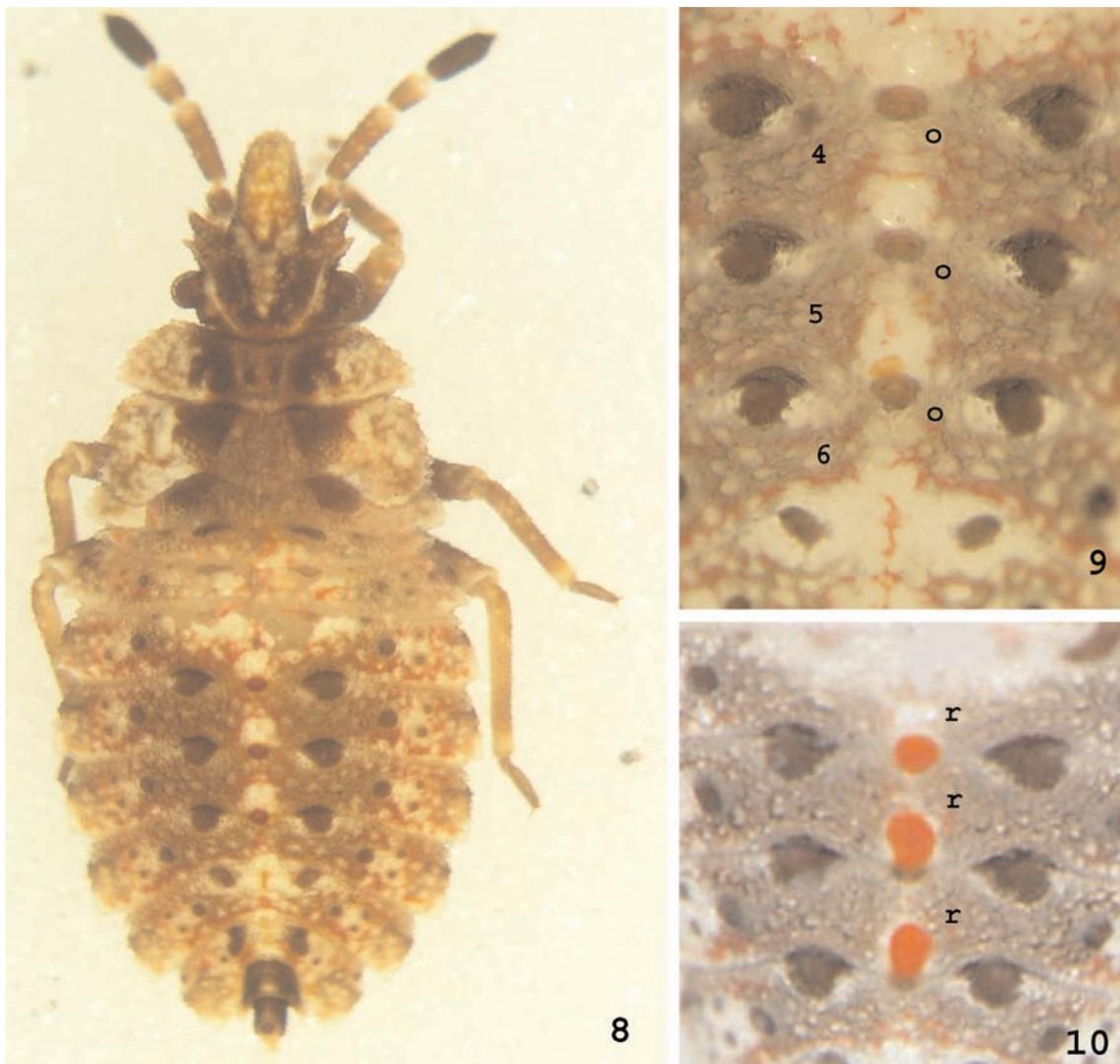
Areas regularly arranged in paired longitudinal lines: marginally (= laterally) on all laterotergites, sublaterally and submedially; largest areas in submedial line. Three unpaired ostioles of DAGs medially on posterior margin of abdominal segments 3, 4, and 5, situated proportionally between submedial lines of glabrous areas.

Glabrous areas larger in younger to older nymphal instars, particularly in submedial lines; roughly of same diameter as ostioles in 2nd instar, distinctly larger in subsequent instars, about 6x larger than diameter of ostioles in 5th instar.

Adults (Figs 16, 24)

Dorsum of abdomen, excluding laterotergites, distinctly separated from mediotergites, covered by scutellum and wings in both sexes. Mediotergites not fused in tergal disk, sutures between tergites distinct, sinuate, more conspicuously in male than in female, medially bent anteriorly. Glabrous areas on mediotergites in two longitudinal lines, sublateral and submedial, more distinct on segments 3-6, generally less contrasting with surrounding cuticle than in nymphs. Three unpaired orange DAGs' reservoirs in medial line, visible through cuticle of mediotergites, less pigmented than lateral parts of abdominal dorsum.

Figs 8-10. *Aradus betulae* (LINNAEUS 1758), 4th instar (**8**) whole body, dorsal view (**9**) detail of DAGs' ostioles, dorsal view (**10**) detail of dissected DAGs' reservoirs, ventral view. 4, 5, 6 - abdominal terga; o - DAG's ostiole; r - DAG's reservoir.



Ostioles and surrounding abdominal cuticle

Nymphs (Figs 2, 3, 5, 6, 9, 12, 13)

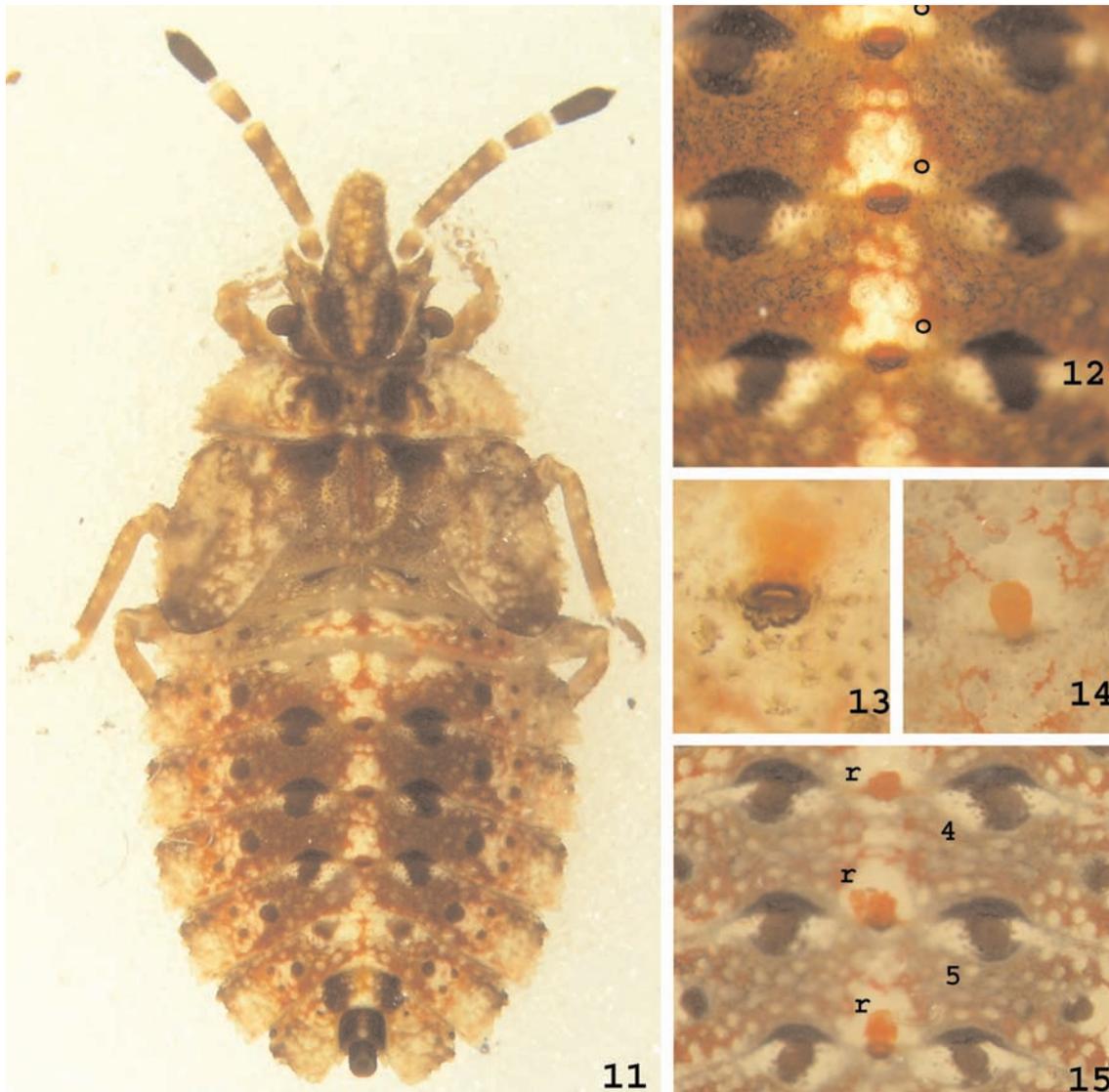
Three unpaired DAGs' ostioles, openings of reservoirs through cuticle, in all instars studied. Ostiole formed by relatively short, narrow, transversally oval slot with parallel sides, anterior side slightly convex only in 5th instar. Ostioles located medially on extreme posterior margins of segments 3, 4 and 5, thus appear situated in intersegmental membranes. All ostioles in particular instar nearly of same size, largest in 2nd instar, smallest in 5th instar: 2nd instar – ostiole about 1/16 of tergite width, 3rd instar – about 1/20 of width, 4th instar – about 1/20 of width, 5th instar – about 1/25 of width. Ostioles in 5th instar narrower than in younger instars.

Ostioles closely surrounded by pigmented and sclerotized cuticle, distinctly differ-

ent from remainder of tergite. Cuticle smooth, without conspicuous structure differing in shape between instars; regular narrow ring in 2nd instar; smooth, narrow strip anteriorly and laterally, crescent posteriorly, anterior part distinctly wider than posterior part of strip in 3rd instar; almost smooth, posterior part with fine tubercles, wide strip anteriorly and laterally, crescent posteriorly, anterior part slightly wider than posterior part of strip in 4th instar; smooth, except conspicuous tubercles posteriorly, wide strip anteriorly and laterally, with slight crescent shape posteriorly, almost of same width around ostiole in 5th instar.

Adults (Figs 17-19, 27)

Three unpaired ostioles medially on extreme posterior margins of medioterga 3, 4, and 5 in both sexes; margins shallowly concave, slightly more in male than in female.



Figs 11-15. *Aradus betulae* (LINNAEUS 1758), 5th instar (11) whole body, dorsal view (12) detail of DAGs' ostioles, dorsal view (13) detail of DAG's posterior ostiole, dorsal view (14) detail of dissected DAG's median reservoir, ventral view (15) dissected DAGs' reservoirs, ventral view. 4, 5 - abdominal terga; o - DAG's ostiole; r - DAG's reservoir.

Intersegmental line medially modified in transversally oval, elevated structure with thickened borders. Small, narrow, transverse opening representing ostiole located close to posterior border of structure. Detailed structure of three ostioles slightly different. Ostiole conspicuously larger, wider in male (about 1/14 of mediotergite width) than in female (about 1/25 of width). Ostiole situated posterior to conspicuous, brightly orange DAGs' reservoirs visible through cuticle, always located entirely beneath preceding mediotergum.

DAGs' reservoirs

Nymphs (Figs 2, 7, 10, 14, 15)

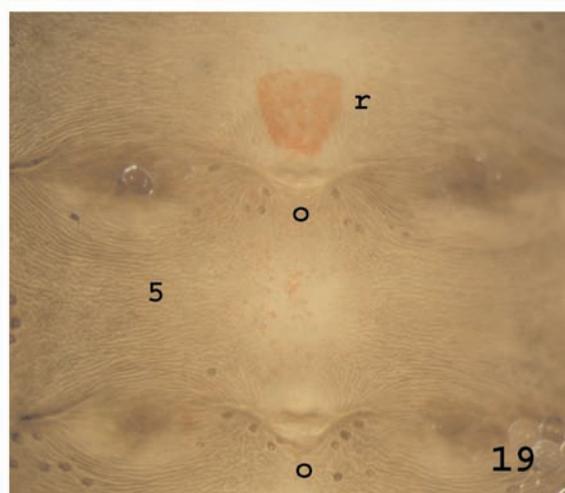
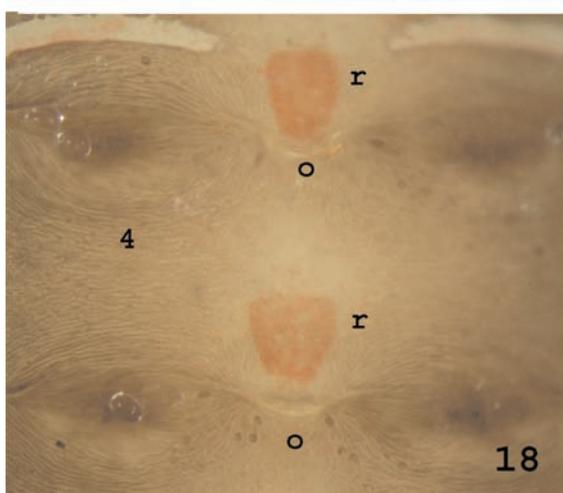
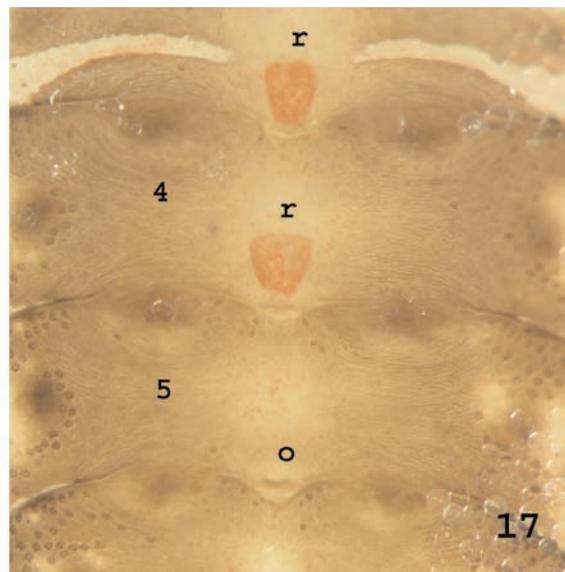
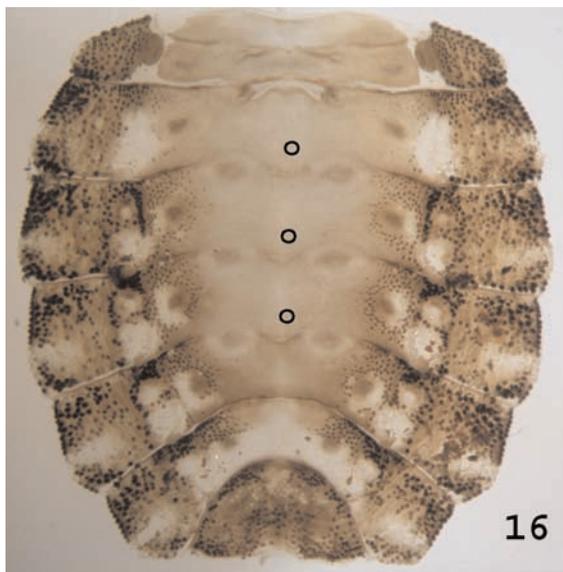
Three unpaired DAGs' reservoirs medially in abdomen, anteriorly (marked also as 3/4) beneath tergum 3, medial (4/5) be-

neath tergum 4, posterior (5/6) beneath tergum 5. All reservoirs globular to short oval sac-shaped, relatively small, always longer than diameters of ostioles but however, never extended beyond 1/2 length of relevant segment. Reservoirs conspicuously brightly orange to reddish, directed anteriorly from their ostioles. Size of all reservoirs in one instar similar, with only slight differences; posterior reservoir largest, anterior reservoir smallest in 2nd instar; all reservoirs nearly same in 3rd instar; medial and posterior reservoirs larger than anterior in 4th instar; all reservoirs of equal size, only slightly larger than diameter of ostiole in 5th instar.

Adults (Figs 17-27)

Three unpaired DAGs' reservoirs medially in abdomen, similar to nymphal reservoirs, dark orange, globular sac-shaped, al-

Figs 16-19. *Aradus betulae* (LINNAEUS 1758), male (16) dissected abdomen, dorsal view (17) detail of dissected DAGs' ostioles and reservoirs, dorsal view (18) detail of dissected DAGs' anterior and medial ostioles and reservoirs, dorsal view (19) detail of dissected DAGs' medial reservoir and posterior ostiole, dorsal view. 4, 5 - abdominal terga; o - DAG's ostiole; r - DAG's reservoir.



ways longer than diameter of ostioles, directed anteriorly. Reservoirs conspicuously larger in male than in female; longitudinally oval, slightly narrowed close to ostiole, reaching maximally 1/3 length of relevant segment; medial reservoir largest, wider than posterior reservoir, anterior reservoir smallest in male; reservoirs nearly globular-shaped, slightly narrowed close to ostiole, reaching maximally 1/5 length of relevant segment, all almost same, anterior reservoir slightly smaller than identical medial and posterior reservoirs in female.

Conclusions and discussion

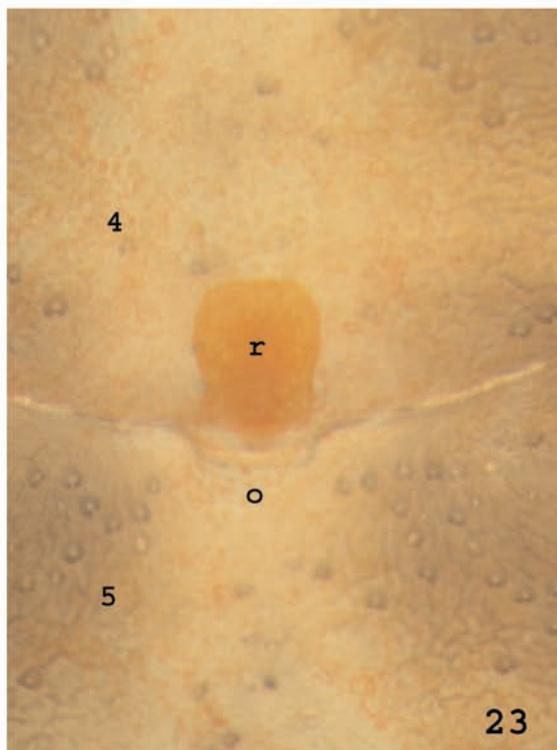
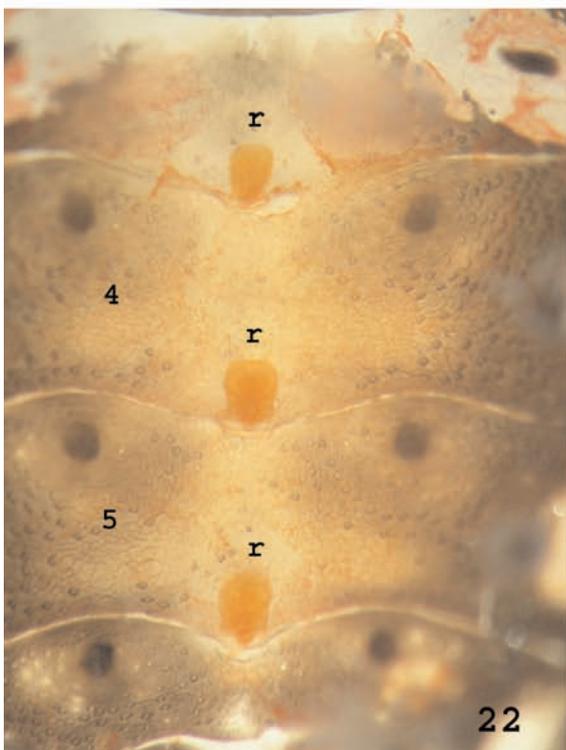
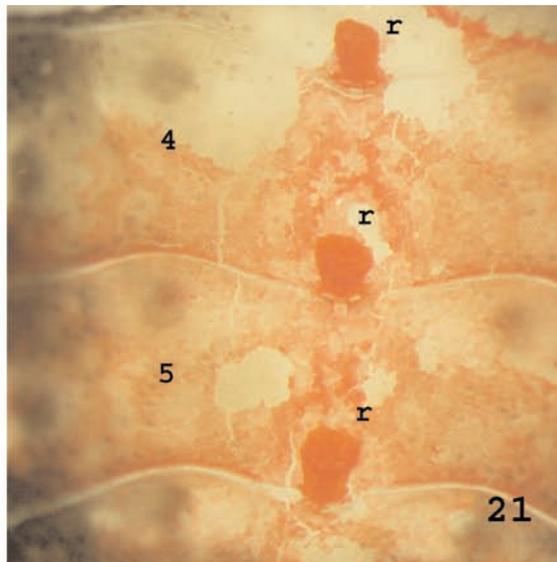
Complete reduction of the DAGs in heteropteran adults has been traditionally assumed, but persistence of these glands in the adult has been reported recently. Confusion probably has been enhanced further by the inconsistent use of various terms. The

following classification of the adult DAGs' conditions is proposed.

1. Functionality of adult DAGs is represented by:

- Presence of secretory units emptying into reservoir(s) (with storied secretion, released externally through the ostiole). The secretory units are composed of glandular units, often destroyed in studied material, and cuticular ductules, mostly conserved (e.g., STADDON 1999).
- Presence of secretion in gland reservoirs.

Functional adult DAGs were confirmed by above listed evidence in the representatives of Cimicomorpha as well as Pentatomomorpha (summarized, for example, by ALDRICH 1988a). Sexual dimorphism in size, shape, and chemical composition of adult DAGs' secretion was found. Slightly larger reservoirs were found in female than in male



Figs 20-23. *Aradus betulae* (LINNAEUS 1758), male (20) dissected abdomen, ventral view (21) dissected DAGs' reservoirs, ventral view (22) dissected DAGs' reservoirs, another specimen, ventral view (23) detail of dissected DAG's medial reservoir, ventral view. 4, 5 - abdominal terga; o - DAG's ostiole; r - DAG's reservoir.

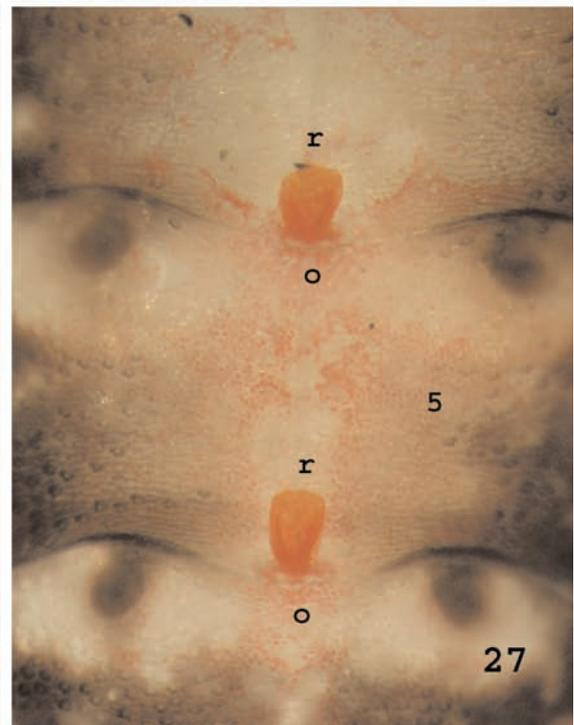
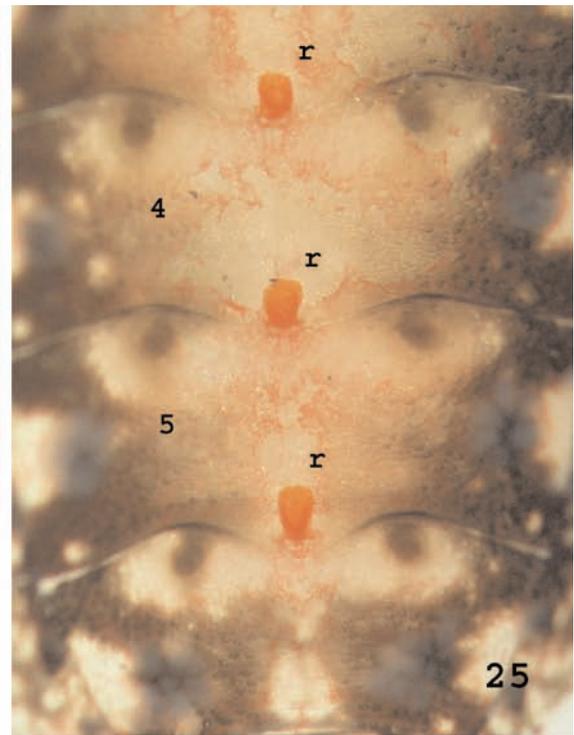
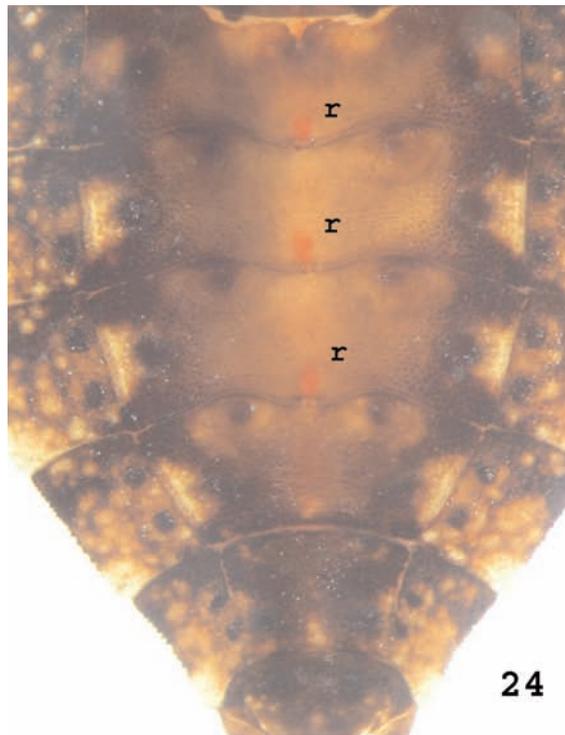
in several pentatomid species (DAVIDOVÁ-VILÍMOVÁ & PODOUBSKÝ 1999); however, functional dimorphism was discovered only in *Nezara viridula* (LINNAEUS 1758) (ALDRICH et al. 1978). Larger reservoirs in males than females is more common, most conspicuous in Pentatomidae: Asopinae (DUPUIS 1947).

2. Distinct DAGs' reservoirs are present in adults and are often more conspicuously coloured than in nymphs, orange to reddish, and either of the same relative size or even larger than in nymphal reservoirs. The sac-shaped reservoirs are swollen, apparently be-

cause they are filled by the secretion. The ostioles are present as a narrow aperture through the cuticle. Although the possible presence of functional secretory units was not studied, the situation is accepted as a manifestation of the functional adult DAGs. Distinct adult reservoirs were reported by the different authors in the representatives of about 21 families. My results confirm the fifty years-old result of LESTON (1955), the first and the last information about the existence of the reservoirs in aradid adults.

3. Either distinct DAGs' ostioles or their remnants are present. This situation often

Figs 24-27. *Aradus betulae* (LINNAEUS 1758), female (24) whole abdomen, dorsal view (25) detail of dissected DAGs' reservoirs, ventral view (26) detail of dissected DAGs' ostioles and reservoirs, ventral view (27) detail of dissected DAGs' medial and posterior reservoirs in tight connection with ostioles. 4, 5 - abdominal terga; o - DAG's ostiole; r - DAG's reservoir.



has been mentioned by earlier authors as an argument for functional DAGs. The terms „scars“ and „scars of scent glands“ have been used for a differently structured cuticle in a position of the nymphal ostioles. These scars can be prominently located (e.g., on tubercles in apterous aradids (USINGER & MATSUDA 1959).)

This above condition represents the weakest evidence of the functional adult

DAGs. Does an aperture through the cuticle really exist? Are the reservoir and the secretory units actually developed? These questions have not been answered as yet. The scars were described in representatives of many heteropteran families and subfamilies (e.g., in all cydnid subfamilies (LIS & HOHOL-KILINKIEWICZ 2002)). The common occurrence of the scars can be expected. If the DAGs are functional in the 5th instar,

then the ostiolar structure is reduced gradually. Thus, the scars can occur in adults of all families with functional nymphal DAGs.

The conclusion of the review of adult DAGs' condition is as follows. The only strong evidence for the adult functional DAGs is either secretion stored in the full reservoirs and/or the presence of secretory units, with distinguishable glandular units and cuticular ductules or only ductules.

The following use of the terms for DAGs is recommended. *Scent gland* means exclusively the functional DAGs with the reservoirs and secretory units developed. *Reservoirs of scent glands* mean the sac-shaped structure with stored secretion from secretory units. *Ostiole* means the aperture of reservoirs externally through the cuticle. *Ostiolar scar* means structures located at the site of nymphal DAGs' ostioles, which can occur in various sizes, shapes and sculpture, if one is not sure that the ostiole is or was connected with functional scent glands.

Although a combination of the DAGs and the MTGs is an autapomorphy of the Heteroptera, the scent glands have never been studied completely in the Aradidae. VÁSÁRHELYI (1987) used the ostiole states in the first cladistic analysis of the aradid subfamilies; however, he only considered nymphal DAGs. Only LESTON (1955) reported adult DAGs in *Aradus cinnamomeus* as three unpaired reservoirs. Other authors described the persistent adult DAGs' ostioles/ostiolar scars in different subfamilies (e.g., Mezirinae – VÁSÁRHELYI 1982; HEISS 1988, 2004; MONTEITH 1997; Isoderminae – HEISS 1981; Chinamyersiinae – MONTEITH 1966, 1980; Aneurinae – JACOBS 1986). Either three ostioles or three scars always are mentioned; this can be considered a general characteristic of the whole family.

USINGER & MATSUDA (1959) characterized the adult DAGs' ostioles complex of the subfamily Aradinae. VERHOEFF (1893) first mentioned three DAGs' ostiolar scars in the adults of *Aradus cinnamomeus* and *A. conspicuus* HERRICH-SCHAEFFER 1835 (as *Aradus dilatatus* DUFOUR 1844). Only sporadic information about other *Aradus* species has been published (e.g., in *Aradus horvathi* VÁSÁRHELYI 1984 (VÁSÁRHELYI

1984).) The adult abdominal dorsum was studied rarely, especially in fully winged taxa (e.g., HEISS & SHONO 2003). The condition reported here for *A. betulae* is identical with that described for *A. cinnamomeus* (LESTON 1955). Thus, *Aradus* can be characterized by three unpaired DAGs' reservoirs in the adults.

No agreement exists concerning polarization of the DAGs' reservoirs states. Either unpaired reservoirs (DUPUIS 1947), or paired reservoirs (summary, see COBBEN 1978), can be ancestral. The DAGs mostly are paired in the superfamily Pentatomoidea (e.g., DAVÍDOVÁ-VILÍMOVÁ & PODOUBSKÝ 1999), the recognized sister group of the Aradidae, and this condition was classified as plesiomorphic by POLIVANOVA (1960). It seems more reasonable that the paired glands represent the ancestral state and the unpaired ones the advanced state in the clade Pentatomoidea + Aradidae. The situation in *Aradus* could be explained by two hypotheses:

(1) By development of the advanced condition, originating by reduction from ancestral condition. If the polarization mentioned above is accepted, the Pentatomoidea have preserved the ancestral condition.

(2) By preserving the ancestral condition, if the polarization mentioned above is not accepted, then the common ancestor of the clade Pentatomoidea + Aradidae had unpaired DAGs, and the prevailing condition in the Pentatomoidea is derived.

The size of the nymphal reservoirs and ostioles does not increase continually from instar to instar. The reservoirs are smallest in the 5th instar relative to total body size, compared to those in the 4th instar and adults. The adult reservoirs are larger than those found in 5th instar, conspicuously swollen, very probably with secretion, and, thus, functional. However, do they represent the modified nymphal glands or the newly developed adult structures? Histological and analytical studies in Aradidae are necessary to prove the functionality of the adult glands. The aradid MTGs are relatively small, with almost inconspicuous ostioles, and are near the coxae. The evaporatorium of *A. betulae* covers a small area laterally on the metapleuron (unpublished results).

Such shift and modification may have resulted from the adaptation to life under bark because it enables easier spraying of the secretion under the bark. The nymphal DAGs generally have a repellent function (e.g., ALDRICH 1988a). VÁSÁRHELYI (1990) described another unique mechanism of defense in *Aradus* larvae (i.e., the use of the anal repellent gland). Adult DAGs could perform varied chemical communication, leading to either aggregation or sexual attraction, or both.

The DAGs' reservoirs are large and distinct in *A. betulae* adults, in contrast to the MTGs. Thus, it is likely that all the adult DAGs are functional because functional adult DAGs are known in the Pentatomoidea, the sister group of Aradidae. Either an anterior DAG is persistent in the Pentatomoidea adults (if a gland is persistent at all, and medial and posterior glands are fully reduced) or all glands are persistent (if so, then the anterior one is the largest). For example, STADDON (1999) described the existence of the DAGs' cuticular gland ductules in almost all pentatomoids studied. Similarly, ALDRICH et al. (1978) and ALDRICH (1995) assumed the persistence of a small but active anterior DAG for all phytophagous Pentatomidae. It is unclear, if this persistence is really most prevalent in the Pentatomoidea or appears to be so just because this group is most frequently studied. LIS & HOHOL-KILINKIEWICZ (2002) suggested the following ground plan in the Pentatomoidea: The nymphs possess three pairs of DAGs, which are reduced in the adults (either their remnants occur or they are entirely absent), and only vestiges of ostioles are visible. However, fully functional adult DAGs were recorded in so many pentatomoids that the persistence of adult DAGs with a modified function is more plausible than their complete reduction and, only in some species their development secondary.

The reservoirs in *A. betulae* males are larger than in females. No sexual dimorphism exists in 5th instars, thus the size of male reservoirs had to increase. Such sexual dimorphism indicates secretion of sexual pheromones. The adult DAGs thus have a different primary function than nymphal glands (i.e. attraction). The occurrence of

sexual dimorphic adult DAGs has been explained mostly by the necessity of contact between sexes before mating facilitated by sexual pheromones, especially in predaceous species with low population densities (e.g., Reduviidae and Asopinae (ALDRICH 1988a; WEIRAUCH 2006).) However, the conspicuous sexual dimorphism in the size of the adult DAGs, which are much larger glands in males, also was found in herbivorous, gregarious species (e.g., *Biprorulus bibax* BREDIN 1900 (Pentatomidae).) The present results indicate possible functional sexual dimorphism in the Aradidae. *Aradus betulae* is gregarious, living mostly in close aggregations, spending most of its life in tight spaces under bark. The above mentioned argument can be partly explained for those species, whose individuals are capable of chemical communication for aggregation (Vásárhelyi in litt.). The functionality of the adult DAGs is not yet proved in Aradidae and most other phytophagous heteropterans. ALDRICH's (1988a) hypothesis can be applied explicitly for the apterous aradids living in wet litter beneath dead wood.

The idea that wings in fully winged adults prevent spraying of DAGs' secretion has long been accepted. However, persistent adult DAGs also were described in winged species. The spraying of secretion can be facilitated either by spreading of the wings or by moving the abdomen ventrally. Nevertheless, it is questionable how the DAGs' secretion is sprayed in aradids in the small spaces under the bark, when the wings are held tightly against the abdomen. Spraying probably does not work under bark but rather in free space, on the bark surface, on fungi, on the ground, or during flying. Thus, the following scenario can be imagined: nymphs and adults of fully winged aradids live gregarious on food resources at isolated patches. Adults disperse while looking for new food resources; in central Europe appropriate climatic conditions occur mostly in May (VÁSÁRHELYI 1990). If successful, they could attract conspecific specimens, particularly those of the opposite sex, using DAGs' pheromonal secretions. Subsequently, they could occupy new space, and mating of individuals from different populations can prevent inbreeding.

The function of adult DAGs is probably more complicated. Attraction before mating could represent only one component of the DAGs complex function (the dispersal flight takes place in May, whereas the DAG's reservoirs still are not reduced during the fall, in October). Further studies are necessary to clarify the entire function of the heteropteran autapomorphic structure, the DAGs, in the Aradidae.

Acknowledgements

I would like to thank my colleagues from Charles University at Prague for their help. Petr Janšta and Jakub Prokop for preparation of the photos, Jan Zima for collecting of material and for comments to the manuscript and Alena Kutíková for technical help. I greatly appreciate comments to the manuscript of Jay E. McPherson (Southern Illinois University, Carbondale), Tamas Vásárhelyi (Hungarian Natural History Museum, Budapest) and Wolfgang Rabitsch (University of Vienna). The study was partly supported by a grant from the Ministry of Education of Czech Republic (MŠMT) MSM 0021620828 and a grant from the Grant Agency of Czech Republic 206/02/0638.

Zusammenfassung

Die dorsalen abdominalen Stinkdrüsen (DAGs) der Larven von *Aradus betulae* (LINNAEUS 1758) sind als drei unpaare Strukturen entwickelt. Die Reservoirs aller drei DAGs bleiben in den adulten Tieren erhalten. Sie sind bei den Männchen deutlich größer als bei den Weibchen und verantwortlich für einen leichten Geschlechtsdimorphismus. Die mögliche Funktion der adulten DAGs bei den Aradidae wird hinsichtlich der speziellen Lebensweise der Aradidae diskutiert.

References

- ALDRICH J.R. (1988a): Chemical ecology of the Heteroptera. — *Annu. Rev. Entomol.* **33**: 211-238.
- ALDRICH J.R. (1988b): Chemistry and biological activity of pentatomoid sex pheromones. — In: CUTLER H.G. (Ed.), *Biologically active natural products: Potential use in agriculture*. Washington D.C., ACS Symposium Series No. **380**: 418-431.
- ALDRICH J.R. (1995): Chemical communication in the true bugs and parasitoid exploitation. — In: CARDÉ R.T. & W.J. BELL (Eds), *Chemical ecology of Insects II*. Chapman & Hall, New York: 318-363.
- ALDRICH J.R. (1996): Sex pheromones in Homoptera and Heteroptera. — In: SCHAEFER C.W. (Ed.), *Studies on Hemipteran phylogeny*. Proc. Thomas Say Publ. Entomol, Maryland, Lanham: 199-233.
- ALDRICH J.R., BLUM M.S., LLOYD H.A. & H.M. FALES (1978): Pentatomid natural products. Chemistry and morphology of the III-IV dorsal abdominal glands of adults. — *J. Chem. Ecol.* **4**: 161-172.
- COBBEN R.H. (1978): Evolutionary trends in Heteroptera. Part II. Mouthpart-structures and feeding strategies. — *Meded. Landbouwhogeschool Wageningen* **78**: 1-407.
- DAVIDOVÁ-VILÍMOVÁ J. & M. PODOUBSKÝ (1999): Larval and adult dorso-abdominal scent glands, and androconia of central European Pentatomidea (Insecta: Heteroptera). — *Acta Soc. Zool. Bohem.* **63**: 37-69.
- DUFOUR L. (1833): Recherches anatomiques et physiologiques sur les Hémiptères. — *Mém Savants Étrang Acad. Sci.* **9**: 129-462.
- DUPUIS C. (1947): Données sur la morphologie des glandes dorso-abdominales des Hémiptères – Hétéroptères. Historique et discussion. — *Feuille Natur.* **49**: 13-21.
- DUPUIS C. (1949): Données nouvelles sur la morphologie abdominale des Hémiptères Hétéroptères et en particulier des Pentatomidea. — *Compte Rendu Seances XIII e Cong. Internat. Zool.* **1948**: 471-472.
- GOUGH A.J.E., HAMILTON J.G.C., GAMES D.E. & B.W. STADDON (1985): Multichemical defense of plant bug *Hotea gambiae* (WESTWOOD) (Heteroptera: Scutelleridae). — *J. Chem. Ecol.* **11**: 343-352.
- GUPTA A.P. (1964): Musculature and mechanism of the nymphal scent apparatus of *Riptortus linearis* H.-S. (Heteroptera: Alydidae) with comments on the number, variation and homology of the abdominal scent glands in other Heteroptera. — *Proc. Entomol. Soc. Wash.* **66**: 13-18.
- HEISS E. (1981): On *Isodermus planus* ERICHSON, 1842, and a new species from Tasmania (Heteroptera, Aradidae). — *Entomofauna* **2**: 247-262.
- HEISS E. (1988): Studies on African Aradidae I. A new species of the apterous genus *Usumbaraia* KORMILEV, 1956 (Heteroptera, Aradidae). — *Ber. nat.-med. Verein Innsbruck* **75**: 191-195.
- HEISS E. (2004): Two new genera and new species of Mezirinae from Mauritius (Heteroptera: Aradidae). — *Linzer biol. Beitr.* **36**: 241-251.
- HEISS E. & Y. SHONO (2003): A new species of the flat bug genus *Aradus* FABRICIUS, 1803 (Het-

- eroptera, Aradidae) from Japan. — Jap. J. Syst. Entomol. **9**: 63-68.
- HENRICI H. (1939): Die Hautdrüsen der Landwanzen (Geocorisae), ihre mikroskopische Anatomie, ihre Histologie und Entwicklung. Teil 1: Die abdominalen Stinkdrüsen, die Drüsenpakete und die zerstreuten Hautdrüsen. — Zool. Jb. Anatomie **65**: 141-228.
- JACOBS D.H. (1986): Morphology and taxonomy of sub-saharan *Aneuris* species with notes on their phylogeny, biology and cytogenetics (Heteroptera: Aradidae: Aneurinae). — Entomol. Mem. Dep. Agric. Wat. Supply Rep. S. Afr. **64**: 1-29.
- JAMES D.G. & G.N. WARREN (1989): Sexual dimorphism of dorsal abdominal glands in *Biprurus bibax* BREDDIN (Hemiptera: Pentatomidae). — J. Aust. Entomol. Soc. **28**: 75-76.
- KÜNKEL M.J. (1866): Recherches sur les organes de sécrétion chez les Insectes de l'ordre des Hémiptères. — Compt. Ren. Acad. Sci. **63**: 433-436.
- LESTON D. (1955): Remarks on the male and female genitalia and abdomen of Aradidae. — Proc. R. Entomol. Soc. London **30**: 63-69.
- LIS J.A. & A. HOHOL-KILINKIEWICZ (2002): Adult dorso-abdominal scent glands in the burrower bugs (Hemiptera: Heteroptera: Cydnidae). — Pol. Pismo Entomol. **71**: 359-395.
- MONTEITH G.B. (1966): A new genus of Chinamyersiinae (Heteroptera: Aradidae) from Australia, with notes on its relationships and male genitalia. — J. Entomol. Soc. Qd. **5**: 46-50.
- MONTEITH G.B. (1969): The relationships of *Kumaressa* MONTEITH and *Tretocoris* USINGER & MATSUDA with a new species of *Kumaressa* (Hemiptera: Aradidae: Chinamyersiinae). — Proc. R. Soc. Qd. **81**: 75-82.
- MONTEITH G.B. (1980) Relationships of the genera of Chinamyersiinae, with description of a relict species from mountains of North Queensland (Hemiptera: Heteroptera: Aradidae). — Pacific Insects **21**: 275-285.
- MONTEITH G.B. (1997): Revision of the Australian flat bugs of the subfamily Mezirinae (Insecta: Hemiptera: Aradidae). — Mem. Qd. Mus. **41**: 1-169.
- POLIVANOVA E.N. (1960): Osobennosti ontogeneza pentatomid (Hemiptera, Pentatomoidea) i yego znacheniye dlya sistematiki i fylogenii (Peculiarities in the ontogenesis of pentatomid-bugs (Hemiptera, Pentatomoidea) and their importance for the taxonomy and phylogeny. — In: HRDÝ I. (Ed.), The ontogeny of insects. Acta symposii de evolutione insectorum, Praha 1959: 75-81 (in Russian, with English summary).
- PRUNER L. & P. MIKA (1996): List of settlements in the Czech Republic with associated map field codes for faunistic grid mapping system. — Klapalekiana **32** Suppl.: 1-175.
- SCHAEFER C.W. (1993): The Pentatomomorpha (Hemiptera: Heteroptera): an annotated outline of its systematic history. — Eur. J. Entomol. **90**: 105-122.
- STADDON B.W. (1979): The scent glands of Heteroptera. — Adv. Insect Physiol. **14**: 351-418.
- STADDON B.W. (1986): Biology of scent glands in the Hemiptera-Heteroptera. — Annl. Soc. Entomol. Fr. **22**: 183-190.
- STADDON B.W. (1990): Male sternal pheromone glands in acanthosomatid shield bugs from Britain. — J. Chem. Ecol. **16**: 2195-2202.
- STADDON B.W. (1999): Notes on glandular structures of the pregenital abdomen of adult British pentatomoids based on a study of cuticular isolates. — Entomol. Mon. Mag. **135**: 177-182.
- USINGER R.L. & R. MATSUDA (1959): Classification of the Aradidae (Hemiptera – Heteroptera). — British Museum of Natural History, London: vii + 1-410.
- VÁSÁRHELYI T. (1982): A study on the relation of *Mezira tremulae* GERM. and two allied species (Heteroptera: Aradidae). — Acta Zool. Hung. **28**: 389-402.
- VÁSÁRHELYI T. (1984): *Aradus horvathi* sp. n. from the Southern Carpathians (Heteroptera, Aradidae). — Ann. Hist.-Nat. Mus. Nat. Hung. **76**: 129-132.
- VÁSÁRHELYI T. (1987): On the relationships of the eight aradid subfamilies (Heteroptera). — Acta Zool. Hung. **33**: 263-267.
- VÁSÁRHELYI T. (1990): Prospects of aradidology in the Westpalaearctics. — Scopolia Suppl. **1**: 27-30.
- VERHOEFF C. (1893): Vergleichende Untersuchungen über die Abdominalsegmente der weiblichen Hemiptera-Heteroptera und -Homoptera, ein Beitrag zur Kenntnis der Phylogenie derselben. — Verhandl. Naturhist. Vereins, Bonn **50**: 307-374.
- WEIRAUCH C. (2006): Abdominal glands in adult Reduviidae (Cimicomorpha, Heteroptera). — Dtsch. Entomol. Z. **53**: 91-102.

Address of the Author:

Dr. Jitka DAVIDOVÁ-VILÍMOVÁ
 Charles University
 Faculty of Science
 Department of Zoology
 Viničná 7
 CZ-128 44 Praha
 Czech Republic
 E-Mail: vilim@natur.cuni.cz

ZOBODAT - www.zobodat.at

Zoologisch-Botanische Datenbank/Zoological-Botanical Database

Digitale Literatur/Digital Literature

Zeitschrift/Journal: [Denisia](#)

Jahr/Year: 2006

Band/Volume: [0019](#)

Autor(en)/Author(s): Davidova-Vilimova Jitka

Artikel/Article: [Dorsal abdominal glands in Aradus betulae \(Heteroptera, Aradidae\) 137-148](#)