The West-Palaearctic species of
Jassidophaga Aczél and Verrallia Mik
described up to 1966 (Diptera: Pipunculidae)

CHRISTIAN KEHLMAIER

Abstract
The paper deals with the western Palaearctic pipunculid species of Jassidophaga Aczél, 1939 and Verrallia Mik, 1899 described up to 1966. The available type material of the six names involved was studied. Lectotypes are designated for Pipunculus fasciatus Roser, 1840, Verrallia pilosa var. setosa Verrall, 1901, Pipunculus villosus Roser, 1840 and Cephalops aucta Fallén, 1817. The following taxonomic changes are proposed: Jassidophaga fasciata (Roser, 1840) (stat. rev.) is reinstated as a valid taxon and regarded as the oldest available name for Jassidophaga setosa (Verrall, 1901) (n. syn.). For the Nearctic species Jassidophaga fasciata (Hardy, 1939) the new name Jassidophaga nearctica Kehlmaier, 2005 n. nom. is introduced. Verrallia helvetica Kuznetzov, 1992 (n. syn.) is considered a junior synonym of Cephalops aucta Fallén, 1817. All species are illustrated and confined by their main characters. New terms are proposed for taxonomic important structures of the male internal genitalia. Finally, an overview of the world fauna of both genera is presented.

Keywords: Pipunculidae, Jassidophaga, Verrallia, Palaearctic, Nearctic.

Zusammenfassung
1 Introduction

Due to their small body-size and dark colouration, Pipunculidae or big-headed flies are rather inconspicuous and hard to detect in the field. On a family level, they can be easily identified by their large compound eyes and their wing venation (Fig. 1). Pipunculid larvae have been found developing as endoparasites of various families of Auchenorrhyncha (Waloff & Jervis 1987) and only lately also in Tipulidae (Skevington 2005). Female adults possess a piercer-like ovipositor for penetrating the intersegmental skin of their hosts. Some 1,300 species have been described world-wide until now (De Meyer 1996, De Meyer & Skevington 2000).

Jassidophaga Aczél, 1939 and Verrallia Mik, 1899 are two species-poor genera of the subfamily Chalarinae. Together with the genus Chalarus Walker, 1834, they form a well-supported monophyletic group (Skevington & Yeates 2000). De Meyer (1996) lists 22 species of Jassidophaga for the world fauna. Yang & Xu (1996) introduce two additional taxa from China. Most of these 24 Jassidophaga species have been described from the Palaearctic but a few also occur in the Nearctic, Oriental and Australasian/Oceanian regions. The geographic distribution of the six species of Verrallia known at present is restricted to the Holarctic region (De Meyer 1996).

The latest revision of the Palaearctic fauna of Jassidophaga and Verrallia was presented by Kuznetzov (1992). In his work, he introduced nine new species and one new synonymy, treating 18 Palaearctic taxa, but missing four additional species, previously described from China and South Korea (see discussion). Also, Kuznetzov (1992) does not explicitly mention that he studied any type material of the “old European species”, i.e., taxa described up to 1966, of the two genera involved. Historically, six names were introduced until then: Cephalops aucta Fallén, 1817, Pipunculus pilosus Zetterstedt, 1838, Pipunculus fasciatus Roser, 1840 [considered as a synonym of P. pilosus since 1897], Pipunculus villosus Roser, 1840, Verrallia pilosa var. setosa Verrall, 1901 and Verrallia beatricis Coe, 1966. Today, prior to this study, six species of Jassidophaga and two species of Verrallia were generally recognized for Europe (De Meyer 2004): Jassidophaga beatricis (Coe, 1966), Jassidophaga pilosa
Zetterstedt, 1838), Jassidophaga pollinosa (Kuznetzov, 1992), Jassidophaga setosa (Verrall, 1901), Jassidophaga verrucosa (Kuznetzov, 1992), Jassidophaga villosa (Roser, 1840), Verrallia aucta (Fallén, 1817) and Verrallia helvetica Kuznetzov, 1992.

The identification key elaborated by Kuznetzov (1992) is currently the only and probably most commonly used one that keys out all European species for both genera. In his work, Kuznetzov (1992) does not present any descriptive diagnosis for the “old European species” but provides drawings for them instead, the female ovipositors of J. beatricis, J. pilosa, J. setosa and J. villosa being drawn after Coe (1966a). In the handbook for the identification of British Pipunculidae, Coe (1966a) provides a key for all “old European species”, figuring male genitalia and female ovipositor, except for female V. aucta. From this and a slightly later paper (Coe 1966a, b) it becomes obvious that Coe studied type specimens of J. beatricis, J. pilosa and J. setosa. Lauterer (1981) gives detailed drawings of the inner genitalia of male J. beatricis, J. pilosa, J. setosa and V. aucta, plus describing and figuring sternite 5 of all “old European species”. Recently, Dunk (1997) published a key for the Central

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**Fig. 1.** Habitus of male Verrallia aucta with indication of vein M₂. – LTC = length of third costal segment; LFC = length of fourth costal segment. – Scale: 1 mm.
European fauna, keying out *J. beatricis*, *J. pilosa*, *J. setosa*, *J. villosa*, *V. aucta* and *V. helvetica*, including the previously unknown male sex of the latter.

The aim of this article is not to revise the European fauna, but simply to enable a better understanding of the taxonomy and variability of the “old European species”, by studying the type specimens available and fixing lectotypes where appropriate. However, a future re-evaluation of the world fauna of both *Jassidophaga* and *Verrallia* would be highly desirable.

**Acknowledgements**

Without the patient help of the following colleagues, this study would not have been possible. DIETER DOCZKAL (Malsch), KLAUS VON DER DUNK (Hemhofen), JOACHIM FLÜGEL (Knüllwald), UWE KALLWÉIT (Dresden), ADRIAN PONT (Oxford), ANDREAS STARK (Halle/Saale) and JENS-HERMANN STUKE (Leer) contributed material. The curators and their teams of the institutional collections mentioned in chapter 2 arranged the loan of type and additional material and/or granted access to their collections. CHRISTIAN SCHMID (Dresden) translated selected parts of the Chinese literature cited into German. MARC DE MEYER (Tervuren), BRAD SINCLAIR (Bonn), JEFF SKEVINGTON (Ottawa) and HANS-PETER TSCHORSNIG (Stuttgart) gave valuable comments on earlier versions of the manuscript.

**2 Material and methods**

Apart from own collecting efforts, material was obtained for study from institutional collections and private collectors. The following acronyms are applied below:

- **ICSP** Imperial College London, Silwood Park Campus, Great Britain (A. BROODBANK)
- **KBIN** Koninklijk Belgisch Instituut voor Natuurwetenschappen, Brussels, Belgium (P. GROOTAERT, P. LIMBOURG)
- **MHNG** Muséum d’Histoire Naturelle, Genève, Switzerland (B. MERZ)
- **NHM** The Natural History Museum, London, Great Britain (N. WYATT)
- **NHRS** Naturhistoriska Riksmuseet Stockholm, Sweden (B. VIKLUND)
- **SMNS** Staatliches Museum für Naturkunde Stuttgart, Germany (H.-P. TSCHORSNIG)
- **ZML** Museum of Zoology, Lund University, Sweden (R. DANELSSON)
- **ZSMC** Zoologische Staatssammlung München, Germany (M. KOTRBA, W. SCHACHT)
- **UMO** University Museum of Natural History, Hope Entomological Collections, Oxford, Great Britain (J. E. HOGAN, M. ACKLAND)

With one exception, terminology follows MCALPINE (1981) and KEHLMAIER (2005). The ratio LTC : LFC refers to the wing venation and describes the length of the third costal segment to the length of the fourth costal segment (Fig. 1). Inner male genitalic nomenclature is according to SINCLAIR (2000) with additional, group specific morphological characteristics introduced in the following. In contrast to MCALPINE (1981) and recent papers dealing with *Verrallia* and *Jassidophaga* (DE MEYER & GROOTAERT 1992, KUZNETSOV 1992, MORAKOTE & HIRASHIMA 1990), the term “phallic processes” is used instead of “parameres”. In the latest revision of the genus *Chalarus*, JERVIS (1992) introduces the term “acuminate processes” for the homologous structure. In Chalarinae, these phallic processes are highly diversified in shape and normally species-specific, and represent a valuable morphological criteria in the systematics of this group. Individual male inner genitalic structures are indicated in Fig. 2 and Figs. 7–8. The phallus consists of a single ejaculatory duct that is embedded by the phallic shaft (phs), ending in the membranous tip of the distiphallus (tdp). The phallic shaft terminates in what is called here tip of distiphallus (ttdp) (called “apical process” by JERVIS 1992), that forms the phallostrema or secondary gonopore. Important morphological features of the phallic processes are its membranous sheath (mspp), the length of its tip (tpp) and the shape, length and number of its lateral branches (lbpp).

In the course of this study, it was tried to verify the host records of *Jassidophaga* mentioned in WALOFF & JERVIS (1987). Attempts to localize any voucher specimens (most probably reared by FORBES BENTON or NADIA WALOFF) staid unsuccessful as the material could not be found at NHM, UMO or ICSP. During this study, it became evident that especially male...
specimens determined in the past turned out to be misidentified due to not dissecting the male terminalia. Therefore, the host records mentioned in the literature have to be taken with care. Nevertheless, this information is included below in the appropriate species chapters.

3 The identity of the “old European species”

3.1 The genera Jassidophaga and Verrallia

There has been considerable dispute in the past, whether Jassidophaga should be regarded as a distinct genus or merely as a subgenus of Verrallia. Enderlein (1936) introduced the name Jassidophaga for the first time in an identification key to European Pipunculidae, giving as a differentiation character the absence of vein M₂ (see Fig. 1). However, Enderlein did not fix any type species for the new genus but merely lists both European species known in his times. This made his proposal invalid and the name unavailable after Art. 13.3 of the 4th edition of the ICZN rules (ICZN 1999). Aczél (1939) then chose P. pilosus as type species, making the name officially available. In 1948, Aczél then comments on both genera, still pointing out the missing vein M₂ as the only diagnostic feature of distinguishing the two. In the following, Coe (1966a), Kapoor et al. (1987), Kuznetzov (1992), Lauterer (1981), Morakote & Hirashima (1990), amongst others, shared Collin’s opinion, that “The forking of the discal vein is a primitive character, and as such may appear in any genus of the family” (Collin 1945: 2), giving Jassidophaga subgeneric rank. Rafael & De Meyer (1992) eventually attributed Jassidophaga generic rank again based on a cladistic analysis, regarding the absence of vein M₂ and the presence of a ventral wart on the base of the front femur in at least one of the sexes as suitable autapomorphies (see also De Meyer & Grootaert 1991). Further proof for a generic independence of Jassidophaga was provided by Skevington & Yeates (2000) through a phylogenetic analysis based on morphology and mitochondrial 12s and 16s ribosomal DNA.

Apart from the two morphological characters mentioned above, two additional morphological and one ecological peculiarities can be added here, that separate Jassidophaga from Verrallia. However, additional taxa of both genera need to be investigated in order to make sure that these points really do have autapomorphic character.

- Vein M₂ absent (present in Verrallia; see Fig. 1).
- At least front and mid femora of females with a distinct or indistinct ventral wart in its middle (none present in Verrallia).
- Sternite 7 of males with a distinct and highly modified projection as in Figs. 14, 18, 22, 26 (no distinct projection present in Verrallia; see Fig. 32).
- Phallic processes stiff and rather straight as in Figs. 2–3, 5–6 (in Verrallia phallic processes soft in distal half and curled or bend; see Fig. 10).
- So far, female Jassidophaga have been found to oviposit exclusively into larvae of Cicadellidae, whereas female Verrallia are only known to parasitize adult Cercopidae.

3.2 Jassidophaga Aczél, 1939

3.2.1 Jassidophaga beatricis (Coe, 1966) (Figs. 2, 11–14)


Type material studied

Great Britain: 1 ♂ (holotype), Herefordshire, Stoke Wood, 30.V.1904, leg. J. H. Wood, coll. NHM (#239455); 1 ♂ (paratype), Lancashire, Lytham, 10.VII.1948, leg. H. Audcent, coll. NHM (#239490); 1 ♂ (paratype), Somerset, Backwell, 11.VII.1925, leg. H. Audcent, coll. NHM (#239444); 1 ♀ (paratype), Oxfordshire, Shotover, 1.VII.1917, coll. NHM (#239449); 1 ♀ (paratype), Hantsshire, New Forest, 1.VII.1905, leg. F. C. Adams, coll. NHM (#239450); 1 ♀ (paratype), Hantsshire, New Forest, 1.V.1902, leg. D. Sharp, coll. NHM (#239445); 1 ♀ (paratype), Sussex, Crowborough, 28.VI.1904, leg. F. Jenkinson, coll. NHM (#239941); 1 ♀ (paratype), Middlesex, Hampstead, 11.VII.1925, leg. O. W. Richards, coll. ICSP.


Originally described by Coe (1966b) from 3 ♂♂ and 12 ♀♀ deposited at NHM, except 1 ♀ stored at ICSP. He points out that the species described by Verrall (1901) as pilosa Zetterstedt, and according to Collin (1956) represents a hitherto undescribed species, is most likely to be conspecific with his J. beatricis.

Males can best be identified via the characteristic inner genitalia (phallic and phallic processes): phs with a distinct membranous bulge in its middle; msp very promi-
nent; tpp and lbpp longer than in other species (Fig. 2). Additional diagnostic features are summarized in Tab. 1. One should note that the strong blunt spines of sternite 5 can be partly broken off occasionally. Female \textit{J. beatricis} can be characterized by the presence of two pairs of strong bristles on the posterior margin of the scutellum, pulvilli of fore legs slightly longer than distitarsi (Fig. 13) and shape of ovipos-

\textbf{Fig. 2.} Inner male genitalia of \textit{Jassidophaga beatricis}. – lbpp = lateral branches of phallic processes; mspp = membranous sheath of phallic processes; mtdp = membranous tip of distiphallus; phs = phallic shaft; tdp = tip of distiphallus; tpp = tip of phallic processes. – Scale: 0.1 mm.
Tab. 1. Diagnostic features of “old European species” of male *Jassidophaga* and *Verrallia*.

<table>
<thead>
<tr>
<th>Character</th>
<th><em>J. beatricis</em></th>
<th><em>J. fasciata</em></th>
<th><em>J. pilosa</em></th>
<th><em>J. villosa</em></th>
<th><em>V. aucta</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>lower bristles of pedicel</td>
<td>variable: light brown to black</td>
<td>black</td>
<td>variable: light brown to black</td>
<td>black (in 1 occ. mid brown)</td>
<td>black</td>
</tr>
<tr>
<td>pollinosity of anepisternum</td>
<td>entirely gray or with trace of brown</td>
<td>normally grayish-brown</td>
<td>entirely gray or with trace of brown</td>
<td>entirely gray or with trace of brown</td>
<td>entirely gray or with trace of brown</td>
</tr>
<tr>
<td>anepimeron</td>
<td>with 2–3 pairs of strong bristles</td>
<td>with 3–4 pairs of strong bristles</td>
<td>with 2 pairs of strong bristles</td>
<td>with 3–4 pairs of strong bristles (in 1 occ. only 2 pairs)</td>
<td>with 2–3 pairs of strong bristles</td>
</tr>
<tr>
<td>posterior margin of scutellum</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LTC : LFC</td>
<td>1.1–2.0</td>
<td>1.8–3.0</td>
<td>1.2–2.2</td>
<td>1.4–2.2</td>
<td>0.9–1.4</td>
</tr>
<tr>
<td>marginal fringe of lower calypter</td>
<td>white to light brown</td>
<td>mid to dark brown (in 1 occ. white)</td>
<td>white to mid brown</td>
<td>light brown; rarely white or mid brown</td>
<td>white to mid brown</td>
</tr>
<tr>
<td>ventral wart of front and mid femora</td>
<td>distinct</td>
<td>indistinct</td>
<td>distinct</td>
<td>mid femora normally with a trace of a wart</td>
<td>absent</td>
</tr>
<tr>
<td>lateral hairs of tergite 1</td>
<td>variable: from entirely white to entirely mid brown to black</td>
<td>black</td>
<td>variable: from entirely white to entirely black</td>
<td>entirely black or partly mid brown in anterior half</td>
<td>white to dark brown in anterior, black in posterior half (occ. entirely black)</td>
</tr>
<tr>
<td>lateral gray pollinosity of tergites 2–5</td>
<td>entirely gray or almost so</td>
<td>posterolaterally with small spots</td>
<td>posterolaterally with large spots</td>
<td>entirely gray or posterolaterally with large spots</td>
<td>tergite 1 gray, tergites 2–5 posterolaterally with small or large gray spots without or partly with a weak median furrow</td>
</tr>
<tr>
<td>sternite 4</td>
<td>without median furrow</td>
<td>without median furrow</td>
<td>without or partly with a weak median furrow</td>
<td>with median furrow (Fig. 9)</td>
<td>with median furrow</td>
</tr>
<tr>
<td>sternite 5</td>
<td>with 3–4 strong, blunt spines (can be broken off!)</td>
<td>variable: with 5–8 spines on each side, situated in 1 or 2 rows (in 1 occ. only 3 spines on each side)</td>
<td>with 3 stronger and 1–3 smaller spines on each side, situated in one or two rows</td>
<td>with 3–4 small spines on each side (in 1 occ. none present)</td>
<td>with 3–4 spines on each side</td>
</tr>
<tr>
<td>gonopod and surstylus</td>
<td>Coe (1966a, fig. 50)</td>
<td>Coe (1966a, fig. 53)</td>
<td>Coe (1966a, fig. 49)</td>
<td>Coe (1966a, fig. 52)</td>
<td>Coe (1966a, fig. 51)</td>
</tr>
<tr>
<td>phallus</td>
<td>Fig. 2</td>
<td>Fig. 3</td>
<td>Fig. 5</td>
<td>Fig. 6</td>
<td>Fig. 10</td>
</tr>
</tbody>
</table>
itor, which has the shortest piercer of the four species treated here (Figs. 11–12). The light colour of various body bristles (ventral bristles of pedicel, femoral fringes of mid and hind femora, lateral hairs of tergite 1) as pointed out, e.g., in COE (1966a) are not considered as suitable identification characters, due to their large variability (see Tabs. 1–2). In the past, HARDY (1972) and LAUTERER (1981) already commented briefly on this circumstance as well. KUZNETZOV’S (1990) idea of female J. beatricis seems to be in contradiction to the diagnosis presented here. His drawing of the ovipositor resembles more to J. fasciata than to J. beatricis.

LAUTERER (1981) states a wide ecological tolerance for J. beatricis, citing it throughout former Czechoslovakia from various biotopes at elevations between 170 and 800 m between early June to mid July. COE (1966a) records the species in Britain between end of May to mid July, whereas DEMPEWOLF (1996) found the earliest specimens in Cologne (Germany) at mid May. The known host species of J. beatricis is the cicadellid Oncopsis alni (Schrank, 1801) (WALOFF & JERVIS 1987).

According to DE MEYER (1996, 2004), J. beatricis is known from Austria, Belgium, Czech Republic, mainland Denmark, Estonia, Germany, Great Britain, Japan, Latvia, Mongolia, Russia (northwest), Slovakia, mainland Spain? and Switzerland. The doubtful record for Spain results from 2 ♀♀ bearing small differences in the shape of the basal part of the female ovipositor (KEHLMAIER 2001).

3.2.2 Jassidophaga fasciata (Roser, 1840) stat. rev. and n. comb.
(Figs. 3–4, 19–22)

Pipunculus fasciatus Roser: ROSER 1840: 55.
Verrallia pilosa var. setosa Verrall: VERRALL 1901: 73, n. syn.

Type material of P. fasciatus studied

Germany: 1 ♀ (lectotype), Baden-Württemberg, leg. Roser, coll. SMNS; 1 ♂ (paralectotype), Baden-Württemberg, leg. Roser, coll. SMNS.

Type material of V. pilosa var. setosa studied

Great Britain: 1 ♂ (lectotype), Hantshire, Lyndhurst, 3.V.1897, leg. J. W. YERBURY, coll. NHM (#239441); 1 ♂ (paralectotype), Hantshire, Lyndhurst, 29.IV.1897, leg. J. W. YERBURY, coll. NHM (#239440); 1 ♂ (paralectotype), Hantshire, Lyndhurst, New Forest, 29.IV.1897, leg. J. W. YERBURY, coll. NHM (#239442); 1 ♀ (paralectotype), Hantshire, Lyndhurst, New Forest, 10.V.1897, leg. J. W. YERBURY, coll. NHM (#239443).

Other material studied (26 ♂♂ 31 ♀♀)

Rosser (1840) very briefly described *P. fasciatus* from an unknown number of specimens in his “First addition to the inventory of two-winged insects present in Württemberg published in 1834” [title translated]. On page 49 he points out that he collected the material by himself in Württemberg, nowadays belonging to the German Federal State of Baden-Württemberg. Unfortunately, Rosser did not spend much time in labelling his flies, as most specimens do not have any label at all. In 1872, his collection went to the SMNS. It is not clear how Rosser himself organized his collection as only few original boxes are left nowadays and even these were reorganized by early custodial staff of the museum. Most likely, Rosser used labels fixed to the ground of the insect boxes bearing the species epithets. It was Lindner who later incorporated most of the specimens into the main collection (Tschornerg in litt.). At SMNS, a single specimen could be obtained showing a label stating “*fasciatus* m.” in Rosser’s hand-writing – the “m.” standing for the Latin word “mihi” (myself) – and another label stating “Type” [written in red] in Lindner’s hand-writing (Fig. 4). The specimen is hereby designated lectotype and was labelled accordingly, in order to fix the name involved and ensure an universal and consistent interpretation of the taxon in the future. Two more male specimens bare a small white quadratic label with a hand-written “17” [significance unknown] plus an identification label of Becker (“*pilosus* Zett.”). As Becker studied Rosser’s collection in preparation to his paper from 1897 – in Becker (1897: 25) he points out that Rosser’s collection comprised 25 species – and synonymized the species with *P. pilosus* (Becker 1897: 95), these two male specimens are considered as part of the type series and were labelled as paralectotypes. When requesting the syntype series of *P. fasciatus* from SMNS, additional material was received, all labelled as “*pilosa* Zett., *fasciata* v. Ros.” by Lindner only, that is not regarded as having type status here: 1 ♂ [= *Eudorylas inferus* Collin, 1956]; 3 ♀♀ [= *J. villosa*].

According to Pont (1995), Verrall (1901) described his *Verrallia pilosa* var. *setosa* from 4 ♂♂ and 1 ♀. A male lectotype for *J. setosa* is hereby designated and was labelled accordingly, in order to fix the name involved and ensure an universal and consistent interpretation of the taxon in the future. One additional male paralectotype deposited at UMO was not obtained for study.

In contrast to Becker (1897), it proved that *P. fasciatus* is not conspecific with *P. pilosus* but represents the senior synonym of *V. pilosa* var. *setosa* instead. It is therefore reinstated as a valid species (stat. rev.) and synonymized with the latter (n. syn.). As a result of this action, the Nearctic *Jassidophaga fasciata* (Hardy, 1939)
[Verrallia fasciatus, see HARDY 1939: 16] is in need of a new name. It is proposed to address it as *Jassidophaga nearctica* Kehlmaier, 2005 *n. nom.* The epithet refers to the geographic distribution of the species, being the first and only representative of the genus originally described from the Nearctic up to date.
Male \textit{J. fasciata} can best be identified by its inner genitalia (phallus and phallic processes) as shown in Fig. 3: tdp and tpp very short; mtdp small. Outer morphological features are the 3–4 pairs of strong scutellar bristles, the large LTC : LFC ratio and the number of peg-like spines on sternite 5. The latter can vary to some extent but is usually more numerous than in the other species treated here (see Tab. 1). \textsc{kuznetzov} (1992: 105) states in his key that sternite 5 of \textit{J. fasciata} [as \textit{setosa}] shows “... two groups of 3 short black spines on each side near posterior margin”, meaning that there are six spines on each side, which is true in many cases. However, in his drawing (\textsc{kuznetzov} 1992, fig. 45) only three spines are shown on each side, indicating that he interprets \textit{J. fasciata} as only bearing three and not six spines on each side of sternite 5 (see also below under \textit{J. kurilensis} \textsc{kuznetzov}, 1992). Female \textit{J. fasciata} is characterized by 3–4 pairs of strong scutellar bristles, pulvilli of front legs shorter than distitarsi (Fig. 21) and shape of ovipositor with its small base and relatively long and slim piercer (Figs. 19–20). Also, the hair tuft present on the anepimeron never seems to be entirely white as in the other species (see Tab. 2).

The flight period of this probably “... euryecious and rather submontanous and montanous species” (between 300–1300 m) (\textsc{lauterer} 1981: 130) ranges in Western and Central Europe from end of April to mid/end of July with a maximum recorded for Belgium at mid/end of May (\textsc{coe} 1966a, \textsc{de meyer} & \textsc{de bruyn} 1989, \textsc{lauterer} 1981). As host species, the Cicadellidae \textit{Oncopsis flavicollis} (Linnaeus, 1761) and \textit{Oncopsis subangulata} (Sahlberg, 1871) are listed by \textsc{waloff} & \textsc{jervis} (1987). \textsc{benton} (1975), cited in \textsc{waloff} & \textsc{jervis} (1987), reports on female \textit{J. fasciata} [as \textit{Verrallia setosa}] attempting to oviposit into birch buds and bud scales, mistaking them for nymphs of \textit{O. flavicollis}.

From the data presented in this study and in \textsc{de meyer} (1996, 2004), \textit{J. fasciata} has been recorded from Austria, Belgium, Czech Republic, mainland Denmark, Es-

\textbf{Fig. 4.} Historic labels attached to the male lectotype of \textit{Jassidophaga fasciata}, in \textsc{Lindner’s} (above) and \textsc{Roser’s} handwriting (below).
### Tab. 2. Diagnostic features of “old European species” of female *Jassidophaga* and *Verrallia*.

<table>
<thead>
<tr>
<th>Feature</th>
<th><em>J. beatricis</em></th>
<th><em>J. fasciata</em></th>
<th><em>J. pilosa</em></th>
<th><em>J. villosa</em></th>
<th><em>V. aucta</em></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>upper bristles of pedicel</strong></td>
<td>mid brown to black</td>
<td>black</td>
<td>mid brown to black</td>
<td>mid brown to black</td>
<td>black</td>
</tr>
<tr>
<td><strong>lower bristles of pedicel</strong></td>
<td>variable: from entirely white to light brown</td>
<td>light to mid brown, few black hairs can be present</td>
<td>entirely white to light brown, but few black hairs can be present</td>
<td>variable: from entirely white to light brown to entirely mid brown to black</td>
<td></td>
</tr>
<tr>
<td><strong>hairs on anepimeron</strong></td>
<td>white</td>
<td>predominantly mid to dark brown with some white hairs present or white to light brown with some dark hairs present</td>
<td>white</td>
<td>white</td>
<td>white</td>
</tr>
<tr>
<td><strong>posterior margin of scutellum</strong></td>
<td>with 2 pairs of strong bristles</td>
<td>with 3–4 pairs of strong bristles (in 2 occ. only 2 pairs)</td>
<td>with 2 pairs of strong bristles</td>
<td>with 3–4 pairs of strong bristles (in 1 occ. only 2 pairs)</td>
<td>with 2 pairs of strong bristles (in 1 occ. 3 pairs)</td>
</tr>
<tr>
<td><strong>LTC : LFC</strong></td>
<td>1.1–1.5</td>
<td>1.8–2.2 (in 1 occ. 1.5)</td>
<td>1.5–2.0</td>
<td>1.0–1.7</td>
<td>0.5–1.0</td>
</tr>
<tr>
<td><strong>pulvilli of front legs</strong></td>
<td>slightly longer than distitarsi (Fig. 13)</td>
<td>as long as or shorter than distitarsi (Fig. 21)</td>
<td>slightly longer than distitarsi (Fig. 25)</td>
<td>almost or more than twice as long as distitarsi (Fig. 17)</td>
<td>1.5 to 2 times as long as distitarsi (Fig. 31)</td>
</tr>
<tr>
<td><strong>ventral wart of front and mid femora</strong></td>
<td>distinct</td>
<td>distinct</td>
<td>distinct</td>
<td>indistinct</td>
<td>absent</td>
</tr>
<tr>
<td><strong>lateral hairs of tergite 1</strong></td>
<td>white</td>
<td>white to mid brown; posterior half can be black</td>
<td>entirely white or posteriorly with few brown to black hairs</td>
<td>white to light brown</td>
<td>white to light brown</td>
</tr>
<tr>
<td><strong>long hair fringes of femora</strong></td>
<td>variable: from entirely white to entire black</td>
<td>on mid leg light brown; others black</td>
<td>mid leg white; others light to mid brown</td>
<td>white to light brown</td>
<td>on mid leg white or light brown; others black</td>
</tr>
<tr>
<td><strong>ovipositor reaching up to anterior margin of sternite 4</strong></td>
<td>anterior margin of sternite 4</td>
<td>anterior margin of sternite 4</td>
<td>anterior margin of sternite 4</td>
<td>anterior margin of sternite 4</td>
<td>anterior margin of sternite 4</td>
</tr>
<tr>
<td><strong>ovipositor, lateral view</strong></td>
<td>Fig. 11, Coe (1966a, fig. 56)</td>
<td>Fig. 19, Coe (1966a, fig. 54)</td>
<td>Fig. 23, Coe (1966a, fig. 57)</td>
<td>Fig. 15, Coe (1966a, fig. 55)</td>
<td>Figs. 27–29, Kuznetzov (1990, fig. 9)</td>
</tr>
<tr>
<td><strong>ovipositor, dorsal view</strong></td>
<td>Fig. 12</td>
<td>Fig. 20</td>
<td>Fig. 24</td>
<td>Fig. 16</td>
<td>Fig. 30, Kuznetzov (1990, fig. 10)</td>
</tr>
</tbody>
</table>

tonia, Finland, Germany, Great Britain, Hungary, Ireland, mainland Italy, Latvia, mainland Norway, Russia (north and northwest), Slovakia, Sweden, Switzerland and The Netherlands. The Japanese record mentioned in *Morakote & Hirashima*
(1990) was later regarded by Kuznetsov (1992) as part of the distinct species *Jassidophaga kurilensis* (Kuznetsov, 1992).

### 3.2.3 *Jassidophaga pilosa* (Zetterstedt, 1838)

(Figs. 5, 23–26)

*Pipunculus pilosus* Zetterstedt: *Zetterstedt* 1838: 579.

**Type material studied**

**Norway:** 1 ♂ (lectotype), Oppland, Dovre, coll. ZML (2433:1–2); 1 ♂ (paratypotype), Finnmark, Bjerkvik, 14.VII.1821, leg. *Zetterstedt*, coll. ZML [specimen not **mentioned in Collin (1956)]; 1 ♂ (paratypotype), Finnmark, Bjerkvik, coll. ZML (2433:3) [= *J. fasciata*; Collin’s specimen no. 195].

**Other material studied (6 ♂♂ 4 ♀♀)**


**Zetterstedt** (1838) based his description on an unknown number of specimens collected at “Björkvik Nordlandiae” in 1821 by himself and on a male and female from “Alpe Dowre Norvegiae” collected in copula by D. Boheman in 1832. **Collin** (1956: 150) mentions “... a pair on one pin labelled Dovre (Norway).”, of which he designates the male as lectotype. He also lists another male (no. 195) collected at “Björkvik”, which he identifies as *J. setosa*. This specimen also represents a paratypotype of *P. pilosus* and is already registered as such, bearing a ZML-label with a type specimen number (2433:3). A re-examination of the fly confirmed Collin’s identification. Apart from the label indicating the collecting locality (Dovre), the pin with the male lectotype and female paratypotype also bears a small quadratic white label. According to Danielsson (in litt.), Zetterstedt used these small white labels to indicate specimens collected by himself on his trip through northern parts of Sweden, Norway and Finland in 1821 – hence, it should be the specimen from “Björkvik”. As the circumstance of this double labelling can not be solved here, it is simply disregarded at present and the specimens treated as being from Dovre. An additional male paratypotype from “Björkvik” could be discovered at ZML in the Wallengren collection. The genitalia were dissected and found to be conspecific with the lectotype. Collin (1956) and Coe (1966b) provide drawings of the ovipositor of this species, the latter also giving a detailed redescription. Today, the female paratypotype is in a rather poor state, with its entire abdomen missing.

In regard to the synonymy of *J. pilosa*, Kertész (1910: 387) and Yang & Xu (1996: 95) list “modestus Schiner” and “ruralis Walker” apart from “fasciatus Roser”, which might cause some confusion. The latter, synonymized by Becker (1897), was demonstrated to represent the senior synonym of *V. pilosa var. setosa* and reinstated as a valid species in this study (see chapter 3.2.2). The name *Pipunculus modestus* Haliday, 1833 was applied by Schiner (1862) to a taxon that should have been addressed by him as *P. pilosa* according to his characterization – note that Schiner (1862) was not aware of Roser’s (1840) publication. Loew followed Schiner’s interpretation as pointed out by Becker (1897: 94f.) and Verrall (1901: 74, 89) who
comment on the matter – at present, *P. modestus* is regarded as a nomen dubium within the genus *Eudorylas* Aczél, 1940 (Kehlmaier 2005). Similarly, Walker’s (1834) redescription of *Pipunculus ruralis* Meigen, 1824 refers to *P. pilosa* as pointed out by Verrall (1900: 10, 1901: 91).

Male *J. pilosa* show a distinctive inner genitalic structure (phallus and phallic processes) (Fig. 5), with phs strongly bent, mtdp large and lbpp very short, as well as projection of sternite 7 (Fig. 26), that clearly differentiates it from the other taxa treated here. Female *J. pilosa* resembles somewhat *J. fasciata* by the shape of the ovipositor. However, in contrast to the latter, *J. pilosa* only bears two pairs of scutellar bristles, entirely white hairs on anepimeron, slightly longer pulvilli on front legs and a longer and stronger curved piercer with its lateral outline showing a weakly

**Fig. 5.** Inner male genitalia of *Jassidophaga pilosa*. – Scale: 0.1 mm.
convex section midventrally (see Tab. 2 and Figs. 23–25). From J. beatricis, the species can be readily separated by the longer ovipositor.

So far, the taxon has been cited in Britain between June and July by COE (1966a), and for Belgium from mid May to beginning of August, with a peak at end of June/beginning of July by DE MEYER & DE BRUYN (1989). The few records gathered in the present paper reach from beginning of June to mid July. A re-evaluation of female collection material of J. pilosa and J. fasciata would be desirable, in order to obtain a better phenological picture for the former. WALOFF & JERVIS (1987) list the Cicadellidae O. subangulata and an unidentified species of Oncopsis as larval hosts. As J. pilosa and J. fasciata share O. subangulata as host species, DE MEYER & DE BRUYN (1989) suspect a mechanism of resource partitioning, as there is significant difference in temporal distribution of both species.

DE MEYER (1996, 2004) summarizes the records for J. pilosa as follows: Austria, Belgium, Bulgaria, Canada, Czech Republic, mainland Denmark, Estonia, Finland, mainland France, Germany, Great Britain, Hungary?, Ireland, mainland Italy?, Japan, Latvia, mainland Norway, Poland, Romania, Russia (northwest), Slovakia, Sweden, Switzerland, The Netherlands, USA and former Yugoslavia. However, it should be tested if the species really does occur in the Nearctic region, as HARDY’s (1943) redescription and figures do not correspond with the concept of J. pilosa presented here.

3.2.4 Jassidophaga villosa (Roser, 1840)
(Figs. 6–9, 15–18)

Pipunculus villosus Roser: Roser 1840: 55.

Type material studied

Germany: 1 ♂ (lectotype), Baden-Württemberg, leg. Roser, coll. SMNS; 1 ♂ (paralectotype), Baden-Württemberg, leg. Roser, coll. SMNS.

Other material studied (14 ♂♂ 92 ♀♀)


It is not known on how many specimens Roser (1840) based the description of P. villosus. As mentioned under J. fasciata, it is evident that Roser collected the specimens himself in Baden-Württemberg, Germany. At SMNS, two specimen could be retrieved apparently belonging to the type series. The male lectotype designated hereby, in order to fix the name and ensure an universal and consistent interpretation of the taxon in the future, bears the original label “villosus, m.” in Roser’s hand-
writing, and an additional label indicating it as “Type”, added by Lindner. The male paralectotype was labelled as “villosus v. Roser” by Becker, who studied Roser’s collection at the end of the 19th century.

Male *J. villosa* can easily be separated from all other European *Jassidophaga* by the numerous lateral branches of the phallic processes (Fig. 6) and the short and blunt projection of sternite 7 (Fig. 18). Also, sternite 4 shows a distinct median furrow that is weaker sclerotized than the rest of the sternite (Fig. 9). Female *J. villosa* are well characterized by their very long pulvilli on front legs and the lateral shape of the...
ovipositor, showing a large base and bearing a weak but characteristic dent on tergite 9 in almost all specimens studied (Figs. 15–17).

Coe (1966a) indicates the species as being generally distributed in Britain and records it between May and August. In Belgium, De Meyer & De Bruyn (1989) summarize data from mid of May until end of July, with a maximum at end of May/beginning of June. In former Czechoslovakia, Lauterer (1981) found J. villosa from early May to mid June and at altitudes between 187–450 m, predominantly in the Pannonicum at wood- and wood-steppe edges and on xeric slopes of hills, missing in colder parts of the country. By netting near the ground, Lauterer (1981) could obtain mainly males (41 : 6-ratio) unlike in the other species where females dominated. He attributes this fact to a different behaviour of the males during mating season, staying closer to the ground and not swarming high up, e. g., like V. aucta. No host species of J. villosa could yet be recorded.

J. villosa has been cited from Austria, Belgium, Czech Republic, mainland Denmark, Estonia, Finland, mainland France, Germany, Great Britain, Hungary, mainland Italy, Japan, Latvia, North Korea, mainland Norway, Poland, Romania, Russia (northwest), Slovakia, mainland Spain, Sweden, Switzerland and The Netherlands as outlined in De Meyer (1996, 2004).

Figs. 7–8. Jassidophaga villosa. – 7. Distal half of phallus, indicating the ejaculatory duct (ej.d.). 8. position of the phallotrema. – Scale: 0.5 mm.
3.2.5 *Pipunculus adpropinquans* Becker nom. nud.

The name is mentioned in Aczél (1948: 40) as a nomen nudum, based on the study of a specimen from the Loew collection at MNHU. The specimen was obtained and turned out to be a male *J. beatricis* with the following label data: “No. 11566, Langenau, VII. 1865, coll. H. Loew”; a red type label in Becker’s handwriting is attached to the specimen. A second specimen under this name at MNHU proofed to be a male *J. pilosa* (Carlsbad, coll. H. Loew, no type label present).

3.3 *Verrallia* Mik, 1899

*Verrallia* Mik: Mik 1899: 137. – Type species: *Cephalops aucta* Fallén, 1817, by original designation.


3.3.1 *Verrallia aucta* (Fallén, 1817)

(Figs. 10, 27–32)

*Cephalops aucta* Fallén: Fallén 1817: 61.


Type material of *C. aucta* studied

**Sweden**: 1 ♂ (lectotype), Esperød (“Esper.”), coll. ZML (2448:1); 1 ♀ (paralectotype), coll. ZML (2448:2).

Other material studied (155 ♂♂ 209 ♀♀)


COLLIN (1956), who studied the Pipunculidae collections in Stockholm and Lund, pointed out that in the FALLÉN collection at NHRS, only one female remained under C. auctus, a second pin being empty, whereas the ZETTERSTEDT collection at ZML holds one male evidently collected at the locus typicus. He points out that this male “... may well be accepted as ‘Lectotype’. ” (COLLIN 1956: 155) but does not designate it as such. In his world catalogue, DE MEYER (1996) lists two syntypes for the species, both deposited at Lund collections (Type Nr. 2448:1–2). When receiving these two “syntypes” from ZML, it turned out that the male represents COLLIN’s number “157” collected at “Esper.”, as noted on the label in ZETTERSTEDT’s handwriting, whereas the female is COLLIN’s number “49” from the ZETTERSTEDT collection and does nor bear any written locality label. However, both specimens show a small quadratic blue label which recognizes them as being collected at Kiviks Es- peröd in eastern part of Province Skåne, most likely by FALLÉN himself who spent most of his time there (DANIELSSON in litt.). ZETTERSTEDT bought FALLÉN’s insect collection after FALLÉN’s death and eventually donated the Diptera to Stockholm. Before he did so, he selectively took out specimens of species he did not have himself and incorporated them into his own collection. It can be assumed that ZETTERSTEDT labelled the specimens with a small blue label because the remaining types of V. aucta in Stockholm do not bear such a label (VIKLUND in litt.). The same applies to the other specimens of V. aucta mentioned in COLLIN (1956) (DANIELSSON in litt.), hence these are not considered as types here. Summarising it, there is the male lectotype of Cephalops aucta, hereby designated in order to fix the name involved and ensure an universal and consistent interpretation of the taxon in the future, and a female paralectotype at ZML whereas the NHRS holds a female paralectotype and an empty pin of a male paralectotype.

KUZNETZOV (1992) described V. helvetica from a female holotype and 4 ♀♀ paratypes all collected in Switzerland and deposited at the Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia. In the diagnosis of this species, he points out that it can be distinguished from V. aucta by “... costal section Cs3 0.4
times as long as Cs4, base of ovipositor angulate (Figs. 7, 8)” (Kuznetsov 1992: 107), i.e., 4th costal section more than twice the length of 3rd costal section. In his identification key on couplet 5, he states that the ratio 4th costal section to 3rd costal section for V. aucta is 1.1–1.2 : 1.0 and for V. helvetica is 1.9 : 1.0, i.e., 4th costal section of V. helvetica is almost twice the length of the 3rd costal section. Unfortunately, the types of V. helvetica could not be obtained for study. However, 152 specimens of female V. aucta from two localities were studied and the variability of the ovipositor and the LTC : LFC-ratio investigated (Tab. 3). In regard to the ovipositor, the lateral shape of its base varies considerably from being round (Fig. 27, form A: 27.6 %) to distinctly angled (Fig. 29, form C: 19.7 %), with an intermediate form B (Fig. 28) comprising 52.6 % of all specimens. In dorsal view, the ovipositor does not seem to be affected by this variability (Fig. 30). The ratio LTC : LFC also shows a large variability from 0.5 to 1.0, with an average of 0.74 and a median of 0.7. From the results obtained, it becomes evident that the average LTC : LFC-ratio is virtually the same for all three forms A–C. Hence, the shape of the ovipositor's base and the LTC: LFC-ratio are not considered as suitable stable morphological characteristics here in order to delimit two species. Therefore, it seems justifiable to synonymize V. aucta with V. helvetica n. syn.

Dunk (1997) figures both sexes of what he considers V. helvetica in his key from material collected in Bavaria. The exact collecting data, not given in Dunk (1997), is as follows: “1 ♂ 2 ♀, Germany, Bavaria, Hammelburg, Truppenübungsplatz, 30.V–13.VI, yellow pan trap, leg. Mandery”. The male and one female are supposed to be deposited at ZSMC but could not be localized. The second female, placed in coll. Dunk, was studied and represents ovipositor “form B” with LTC : LFC = 0.6.

Also, Dunk (1997) mentions various characteristics in order to differentiate male V. helvetica from V. aucta, based on the single male. In the following, his points not treated in Tab. 1 are shortly discussed, based on the examination of 136 male specimens from the “Location B-W”:

- Position of cross-vein r-m in regard to pterostigma: varying from opposite of base to opposite of basal third of pterostigma. The position of r-m in re-

<table>
<thead>
<tr>
<th>LTC : LFC</th>
<th>B-W (n = 64)</th>
<th>Bavaria (n = 88)</th>
<th>both locations</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>A  B  C</td>
<td>A  B  C</td>
<td>A  B  C</td>
</tr>
<tr>
<td>0.5</td>
<td>5  4  2</td>
<td>5  6  1</td>
<td>10  10 3</td>
</tr>
<tr>
<td>0.6</td>
<td>9  13 4</td>
<td>18  30 12</td>
<td>60</td>
</tr>
<tr>
<td>0.7</td>
<td>3  17 9</td>
<td>12  28 13</td>
<td>53</td>
</tr>
<tr>
<td>0.8</td>
<td>2  7  1</td>
<td>2  10 1</td>
<td>13</td>
</tr>
<tr>
<td>1.0</td>
<td>1  1</td>
<td>1  1</td>
<td>2</td>
</tr>
<tr>
<td>Σn</td>
<td>42  80 30</td>
<td>152</td>
<td></td>
</tr>
<tr>
<td>average</td>
<td>0.71 0.75 0.75</td>
<td>0.74</td>
<td></td>
</tr>
<tr>
<td>median</td>
<td>0.7 0.7 0.75</td>
<td>0.7</td>
<td></td>
</tr>
</tbody>
</table>
lation to the pterostigma depends on the ratio LTC : LFC, which shows considerable variation (0.9–1.4), and on its position in regard to cell dm, on which it can be placed from slightly before to slightly beyond middle of cell dm.

• **Length of hypopygium in dorsal view:** in the material studied, the hy-

---

*Fig. 10. Inner male genitalia of *Verrallia aucta*. – Scale: 0.1 mm.*
Popygium is normally as long as or slightly longer than tergite 3, 4 or 5. Very rarely, it can be slightly shorter than tergite 3, 4 or 5.

- Pterostigma normally complete or narrowly incomplete. Very rarely distinctly abbreviated.
- Halteres with base of stem and head distinctly darkened. However, the latter can be paler (light brown) occasionally.
- Posterior margin of scutellum with 2 to 3 pairs of strong marginal bristles and additional pairs of thinner and normally also shorter marginal hairs. Note that the marginal bristles can be broken off. Occasionally, they also can be somewhat weaker and hence do not differ so distinctly from the marginal hairs.
- Projection of surstyli: surstyli viewed dorsally (= abdomen viewed ventrally) with convex margin, meeting in one point (one might argue that they show a blunt projection).
- Also, the shape of the phallic processes can vary as indicated in Dunk (1997: 324). Distally, they can be coiled from once (Fig. 10) to twice, but then the diameter is smaller, or be somewhat “out of shape”, i. e., the apical part being not circular but ovate or showing small bends or breaks. Most probably, this should depend on whether the male already copulated or not, apart from the fact that the phallic processes are soft and flexible in their distal half.

In central and Western Europe, the flight-period of V. aucta is restricted to the summer months. Demewolf (1996), de Meyer & de Bruyn (1989) and Lauterer (1981) all indicate a time-span between end of May/beginning of June until mid August, with a maximum at end of June/beginning of July. The latter author records the species from various habitats in former Czechoslovakia, “… from hygrophilous (peatlands) to xerophilous (steppes), in meadows and woods, mainly near the edges of wood roads …” (Lauterer 1981: 126) and at altitudes between 150 and 850 m.

Males of V. aucta can rather frequently be found swarming. Verrall (1901: 76) mentions that Collin “… saw the males in swarms at Chippenham Fen, flying in similar fashion to many Anthomyidae only rather steadier, about seven feet from the ground over pathways …”, while the females appeared to be close to the ground. Coe (1966a: 31) states that he “… observed aucta behaving similarly over a path at the fringe of Selsdon Wood in Surrey. The remaining species of the genus [i. e. Jassidophaga] occur less commonly in suitable situations.” Another observation in this respect was made by Pont (in litt.) at the German Baltic coast on 10.VI.2003 around mid-day along a path between sand dunes and a street, the vegetation being a mixture of grasses, bushes and rather mature trees. There, he could observe several groups of about a dozen flies swarming rapidly in the shadow of trees at a height of about 3 m, collecting several specimens as voucher specimens (see above).

Lauterer (1981: 126, in litt.) describes part of the copulation of V. aucta. On 3.VI.1976, he was able to observe a couple flying motionless 1 m above the ground of a shadowed pathway in an almost straight horizontal line. Both, male and female, were actively hovering on the spot for about 5 minutes, being connected by their copulatory organs. The female was orientated with its legs towards the ground, whereas the male was “… turned upside down, with its legs pressed close to the thorax”. Mc Alpine (1981: 56ff.) comments on the different mating positions in Diptera, stating that permanent ventroflexion of the male terminalia – as is the case in V. aucta – is always correlated with circumversion, i. e., rotation of the latter through 360°, what represents a synapomorphic character of the Muscomorpha.
However, he also points out that an “upside down” situation of one of the mating partners represents the final mating position of species characterized by unrotated male terminalia, the latter not being the case in *V. aucta*.

As host species of *V. aucta*, the Cercopidae *Neophilaenus lineatus* (Linnaeus, 1758) and *Philaenus spumarius* (Linnaeus, 1758) were recorded in the past (Sander 1985, Waloff & Jervis 1987). Lauterer (1981) reports on a population of *Ph. spumarius* observed at Lednice, southern Moravia (nowadays Czech Republic),

showing a parasitization rate of 5 %. WHITTAKER (1969) studied populations of Ph. spumarius and N. lineatus in southern England (Berkshire) over a period of four years and records a mean rate of parasitism of 37 % for Ph. spumarius and 25 % for N. lineatus. The species of Verrallia are known for only parasitizing adult Cercopidae. WHITTAKER (1969) suspects that the hosts get attacked by V. aucta most probably after emerging from the spittle mass while they are still soft and unpigmented. WHITTAKER (1973) conducted further studies on the interactions of V. aucta and its hosts.

Figs. 27–32. Details of Verrallia aucta. – 27. Female ovipositor, lateral view, form A. 28. Female ovipositor, lateral view, form B. 29. Female ovipositor, lateral view, form C. 30. Female ovipositor, dorsal view, form A–C. 31. Female tarsal segment 4, distitarsus, claws and pulvilli of front leg. 32. Projection of male sternite 7. – Scales: 0.1 mm.
According to De Mey er (1996, 2004), *V. aucta* has been recorded from Austria, Belgium, Bulgaria, Czech Republic, mainland Denmark, Estonia, Finland, mainland France, Germany, Great Britain, Hungary, Ireland, Israel, mainland Italy, Kazakhstan, Latvia, Lithuania, mainland Norway, Poland, Romania, Russia (northwest), Slovakia, mainland Spain, Sweden, Switzerland and The Netherlands.

4 Brief discussion of additional species

Apart from the five taxa treated above, the following species of *Jassidophaga* and *Verrallia* are currently known for the world fauna. The identity of most species is rather obscure at present and a revision of both genera on a world-wide level would be highly desirable.

4.1 Species of *Jassidophaga*

*Jassidophaga abscissa* (Thomson, 1869) – only ♀ known

Described and only recorded from Taiwan in the past (locus typicus according to Yang & Xu 1996), its identity is insufficiently known. The species is not included in Kuznetzov (1992). Sack (1935) provides a short paragraph at the end of his work on the characteristics of this species taken from the original description.

*Jassidophaga argentisegmentata* (Brunetti, 1912) – only ♂ known

Described from two males and only recorded from Myanmar (formerly Burma) in the past. The original description gives a fairly good idea of the outer morphological features, interesting ones being the yellow antenna and uniformly yellow legs (except brown coxae) (Brunetti 1912). According to Churkin (1990), the species stands close to *J. villosa* and *Jassidophaga pala* (Morakote, 1990). Hardy (1972) comments extensively on a male specimen from Myanmar that he attributes to this or a closely allied taxon. He provides figures of the antenna, sternite 5 and tip of abdomen in ventral view.

*Jassidophaga armata* (Thomson, 1869) – only ♂ known

Described and only recorded from Taiwan (locus typicus according to Yang & Xu 1996), its identity is insufficiently known. The species is not included in Kuznetzov (1992). Sack (1935) summarizes the available information.

*Jassidophaga chiiensis* (Ôuchi, 1943) – only ♂ known

Described from a single male captured in South Korea, the identity of this species is insufficiently known at present. *J. chiiensis* is not included in Kuznetzov (1992). Ôuchi (1943) figures the antenna, wing as well as thorax and abdomen in dorsal view. He places the species close to *J. pilosa*, differentiating it by the shape of the flagellum and the colouration of the legs.

*Jassidophaga contracta* Yang & Xu, 1996 – only ♀ known

The identity of this species is insufficiently known at present. Yang & Xu (1996, pl. 17, no. 54) describe the female from the holotype and figure wing, antenna, ovipositor and (assumably) fore leg. According to them, *J. contracta* is allied to Jas-
**sidophaga nearctica** Kehlmaier, 2005 [quoted as *Jassidophaga fasciata* (Hardy, 1939)] but differs in the shape of the ovipositor.

*Jassidophaga eximia* (Kuznetzov, 1992) – only ♀ known

The description of this very small species is based on the female holo- and a paratype collected in Primorsk territory, Asian part of Russia. The following features, taken from the original description, should enable an identification of *J. eximia*, which seems to be closest to *J. beatricis*: body length 2.6 mm, wing length 3.6 mm, 2 pairs of long scutellar bristles, pulvilli as long as distitarsi, shape of ovipositor figured in Kuznetzov (1992, figs. 78, 79).

*Jassidophaga flavidipes* De Meyer & Grootaert, 1992 – only ♀ known

Known from a single female captured in Australia, De Meyer & Grootaert (1992) present a thorough diagnosis of this taxon and figure its ovipositor. As *J. argentisegmentata*, the species has yellow antennae and legs (except coxae and trochanters).

*Jassidophaga guangxiensis* Yang & Xu, 1996 – only ♀ known

The identity of this species is insufficiently known at present. Yang & Xu (1996, pl. 17, no. 55) describe the female from the holotype and figure wing and ovipositor. According to them, *J. guangxiensis* is supposed to be close to *J. pilosa* but differs from the latter by the longer fourth costal section.

*Jassidophaga hodosa* (Kuznetzov, 1992) – only ♀ known

Described from the female holotype collected on Sakhalin Island (Asian part of Russia). The following key characters are obtained from the original description: scutellum with 2 pairs of long bristles, LTC : LFC = 1.5, pulvilli 0.8 times distitarsi, fore and middle femora with distinct ventral wart, shape of female ovipositor figured in Kuznetzov (1992, figs. 41–42). In his identification key, this author characterizes *J. hodosa* by bearing 8–10 strong marginal bristles. However, from the original description, one gets the impression that the scutellum only bears “… 4 very long …” marginal bristles amongst an additional “… 4 short black bristles on hind margin” (Kuznetzov 1992: 112). Kuznetzov places the species near *J. fasciata*.

*Jassidophaga japonica* ssp. *japonica* (Morakote, 1990) – ♂ ♀

The species was described from Japan and male genitalia and female ovipositor are nicely illustrated in Morakote & Hirashima (1990). It is related to *J. beatricis* and *J. pilosa*.

*Jassidophaga japonica* ssp. *melanosa* De Meyer & Grootaert, 1992 – only ♂ known

De Meyer & Grootaert (1992) describe the subspecies from five males collected in Papua New Guinea and Australia and figure its genitalia and sternite 5.

*Jassidophaga kurilensis* (Kuznetzov, 1992) – ♂ ♀

Kuznetzov (1992) regards *J. setosa* sensu Morakote & Hirashima (1990) as a distinct species, also recording it from Kuril Islands (Asian part of Russia), and subsequently describing it as *J. kurilensis*. Descriptions and figures are provided by Morakote & Hirashima (1990) and Kuznetzov (1992). For the time being,
Kuznetzov’s point of view is followed here. However, his hypothesis of two independent taxa may well be questioned and should be tested by additional morphological studies and DNA sequencing. Dempewolf & Colln (1999) recorded 1♂ and 2♀ in Western Germany (Eifel region), stating that the specimens keyed out towards J. kurilensis but treating them as Jassidophaga sp.

For a differentiation of the two species, Kuznetzov (1992) uses the shape of the surstyli, being shorter and wider in J. kurilensis, and the “... presence of two groups of 9–12 short stoutish black spines in two rows sublaterally on the sternite 5 ...” (Kuznetzov 1992: 111). However, in his identification key on page 105 he erroneously states “Fifth sternite with two groups of 10–12 short black spines on each side near posterior margin ...”, i.e., with 20–24 spines on each side. This is especially interesting, because Kuznetzov (1992) interprets J. fasciata as only bearing three spines on each side of sternite 5 (see also under J. fasciata).

Jassidophaga makarkini (Kuznetzov, 1992) – only ♀ known

The female holotype and only specimen known at present was collected at Kun-dur, Khingan Nature Reserve, Amur Province, Asian part of Russia. The following features taken from the original description should enable an identification of J. makarkini, a species apparently allied to J. fasciata: 3 pairs of long scutellar bristles, LTC : LFC = 1.5, pulvilli shorter than distitarsi, fore and middle femora with a distinct wart, fore and middle tibiae yellow, shape of ovipositor figured in Kuznetzov (1992, figs. 55, 56).

Jassidophaga nearctica Kehlmaier, 2005 n. nom. – ♂ ♂

Due to the resurrection of Jassidophaga fasciata (Roser, 1840) from synonymy, a new name had to be chosen for Jassidophaga fasciata (Hardy, 1939) (see above under 3.2.2). J. nearctica was originally described from the female only (Hardy 1939). In his revision of Nearctic Pipunculidae, Hardy (1943) then describes the male and figures the dorsal aspect of its abdominal tip, the female ovipositor in dorsal and lateral view and the antenna (no sex given). Therefore, female J. nearctica may be identified via its ovipositor but the identity of the male has to be regarded as insufficiently known.

Jassidophaga pala (Morakote, 1990) – ♂ ♂

The species could be recorded from the Asian part of Russia and Japan in the past. J. pala stands close to J. villosa and is nicely described and figured in Morakote & Hirashima (1990). It differs from the former, amongst other small morphological features, by a pale flagellum, instead of a dark brown or black one. Kuznetzov (1992) synonymizes J. pala with Verrallia pseudovillosa Churkin, 1990.

Jassidophaga plumbella (Brunetti, 1912) – only ♂ known

Described from the female holotype and only recorded from India in the past, the identity of this taxon is insufficiently known. Due to the poor state of the holotype, Kapoor et al. (1987) reproduce the redescription of J. plumbella presented by Brunetti (1923). Hardy (1972) comments extensively on one male and three females that he attributes to this species with a question mark. He figures male sternite 5, tip of abdomen in ventral view and female ovipositor.
Jassidophaga pollinosa (Kuznetzov, 1992) – only ♀ known

The only known specimen so far, the female holotype, was collected at Yukki (Leningrad Province, European part of Russia). The following features are taken from the original description and indicate a close relationship with J. villosa rather than J. fasciata as pointed out by Kuznetzov (1992): 4 pairs of long marginal scutellar bristles, pulvilli 1.9 times as long as distitarsi, LTC:LFC = 1.6, fore and mid femora with a distinct wart, shape of ovipositor figured in Kuznetzov (1992, figs. 58, 59).

Jassidophaga sidorenkoi (Kuznetzov, 1992) – only ♀ known

At present, only known from the female holotype collected on Kunashir Island (Kuril Islands, Asian part of Russia). The species is characterized by 2 pairs of long scutellar bristles, pulvilli as long as or slightly longer than distitarsi, LTC:LFC = 1.5 and shape of ovipositor as figured in Kuznetzov (1992, figs. 80, 81). The species should stand very close to J. beatricis.

Jassidophaga speciosa (Kuznetzov, 1992) – only ♀ known

Only known from the female holotype so far, collected on Kunashir Island (Kuril Islands, Asian part of Russia). The following features taken from the original description should enable an identification of J. speciosa: 4 pairs of long scutellar bristles, pulvilli 1.25 times distitarsi, LTC:LFC = 1.6, fore and middle femora with a distinct wart, shape of ovipositor similar to J. pilosa and figured in Kuznetzov (1992, figs. 60, 61).

Jassidophaga triloba (Yang & Xu, 1989) – only ♂ known

Described from male material collected in China, Shaanxi Province, Nanwutai, the species is not included in Kuznetzov (1992). Yang & Xu (1989) give a brief differential diagnosis from the related J. chiensis in English and figure the wing and the tip of the abdomen in dorsal view. Although they point out that sternite 9 is composed of three plates instead of two, as in other members of the genus, the identity of J. triloba has to be regarded as insufficiently known.

Jassidophaga verrucosa (Kuznetzov, 1992) – only ♀ known

The female holo- and paratype were collected in the Leningrad Province, European part of Russia. In his identification key, Kuznetzov (1992) characterizes J. verrucosa by bearing 8–10 strong marginal bristles. However, in the description, he states that the scutellum bears “…4 very long black bristles on hind margin” (Kuznetzov 1992: 112). The following features taken from the original description indicate a close relationship with J. beatricis: 2 pairs of long marginal scutellar bristles, pulvilli longer than distitarsi, LTC:LFC = 1.0, fore and mid femora with a distinct wart, shape of ovipositor figured in Kuznetzov (1992, figs. 62, 63).

4.2 Species of Verrallia

Verrallia ciskii Aczél, 1940 – only ♀ known

V. ciskii was originally described from a single female specimen by Williston (1886) as Pipunculus opacus Williston, 1886 and later renamed by Aczél (1940). In his revision of Nearctic Pipunculidae, Hardy (1943) quotes the original description of Williston and points out that he was not able to study the taxon, due to the un-
known deposition of the holotype. The species seems to be a member of *Verrallia* but its exact identity is insufficiently known.

*Verrallia rebunensis* Morakote, 1990 – ♂♀

Morakote (in Morakote & Hirashima 1990) describes the taxon from a single male and figure its antenna, thorax, sternite 5 and genitalia. Kuznetzov (1992) records an additional male and 5 female specimens. Unfortunately, he does not provide a drawing of the female ovipositor. Also, female *V. rebunensis* is not included in his identification key. An attempt to inquire if Kuznetzov (1992) accidentally mixed up the genus signs failed. The species is known from the Asian part of Russia and Japan.

*Verrallia spectabilis* Collin, 1941 – ♂♀

Collin (1941) describes both sexes and figures the female ovipositor, but does not comment on the male genitalia in detail. Kuznetzov (1992, figs. 11–13) figures the male genitalia, sternite 5 and projection of sternite 7. Morakote & Hirashima (1990) give a redescription of female *V. spectabilis* and provide a nice habitus figure of a female specimen. The species is known from the Asian part of Russia and Japan.

*Verrallia virginica* Banks, 1915 – ♂♀

According to Thompson (1977), who resurrected *V. virginica* from its synonymy with *V. aucta*, the male genitalia and female ovipositor of the latter two species are identical. However, he lists several distinct and apparently stable colour differences that separate the two. Also, host records and life history data seem to indicate the existence of two independent taxa, with *V. virginica* known to parasitize the Cerocopidae *Aphrophora saratogensis* (Fitch, 1851) (Linnane & Osgood 1977).

5 References


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