

Revision of the cluster-flies of the *Pollenia venturii* species-group, with a cladistic analysis of Palaearctic species of *Pollenia* Robineau-Desvoidy (Diptera: Calliphoridae)

KNUT ROGNES

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Within *Pollenia* Robineau-Desvoidy a *venturii* species-group is defined and revised. It consists of a single species *P. venturii* Zumpt. *P. solitaria* Grunin is proposed as a junior synonym. It is characterized by unique features in the male aedeagus and the lateral sacs of the internal female reproductive organs. Male and female terminalia are illustrated, the latter for the first time. A preliminary cladistic analysis of all known Palaearctic species of *Pollenia* (except *P. japonica* Kano & Shinonaga) suggests that the sister-group of *P. venturii* is a clade consisting of the *viatica* + *vagabunda* + *amentaria* + *haeretica* species-groups. A sclerotized internal wall of the lateral sacs in the internal reproductive system of female *Pollenia* appears to be a parallelism developed independently in the *venturii*, *rudis*, most members of the *tenuiforceps* and some members of the *semicinerea* groups, rather than an underlying synapomorphy. *P. venturii* is known from France, Germany, Greece, Italy and Russia. A key is provided to species-groups in *Pollenia*.

K. Rognes, Stavanger Lærerhøgskole, Postboks 2521 Ullandhaug, N-4004 Stavanger, Norway.

Introduction

The present paper is a sequel to earlier ones revising various species-groups in the cluster-fly genus *Pollenia*, some members of which, in the larval stages, are known to be parasites or predators of earthworms (Rognes 1987a, b, 1988, 1991b, 1992). Its purpose is to define a *venturii* species-group within this genus and revise its nominal species. To clarify its relationship with other species-groups within *Pollenia* a cladistic analysis of all known Palaearctic species of *Pollenia* (except the Japanese *Pollenia japonica* Kano & Shinonaga) has been performed. The analysis is based partly on data in my already published species-group revisions, and partly on data from species-group revisions still under preparation (*amentaria*, *griseotomentosa*, *tenuiforceps*, *haeretica* and *japonica* species-groups).

Material and methods

The study is based primarily on material in the following collections (followed by the depository acro-

nym used in the text): Department of Entomology, The Natural History Museum, London (BMNH); Muséum National d'Histoire Naturelle, Paris (MNHN); the Venturi collection in Università degli Studi, Istituto d'Entomologia Agraria, Pisa (PISA); Staatliches Museum für Naturkunde, Stuttgart (SMNK); United States National Museum, Smithsonian Institution, Entomology, Washington (USNM); Universitetets Zoologiske Museum, København (ZMUC) and the Zoological Museum, Moscow Lomonosov State University, Moscow (ZMMSU).

Morphological terms and abbreviations follow Rognes (1991a).

Cladistic analyses were performed using Farris' parsimony program HENNIG86 (Farris 1988). It is based on the 40 Palaearctic species of *Pollenia* listed (with abbreviations) in Appendix 1. 43 characters (with numbers 0–42) employed in the analysis and their coding are explained in Appendix 2. The data matrix is shown in Appendix 3. A group consisting of *Morinia* + *Melanodexia* + an hypothetical 'outgroup' assumed to embody the ground plan fea-

tures of the subfamily Polleniinae (cf. Rognes 1991a) was used as outgroup for rooting the cladogram. Trees were first calculated by the command sequence *mh**; *bb**; with all characters given unity weight (UNWEIGHTED). This resulted in 108 equally parsimonious trees (length 107 steps, consistency index 0.55, retention index 0.82). Subsequently, the successive weighting procedure of HENNIG86 (Farris 1988, 1989; see also Seberg 1989: 189) was employed by repeating the command sequence *mh**; *bb**; *xsteps w*; *cc*; until the weights no longer changed (SUCCESSIVE WEIGHTING). This resulted in 756 equally parsimonious trees (after 4 rounds of the command sequence) (length 468, *ci* 0.83, *ri* 0.94). From the latter trees a strict consensus cladogram was calculated using the *nelsen* option which retains only the monophyletic groups present in all the 756 trees (Fig. 11).

A second series of analyses was performed in which character 20 (♀ lateral sacs, unordered) was coded instead by ordinal branched coding as outlined by Mickevich & Weller (1990). Position 20 in the data-matrix was replaced by the following codes (the position 20 score in Appendix 3 in parenthesis): unsclerotized tubes 00 (0), sclerotized tubes 10 (1), sclerotized fused spheres 20 (2), sclerotized disks 11 (3), and treated as additive characters (ordered). This character state tree for the lateral sac character assumes that sclerotized fused spheres as well as sclerotized disks derive independently from sclerotized tubes. Otherwise the data matrix was identical to the one showed in Appendix 3. The command sequence *mh**; *bb**; resulted in 144 equally parsimonious trees (length 108 steps, *ci* 0.54, *ri* 0.82). A subsequent successive weighting procedure resulted in 658 equally parsimonious trees (length 466, *ci* 0.83, *ri* 0.94) after 3 iterations. The strict consensus cladogram calculated using the *nelsen* command contained exactly the same groups as the tree in Fig. 11.

Genus *Pollenia* Robineau-Desvoidy

Pollenia Robineau-Desvoidy, 1830: 412. Type-species: *Musca rudis* Fabricius, by original designation. For a comprehensive list of generic synonyms and a diagnosis of the genus, see Rognes (1991a).

Key to species-groups of Palaearctic *Pollenia*

Dissection of male and female terminalia is necessary before the key can be used. It will not work for

all females, as they are insufficiently known in many species-groups. The key does not cover the East Palaearctic genus *Xanthotryxus*, even if it will probably be relegated to the status of a separate species-group within *Pollenia* in the future because of its profuse vestiture of yellow-white curly '*Pollenia*-hairs'. Its species are very large and have the parafacialia entirely bare. The composition of the species-groups is indicated in Appendix 1.

1. Costa hairy below to about halfway between junctions with R_1 and R_{2+3} (i.e. second and at least half of third costal sector hairy below) *japonica* group (1 species)
- Costa hairy below only to junction with Sc, occasionally some hairs between junctions with Sc and R_1 (i.e. second costal sector bare below) 2
2. Aedeagus with a median midventral hypophallic lobe (absent in one member of the *griseotomentosa* group); each lateral hypophallic lobe more or less triangular with a central sclerotization (sclerotization absent in another member of the *griseotomentosa* group); ovipositor only with soft wavy setae on tip, no spines 3
- Aedeagus without a median hypophallic lobe; each hypophallic lobe differently shaped and absolutely without central rod-like sclerotization; ovipositor with or without spines on tip 7
3. Male hind tarsi shorter than hind tibia; basicosta black 4
- Male hind tarsi longer than hind tibia; basicosta yellow or black 6
4. Hind leg of male with specialized vestiture of tibia and tarsus (except *tenuiforceps*); facial carina distinct; male cerci of normal width; aedeagus with blunt rounded apex of each hypophallic lobe; each paraphallic process appearing somewhat thickened apically in some views and apically curving strongly inwards towards midline; median hypophallic lobe fully sclerotized; female lateral sacs when sclerotized shaped as flat disks . . . *tenuiforceps* group (4 species)
- Male hind leg usually without modified vestiture (except *pectinata* of the *semicinerea* group); male cerci very narrow; apex of paraphallic processes usually not curving strongly towards midline, nor apically thickened; median hypophallic lobe at most sclerotized in posterior part 5
5. Outer *ph* seta present; facial carina usually conspicuous; body size typical for a *Pollenia*; aedeagus with triangular distally very sharp hypophallic lobes, these lobes with a very distinct central sclerotization; female lateral sacs when sclerotized shaped as long tubes *semicinerea* group (5 species)
- Outer *ph* seta usually absent; facial carina absent or very indistinct; body size small for a *Pollenia*; abdomen with dusted tessellations in an unusual pattern (dark blackish longitudinal band occupying central half of tergites or broad blackish anteriorly narrowing triangles); lateral hypophallic lobes often with indistinct central sclerotization (*mayeri*, which has a very dense 'brush'

- of long setae on male ST5); median hypophallic lobe sometimes absent (*griseotomentosa*); female lateral sacs unsclerotized
 *griseotomentosa* group (2 species)
6. Basicosta most often yellow, sometimes darkened; lappets of metathoracic spiracle yellow; facial carina conspicuous; paraphallic processes proceeding distad parallel with long axis of aedeagus, thus not curving toward midline; female with sclerotized lateral sacs in the shape of long sometimes coiled tubes *rudis* group (7 species)
- Basicosta black; lappets of metathoracic spiracle dark matt brown; facial carina absent or very indistinct; paraphallic processes curving conspicuously towards midline; female with unsclerotized lateral sacs *labialis* group (2 species)
7. Aedeagus with very long lateral hypophallic lobes, apically these are shaped like a kind of gutter; acrophallus tending to appear as a small appendix inserted dorsally on the apex of the distiphallus; female ovipositor with microtrichiae on ST8 and pleural membrane 8; female lateral sacs shaped as fused spheres with sclerotized internal walls *venturii* group (1 species)
- Aedeagus without a gutter-like structure apically on the hypophallic lobe; acrophallus long and proceeding in same direction as distiphallus; female ovipositor without microtrichiae on ST8 and pleural membrane 8; female lateral sacs unsclerotized 8
8. Basicosta yellow; facial carina very conspicuous and broad, rounded on top; aedeagus with long ventral plates; female ovipositor with numerous straight stiff spines on tip, without microtrichiae on epiproct and most of pleural membrane 7 *viatica* group (7 species)
- Basicosta black; facial carina narrower, less conspicuous or absent 9
9. 2 inner *ph* setae; very often with supplemental strong setae in front of the normal 3 *h* setae; male cerci bent backwards when seen in profile; some species with median presutural undusted vitta and 2 *pv* setae on front tibiae; others without median undusted vittae and with a single *pv* seta on front tibia *vagabunda* group (5 species)
- 1 inner *ph* seta; no supplemental setae in front of the 3 *h* setae; male cerci straight when seen in profile 10
10. Scutellum with 4(–5) pairs of marginal setae; male frons very broad for a *Pollenia*; male cerci with a dense brush of short hairs on apex *haeretica* group (2 species)
- Scutellum with 5–6 pairs of marginal setae; male frons normal; male cerci without a dense brush of short hairs on apex (except in *leclercqiana* which has the cell r_{4+5} stalked) *amentaria* group (5 species)

Autapomorphies of the *venturii* species-group

At present only a single species is known in the *venturii* species-group: *P. venturii* Zumpt, which is

now recognizable in both sexes (the female has hitherto been unidentifiable). It is characterized by the following two autapomorphies which also are unique in *Pollenia*:

(1) A peculiar aedeagus (Figs 3–4) [character 0(2)].

The aedeagus is equipped with long hypophallic lobes apically furnished with a kind of longitudinal gutter, open dorsally and distally with an almost circular opening. The paraphallic processes are housed in but not projecting beyond the distal end of this gutter. There is no mesohypophallic sclerotization proceeding distad beyond the ventro-apical end of the ventral plate sclerotization. The acrophallus is strikingly short and projects somewhat dorsally. It often has the appearance of a short sclerotized dorsal appendix implanted distally on the aedeagus since most of the unsclerotized membrane is invisible in the stereomicroscope unless examined with a dark background.

(2) Peculiar lateral sacs of the internal female reproductive organs (Figs 9–10) [character 20(2)].

These are almost spherical, firmly fused in the midline and furnished with a very thick wall. The lumen of the composite structure appears double, each half probably receiving the apex of a single hypophallic lobe with one paraphallic process during mating. The internal walls are strongly sclerotized.

According to the cladogram (Fig. 11) the following autapomorphies, all non-unique in *Pollenia*, also define the *venturii* species-group:

(3) Broad male cerci [character 11(2)].

(4) Weak abdominal dusting [character 41(1)].

(5) Black katepisternal ground vestiture [character 30(1) (only under some optimizations of interior node character states)].

Taxonomic history of the *venturii* species-group

Lehrer (1963, 1967) grouped *Pollenia venturii* with *P. fulvipalpis* Macquart (as *bisulca*), *P. viatica* Robineau-Desvoidy (as *pallida*) and *P. bulgarica* Jacentkovský mainly on the basis of alleged shape and length of the hypophallic lobes. Rognes (1991b) pointed out that the structure of the ovipositor of *venturii*, unknown to previous workers, did not support such an assignment, and he rejected Lehrer's classification. When Grunin (1970) described *Pollenia solitaria* he did not mention the

close resemblance of the male genitalia to those of *Pollenia venturii* as described by Zumpt (1956), probably because the latter species was unknown to him, even though Zumpt's figures of these organs might have suggested such an idea. Zumpt erroneously described the abdomen of his *venturii* as totally devoid of dusting ('glänzenschwarz, völlig ohne Bestäubung'), but the material I have examined has at least some dusting on abdomen when seen in tangential view. This may also have misled Grunin into believing that *solitaria* was a separate species.

Relationships of the *venturii* species-group

The large number of trees (108, 144, respectively) obtained from both series of cladistic analyses (regardless of the coding of character 20) (both UNWEIGHTED, above) varied in the position of the *venturii* group in only two ways. One group of trees showed *venturii* as the sister group of a clade consisting of 20 species belonging to the *rudis*, *labialis*, *griseotomentosa*, *tenuiforceps* and *semicinerea* groups. The monophyly of this clade is based on common possession of sclerotized lateral sacs of whatever shape (character 20). The other group of trees showed the *venturii* group as the sister-group of a clade consisting of the *haeretica* + *amentaria* + *vagabunda* + *viatica* groups (as in Fig. 11, node 62). The nelsen trees resulting from both SUCCESSIVE WEIGHTING analyses also gave the latter grouping. This sister-group relationship is based on character 17(1), the position of the marginal setae on the T8 in the ovipositor definitely in front of the hind margin of this sclerite (Appendix 5). This character state is a synapomorphy also for node 46 (the *semicinerea* group) and node 51 (the *rudis* group). It has a weight of 2 (Appendix 4). For the time being the position of *venturii* is therefore rather precarious.

Relationships of the *rudis* species-group

The monophyletic group determined by node 61 on the cladogram of Fig. 11 encompasses the same species as analyzed by Rognes (1988: 342, fig. 59). Although all species-groups turn out to be monophyletic and reasonably well founded (Appendix 5), their interrelationships as revealed by the HENNIG86 parsimony analysis are quite different from those presented in my earlier paper. This is due among other things to the fact that my former anal-

ysis was based on the concept of underlying synapomorphy, which I now believe is impossible to use as evidence for grouping (Farris 1986; in spite of Sæther 1988). Neither can it be coded, since it is impossible to get any clues by inspecting specimens as to which terminal taxa one should assign 'the common capacity to develop the same feature' (Sæther 1988: 48). Apparently, it can be invoked for any imaginable group. Undoubtedly the phenomenon may occur, but this can only be revealed after a parsimony analysis has been performed (Farris 1986). The tree presented in my earlier paper is not a most parsimonious tree for the data employed and not one best supported by available data. Since extra-Palaeartic relatives of *Pollenia*, including the Japanese *P. japonica* Kano & Shinonaga, have not yet been analyzed in sufficient detail, the above HENNIG86 analysis should still be regarded as preliminary.

Pollenia venturii Zumpt

(Figs 1-10)

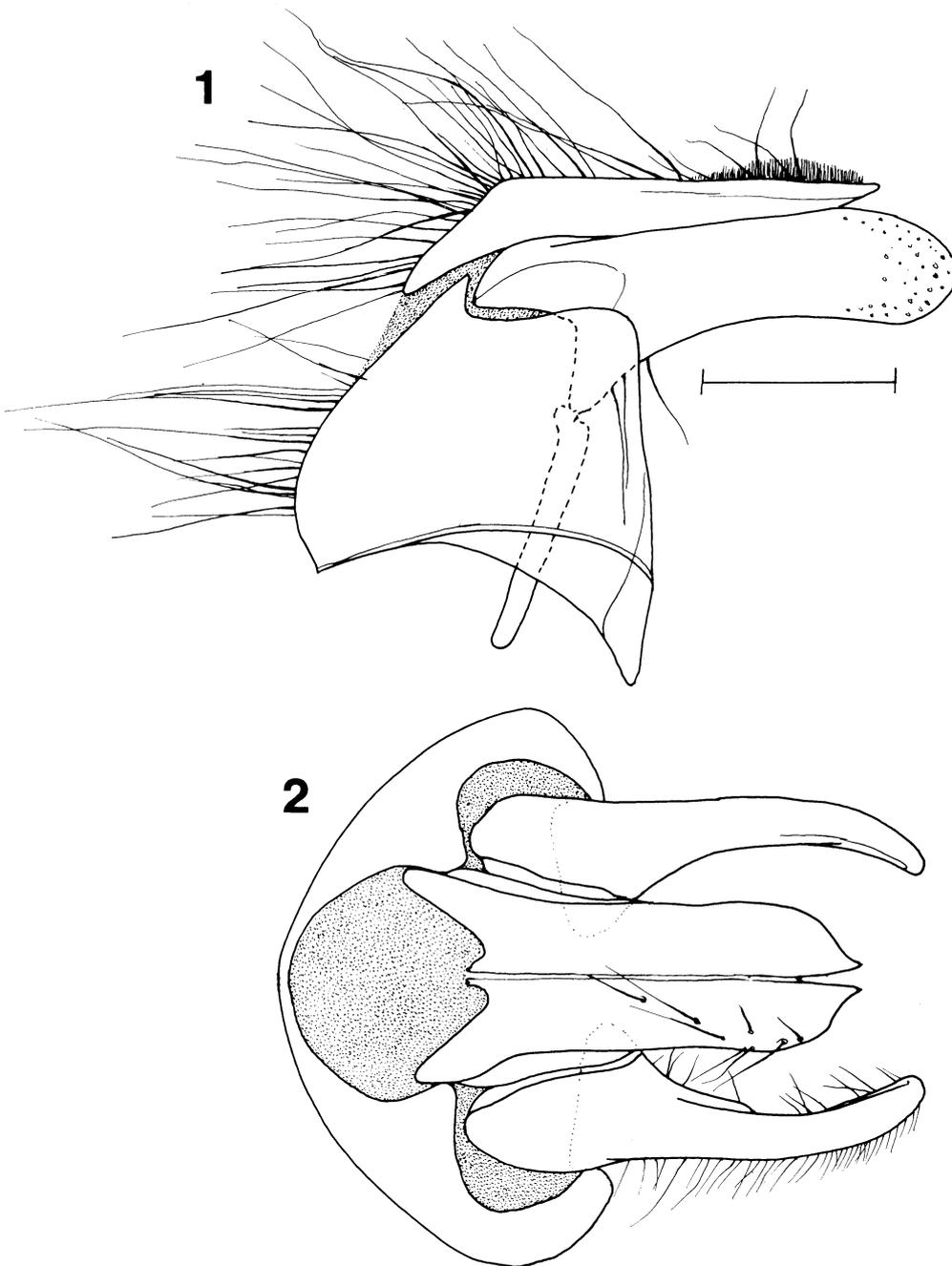
Pollenia venturii Zumpt, 1956: 79 (description), Tafel VI, fig. 75 (aedeagus in profile), Tafel VII, fig. 78 (cerci and surstyli, flattened mount); Loi & Raspi, 1983: 233 [63] (Venturi collection catalogue entry); Schumann, 1986: 47 (Palaeartic catalogue entry); Rognes, 1991b: 442 (rejection of close relationship with *viatica* species-group). Holotype ♂, ITALY (BMNH) [examined].

Pollenia solitaria Grunin, 1970: 480 (description), 481 figs. 44-47 (cerci, surstyli and aedeagus, in profile and frontal views); Schumann, 1986: 47 (Palaeartic catalogue entry). Holotype ♂, RUSSIA (ZMMSU) [examined]. **Syn. n.**

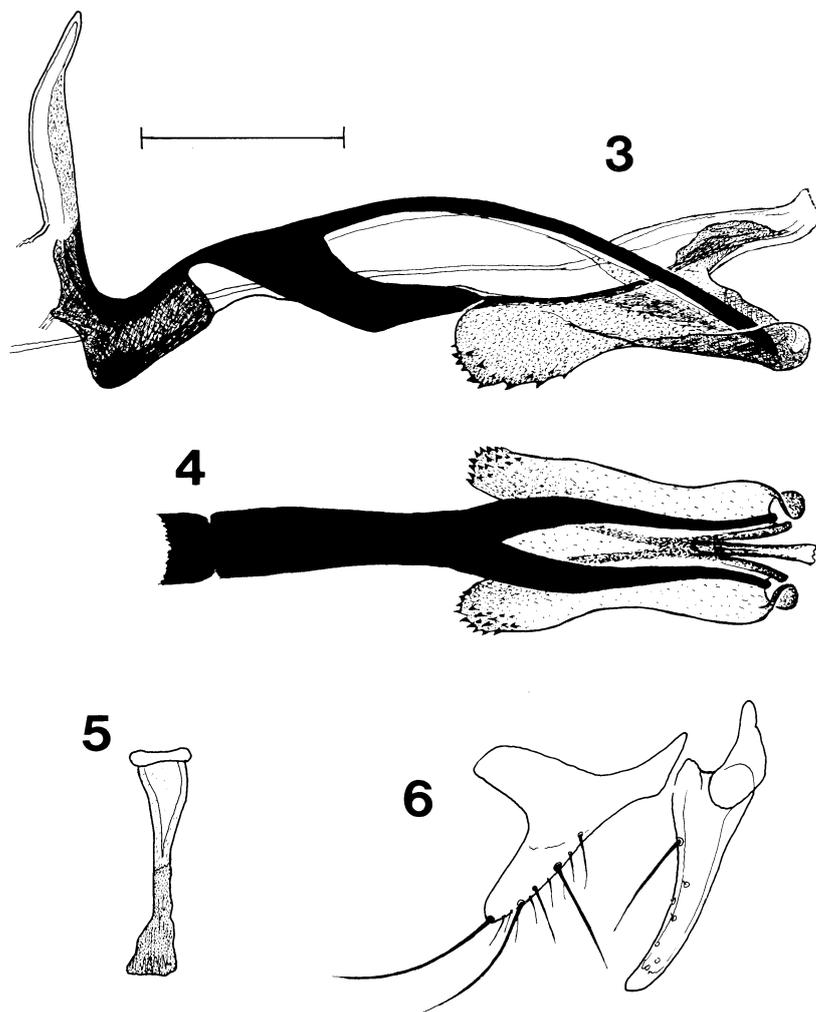
Sachtlebeniola venturi (Heinz); Lehrer, 1963: 292 (proposed assignment to *viatica* species-group).

Nitellia venturi Zumpt; Lehrer, 1967: 258 (proposed assignment to *viatica* species-group).

Diagnosis. - *Pollenia venturii* is reliably separable from all other Palaeartic *Pollenia* on the structure of the male aedeagus and the female lateral sacs. On external features it differs from other *Pollenia* species with black mostly shining abdomen, as follows: from *amentaria* (Scopoli) and *moravica* (Jacentkovský) (♂ ♀) on the black katepisternal vestiture and fewer marginal scutellar setae, the females also on the rather narrow fronto-orbital plates, being much narrower than half the frontal vitta, and being black and shiny in the dorsal part; from *leclercqiana* Lehrer on the open unstalked cell r_{4+5} ; from *atramentaria* (Meigen) on the dorsally bare stemvein; from *mystica* Rognes and *paragrunini* Rognes on the presence of 2 *pv* setae on front tibia, longer



Figs 1-2. *Pollenia venturii* Zumpt (F, Lardy, USNM), ♂ terminalia: (1) cerci, surstylus, epandrium and bacilliform sclerite, lateral view; (2) cerci, surstyli and epandrium, posterior view. Scale 0.2 mm.



Figs 3–6. *Pollenia venturii* Zumpt (F, Lardy, USNM), ♂ terminalia: (3) aedeagus, lateral view; (4) distiphallus, posterior view; (5) ejaculatory sclerite; (6) pre- and postgonites. Scale 0.2 mm.

hind tarsi, smaller facial carina and broader frons (in the male) and brown thoracic spiracles; from *alajensis* Rodendorf on the longer hind tarsi and broader frons (in the male).

Description. – ♂ ♀. Black body with very little dust. Head black, except for reddish colour of lunula, facial ridges, vibrissal corner, and edge of oral opening carrying subvibrissal setae. Genal dilation shining black, very thinly dusted, with black vestiture. Upper parts of fronto-orbital plates black and shiny, very thinly dusted. Parafacialia, area between

eye and postocular cilia, and anterior half of fronto-orbital plates densely silvery dusted, sometimes with an additional golden sheen. Facial keel distinct, narrow, black, convexity directed forwards in profile. Occiput with 3–4 irregular rows of black setulae behind postocular row of setae, pale hairs centrally, but these never invading genal dilation from behind. Parafacial vestiture short, not as long as width of first flagellomere and much shorter than longest arisal hairs. Antenna with scape and pedicel yellow or brown, first flagellomere black; parts of pedicel and first flagellomere closest to

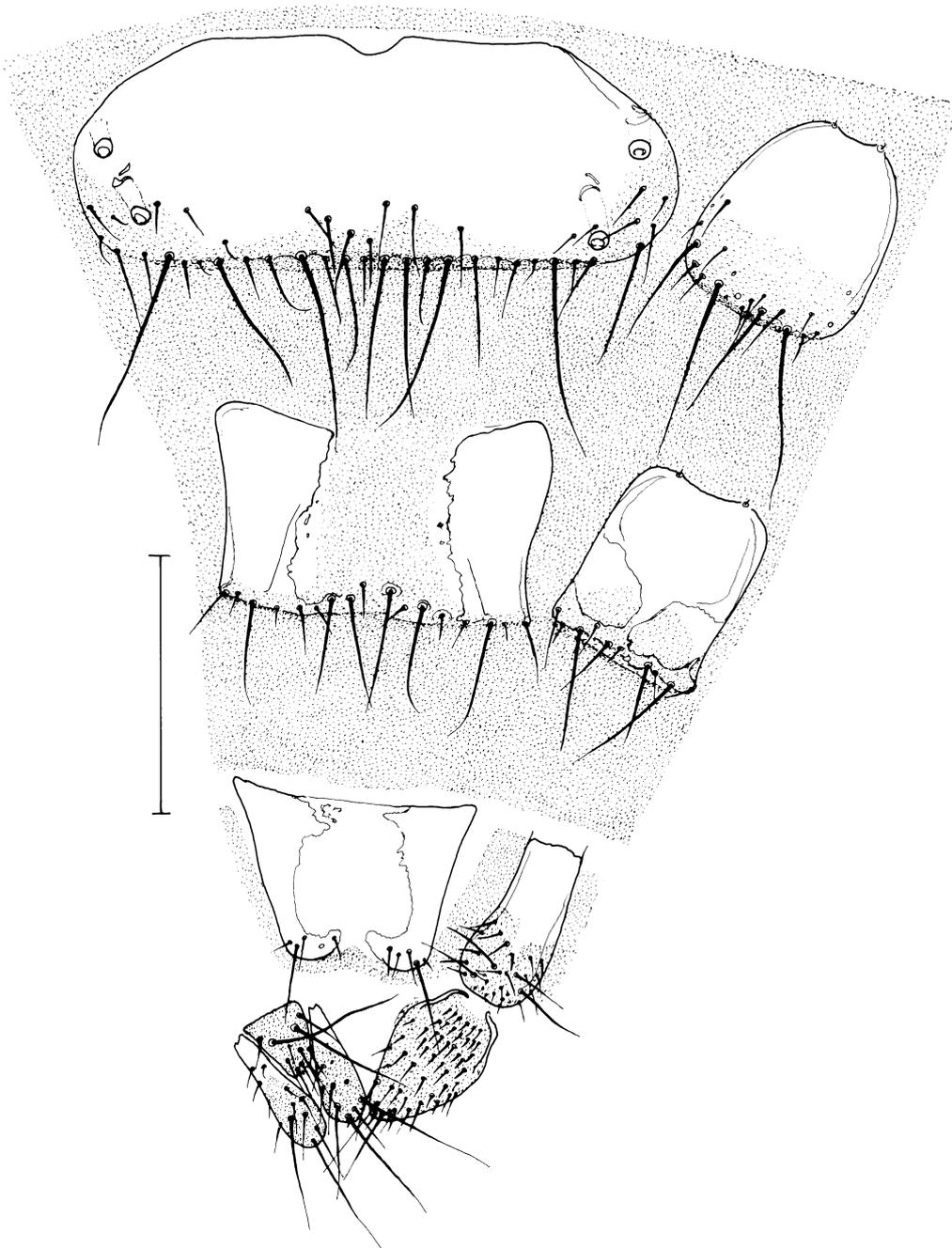


Fig. 7. *Pollenia venturii* Zumpt (F, Lardy, USNM), ♀ terminalia (G. pr. 304): ovipositor (stipple indicates extent of microtrichiae). Scale 0.5 mm.

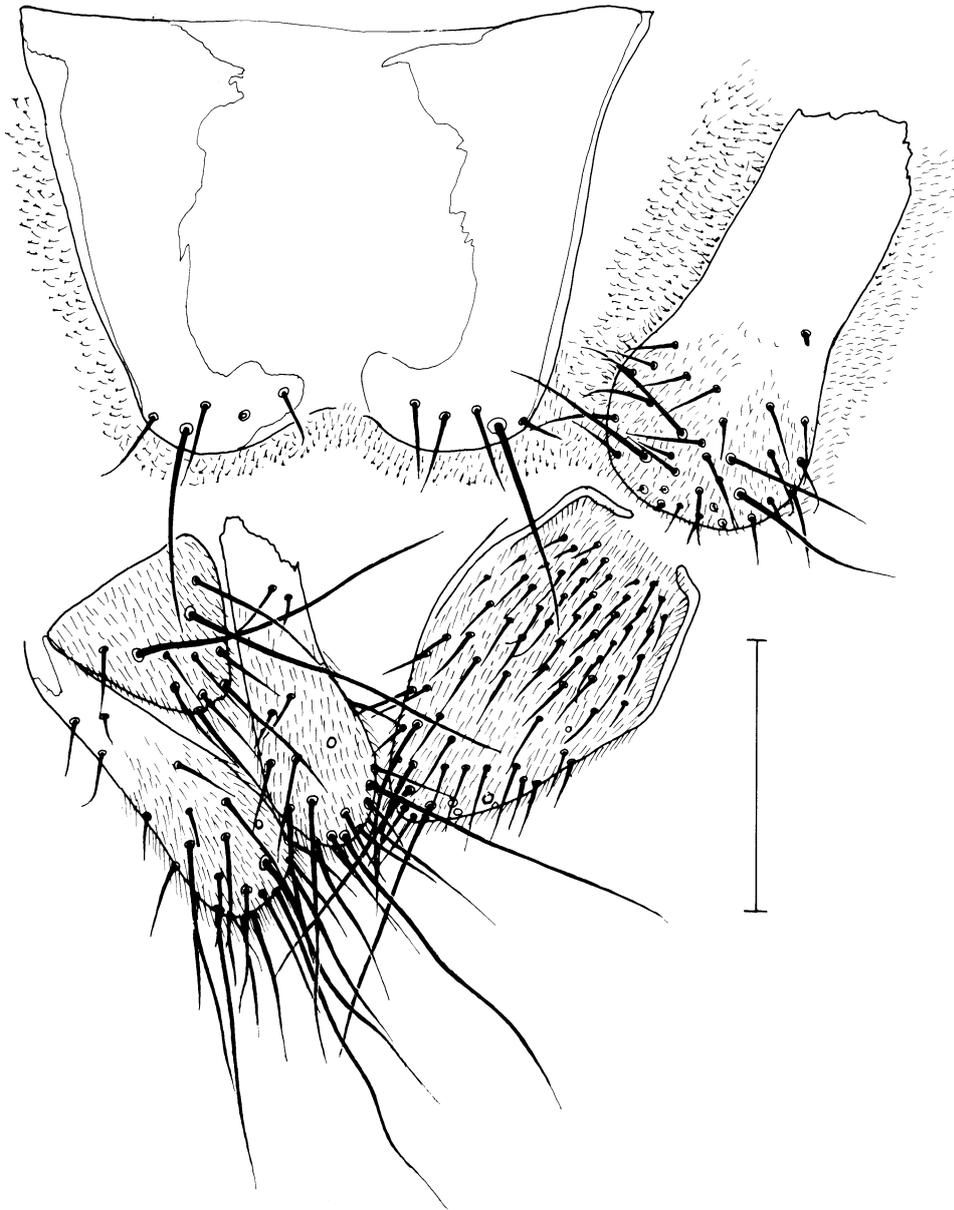
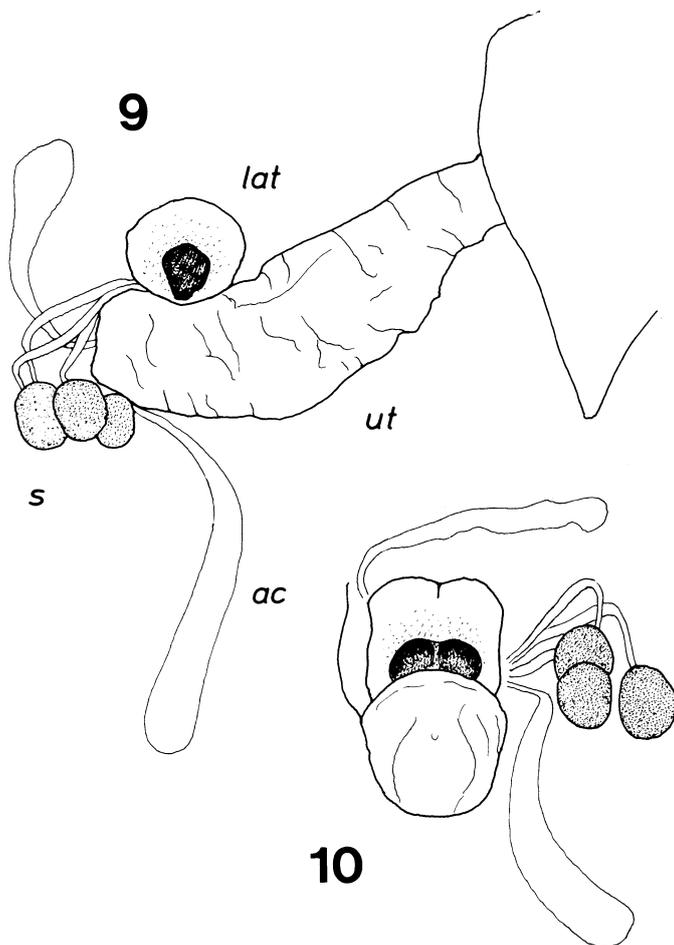


Fig. 8. *Pollenia venturii* Zumpt (F, Lardy, USNM), ♀ terminalia (G. pr. 304): T8, epiproct, cerci, ST8 and hypoproct. Scale 0.2 mm.

junction always bright yellow. Thorax black with very little dusting, no vittae discernible. Outer *ph* seta often absent (see below). Katepisternal ground vestiture black. 4–5 pairs of marginal scutellar setae, 1 pair of discal scutellar setae. Spiracles brown

(darker than *rudis* group). Lower calypter brownish in male, white in female. Wing veins paler in female than in male. *bc* black. Cell r_{4+5} always widely open. t_1 with (1–)2 *pv* setae; t_2 with 2–3 *ad* setae, t_3 with 2–3 *av* setae. Tarsi as long as tibiae. Abdomen



Figs 9-10. *Pollenia venturii* Zumpt (F, Lardy, USNM), ♀ terminalia (G. pr. 304): (9) uterus, lateral sacs, spermathecae and accessory glands, lateral view of dissection; (10) same dissection seen towards end of uterus. *ac* - accessory glands, *lat* - lateral sacs, *s* - spermathecae, *ut* - uterus.

shining black, usually with only a thin layer of dust, usually visible only in low tangential view, and shifting at midline according to angle of view. In a few cases (males from Greece and Russia) the layer of dusting is rather dense, visible from all directions and not shifting.

♂. Body length: 7-9 mm (n=15). Frons at narrowest point 0.055-0.081x head width (mean 0.066, n=14). Outer *ph* seta absent in 5 of 15 males examined, in two specimens asymmetrically developed. Dorsum of thorax most often without yellow crinkly *Pollenia* vestiture. Anepisternal vestiture behind anepisternal row of setae mostly black.

Postalar wall with mostly black vestiture. Genitalia as in Figs 1-6. Cerci broad, apical cleft small. Surstyli very broad in lateral view, longer than cerci, curving towards midline apically. Aedeagus as described above. Paraphallic tips do not project beyond hypophallic lobe apices. These latter each folded to a sort of apical canal guiding the movement of distal paraphallic tips. Distiphallus very characteristic in dorsal view. Acrophallus very short, projecting dorsally in profile view. Postgonites with a basal seta. Ejaculatory sclerite small.

♀. Body length: 6.5-7.5 mm (n=5). Frons at narrowest point 0.302-0.328x head width (mean 0.315,

n=5). Fronto-orbital plates much narrower than half width of frontal vitta. In posterior half the fronto-orbital plates are black and shiny, almost without dusting. Outer *ph* seta absent in 4 of 5 specimens examined, in the fifth specimen it was very weak on both sides. Dorsum of thorax most often with some yellow crinkly *Pollenia* vestiture. Anepisternal vestiture behind anepisternal row of setae mostly yellow. Postalar wall with mostly yellow vestiture, with some admixture of black setae. Ovipositor as in Figs 7-8. Cerci with soft wavy hairs, no spines present. Ovipositor sclerites short. T7 invaded by microtrichiae all over middle portion. ST8 with cover of microtrichiae on posterior half. Pleural membrane 8, epiproct and apical $\frac{3}{4}$ of cerci microtrichiose. Lateral sacs (Figs 9-10) almost spherical, firmly fused in the midline and furnished with a very thick wall. The lumen of the composite structure appears double. The internal walls are strongly sclerotized. Spermathecae as in Figs 9-10.

Type material. - *Pollenia venturii* Zumpt. Holotype σ , ITALY, Firenze province, Tavarnuzzo, 18.vii.1945 (Venturi) (BMNH). Paratypes, 8 σ , as follows: ITALY: 1 σ , Pesaro Urbano, Fano, 11.iv.1952 (Venturi) (PISA); 1 σ , Pisa, Cascina 17.vi.1951 (Venturi) (PISA); 2 σ , same 28.v.1952 (Venturi) (PISA); 1 σ , same vi.1952 (Venturi) (PISA); 1 σ , Firenze, 14.vii.1945 (Venturi) (dissected by Heinz, dried genital capsule glued to card) (PISA); 1 σ , Firenze, Galluzzo, 26.v.1949 (Venturi) (postabdomen dissected by Zumpt and mounted on slide no. 53) (BMNH); 1 σ , no labels (Venturi) (dissected by KR) (PISA).

Pollenia solitaria Grunin. Holotype σ , RUSSIA: Krasnodar Kray, village of Lvovskoe, 20.vii.1956 (Viktorov) (dissected by Grunin) (ZMMSU).

Notes on type material. - It is very difficult to decide how many specimens were actually seen by Zumpt, as only a single specimen carries his determination label (the paratype in BMNH), and no dates are given in the original publication (Zumpt 1956). From the description it is evident that he saw other specimens than the 'Holotypus' which 'wurde freundlichst der Entomologischen Abteilung des South African Institutes for Medical Research, Johannesburg, überlassen'. He mentions that 'Diese Art wurde von Herrn Prof. Dr. F. Venturii in 6 Exemplaren in der Provinz Firenze, Italien, gesammelt'. However, he does not state how many of these he saw. In BMNH there are now 2 specimens, and in the Venturi collection (PISA) are 7 more, so that Venturii actually collected 9 specimens before 1952. The BMNH specimens carry a holotype and a paratype label, respectively, the holotype carries an additional red Heinz determination label from 1952, and the paratype an additional Zumpt determination label. None of the specimens in PISA carries a Zumpt label, but two (collected in 1945 and 1951) each carry a yellow paratype label in addition to a blue Heinz determination label from 1952. I accept the reference to the 'Holotypus' and the presence in BMNH of a specimen labelled both as holotype and as having been presented to the BMNH from the

South African Institutes for Medical Research as evidence that Zumpt validly designated a holotype. As it seems impossible to decide which specimens actually were before Zumpt when he described *venturii* I have decided to regard all the remaining specimens collected by Venturi as paratypes. I have labelled them as such.

Remarks on authorship. - Zumpt (1956) published the name of this species in the following way: '*Pollenia venturii* Heinz i. litt.'. Heinz seems to have been the one who coined the name and recognised the species as new. However, since no part of Heinz's letter was printed in Zumpt's work, Zumpt, and not Heinz, is actually the one who provided the taxonomic characters and thus also the one 'satisfying the criteria of availability other than publication' required by the Code (cf. ICZN, Article 50 (a), also Example). Therefore I regard Zumpt, and not Heinz, as the author of the specific name in the sense of the Code, even if the name itself obviously was provided by Heinz.

Other material examined. - FRANCE: 1 σ , Indre, Abloux, no date (Alluud) (dissected by KR) (MNHN); 1 σ , Essonne, Bouray, 8.ix.1912 (Surcouf) (dissected by KR) (MNHN); 1 σ 1 σ , Essonne, Lardy, 10.iii.1912 (Surcouf) (σ dissected by KR) (MNHN); 1 σ 1 σ , same, no date (Ségu) (both sexes dissected by KR, σ G. pr. 304) (USNM). GERMANY: 1 σ Brandenburg, Frankfurt an der Oder, 23.ix.1933 (Riedel) (USNM); 1 σ Baden-Württemberg, Hagnau a. Bodensee, 29.iv.1934 (Lindner) (postabdomen dissected by Zumpt and mounted on slide no 34 (not seen)) (SMNK, except slide); 1 σ Hessen Land, Wallau, 12.iii.1960 (Gruhl) (dissected by KR) (SMNK). GREECE: 1 σ Achaia, Panagitsa 40km NW Tripolis (600m) 14.vii.1982 (Skule & Langemark) (dissected by KR) (ZMUC).

Biology. - Examined material has been captured in the months of March, April, May, July and September. Nothing is known of the immature stages, life-cycle or habits.

Distribution. - *Pollenia venturii* is known from France, Germany (both the former East and West Germany), Greece, Italy and the Russian Republic of the former Soviet Union.

Discussion. - *Pollenia venturii* is apparently an extremely rare species, a total of only 20 specimens are known to this date. Apart from material examined by Heinz, Zumpt and Grunin, all specimens have been misidentified in the collections that I have examined: either as *Pollenia amentaria* (Scopoli) (as '*P. vespillo* Fabr.') or as *P. atramentaria* (Meigen). The male from Germany in SMNK dissected and identified by Zumpt was evidently not included in his 1956 monograph, as he only gives the distribution as Italy, but the reason for this is not clear.

Grunin described *solitaria* mainly on the basis of the relatively dense abdominal dusting of the specimen available to him. A similar strong dusting oc-

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Appendix 1. – Abbreviations of the 38 terminals used in the cladistic analysis grouped according to species-group. Taxa with identical scores for the characters selected for the analyses are listed under a single entry.

rudis species-group:

- paupera – *Pollenia paupera* Rondani, 1862
- luteovi – *Pollenia luteovillosa* Rognes, 1987b
- pedicul – *Pollenia pediculata* Macquart, 1834
- rudis – *Pollenia rudis* (Fabricius, 1794)
- *Pollenia angustigena* Wainwright, 1940
- *Pollenia hungarica* Rognes, 1987b
- *Pollenia* sp. “Unknown species No. 1” of Rognes, 1987b

semicinerea species-group:

- grunini – *Pollenia grunini* Rognes, 1988
- mystica – *Pollenia mystica* Rognes, 1988
- paragru – *Pollenia paragrunini* Rognes, 1988
- pectina – *Pollenia pectinata* Grunin, 1966
- semicin – *Pollenia semicinerea* Villeneuve, 1912

labialis species-group:

- labiali – *Pollenia labialis* Robineau-Desvoidy, 1863
- pseudin – *Pollenia pseudintermedia* Rognes, 1987a

griseotomentosa species-group:

- griseot – *Pollenia griseotomentosa* Jacentkovský, 1944
- mayeri – *Pollenia mayeri* Jacentkovský, 1941

tenuiforceps species-group:

- alajens – *Pollenia alajensis* Rodendorf, 1926
- dasypod – *Pollenia dasyпода* Portschinsky, 1881
- similis – *Pollenia similis* Jacentkovský, 1941
- tenuifo – *Pollenia tenuiforceps* Séguy, 1928

venturii species-group:

- venturi – *Pollenia venturii* Zumpt, 1956

viatica species-group:

- bicolor – *Pollenia bicolor* Robineau-Desvoidy, 1830
- ruficru – *Pollenia ruficrura* Rondani, 1862
- ponti – *Pollenia ponti* Rognes, 1991b
- bulgari – *Pollenia bulgarica* Jacentkovský, 1939
- fulvipa – *Pollenia fulvipalpis* Macquart, 1835
- viatica – *Pollenia viatica* Robineau-Desvoidy, 1830
- *Pollenia mediterranea* Grunin, 1966

vagabunda species-group:

- bezzian – *Pollenia bezziana* Rognes, 1992
- verneri – *Pollenia vernerii* Rognes, 1992
- stigi – *Pollenia stigi* Rognes, 1992
- contemp – *Pollenia contempta* Robineau-Desvoidy, 1863
- vagabun – *Pollenia vagabunda* (Meigen, 1826)

amentaria species-group:

- amentar - *Pollenia amentaria* (Scopoli, 1763)
Pollenia moravica (Jacentkovský, 1941)
 atramen - *Pollenia atramentaria* (Meigen, 1826)
 vera - *Pollenia vera* Jacentkovský, 1936
 leclerc - *Pollenia leclercqiana* Lehrer, 1978

haeretica species-group:

- haereti - *Pollenia haeretica* Séguy, 1928

ibalia - *Pollenia ibalia* Séguy, 1930

other taxa:

- morinia - *Morinia melanoptera* (Fallén, 1817)
Morinia argenticincta (Senior-White, 1923)
 melanod - *Melanodexia* Williston
 outgrou - assumed ground plan characters of
 Polleniinae

Appendix 2. - Characters used in the cladistic analysis (number to the left) and codings of states (* = unordered coding for multistate characters) below.

Aedeagus:

- 0 - *shape of lateral hypophallic lobes
 0 - *rudis* type
 1 - *tenuiforceps* type
 2 - *venturii* type
 3 - *viatica* type
 4 - *vagabunda* type
 5 - *bezziana* and *verneri* type
 6 - *amentaria* type
 7 - *haeretica* and *ibalia* type
 9 - *Melanodexia* type
- 1 - median midventral hypophallic lobe
 0 - absence
 1 - presence
- 2 - central sclerotization in lateral hypophallic lobes
 0 - absence
 1 - presence
- 3 - sclerotization of median midventral hypophallic lobe
 0 - in posterior part only
 1 - fully sclerotized
- 4 - paraphallic processes, curvature
 0 - parallel
 1 - inwardly curved
- 5 - paraphallic processes, apex
 0 - not thickened
 1 - thickened
- 6 - paraphallic processes, apical armature
 0 - unarmed
 1 - armed with minute teeth
- 7 - paraphallic processes, apical truncation
 0 - not truncated
 1 - apically transversely truncated
- 8 - *ventral plate
 0 - moderate
 1 - long, continuous with mesohypophallic rod
 2 - very short
 3 - absent or reduced

Male cerci:

- 9 - form in profile
 0 - straight
 1 - bent backwards
- 10 - apical ornamentation
 0 - no brush
 1 - with apical golden brush
- 11 - *width
 0 - normal
 1 - narrow
 2 - very broad
- Ovipositor:
- 12 - spines on tip
 0 - absent
 1 - present
- 13 - epiproct
 0 - with microtrichiae
 1 - without microtrichiae
- 14 - pleural membrane 7
 0 - with microtrichiae
 1 - without microtrichiae on at least anterior half
- 15 - pleural membrane 8
 0 - with microtrichiae
 1 - without microtrichiae
- 16 - cerci
 0 - with microtrichiae
 1 - without microtrichiae
- 17 - T8 marginal setae
 0 - marginal
 1 - in front of margin
- 18 - ST8
 0 - with microtrichiae
 1 - without microtrichiae
- 19 - sclerite length
 0 - short
 1 - long

- 20 - *lateral sacs
 0 - unsclerotized
 1 - sclerotized elongate tubes
 2 - sclerotized fused spheres
 3 - sclerotized flattened disks
- 21 - *spermathecae
 0 - spherical
 1 - elongate
 2 - *Morinia* type
- Head:
 22 - *facial carina
 0 - normal
 1 - absent
 2 - very broad
- 23 - male frons
 0 - normal
 1 - very broad
- Thorax:
 24 - yellow crinkly hairs on scutum and pleura
 0 - absent
 1 - present
- 25 - presutural intraalar seta
 0 - present
 1 - absent
- 26 - inner posthumeral seta(e)
 0 - single
 1 - double
- 27 - humerus, supplemental setae in front of 3 normal setae
 0 - absent
 1 - present
- 28 - *scutellum
 0 - 4 to 5 pairs of marginal setae
 1 - 5 to 6 pairs of marginal setae
 2 - 3 pairs of marginal setae
 3 - 2 pairs of marginal setae
- 29 - middorsal presutural stripe
 0 - absent
 1 - present
- 30 - katepisternal ground vestiture, colour
 0 - yellow
 1 - black
- 31 - colour of lappets of metathoracic spiracle
 0 - yellow
 1 - brown, dark brown
- 32 - outer posthumeral seta
 0 - present
 1 - absent
- Legs:
 33 - front tibiae, number of *pv* setae
 0 - 1 *pv* seta
 1 - 2 *pv* setae
- 34 - hind tibiae, *pd* preapical seta
 0 - absent
 1 - present
- 35 - hind tarsi in male, length
 0 - as long as or longer than hind tibia
 1 - shorter than hind tibia
- 36 - hind leg in male, vestiture
 0 - unmodified vestiture
 1 - specialized vestiture
- Wings:
 37 - basicosta
 0 - black or very dark
 1 - yellow
- 38 - node at base of vein R_{4+5}
 0 - with small setulae
 1 - no setulae
- 39 - cell r_{4+5}
 0 - open
 1 - stalked
- 40 - Lower calypter, shape
 0 - broad, inner margin converging with long axis of fly
 1 - narrow, inner margin diverging from long axis of fly
- Abdomen:
 41 - abdominal dusting
 0 - rather dense, chequered
 1 - weak or absent
- 24 - general size
 0 - normal
 1 - small
-

Appendix 3. - Data matrix for cladistic analysis.

char #	01234	56789	11111 01234	11111 56789	22222 01234	22222 56789	33333 01234	33333 56789	444 012
paupera	01100	00000	00000	00100	11001	00000	00000	00100	000
luteovi	01100	00100	00000	00100	11001	00000	00110	01100	000
pedicul	01100	00100	00000	00100	11001	00000	00010	00100	000
rudis	01100	01100	00000	00100	11001	00000	00010	01100	000
grunini	01100	01000	01000	00100	10001	00000	00010	10000	000
mystica	01101	00000	01000	00100	00001	00000	10000	10000	010
paragru	01101	01101	01---	-----	---01	00000	10000	10000	0-0
pectina	01100	00000	01000	00100	00001	00000	00000	11000	000
semicin	01100	01001	01000	00100	10001	00000	100-0	10000	010
labiali	01101	00000	00000	00000	01101	00000	01010	00000	000
pseudin	01101	00000	00000	00000	01001	00000	01010	00000	000
griseot	001-0	00010	01000	00000	00101	00000	00110	10000	001
mayeri	01000	00010	01000	00000	00101	00000	00110	10000	001
alajens	11111	10000	00000	00---	30001	00000	-0010	11000	010
dasytod	11111	10000	00000	00000	30001	00000	00010	11000	000
similis	11111	10000	00000	00000	00001	00000	00010	11000	000
tenuifo	11111	10000	00000	00-0	30001	00000	00010	10000	000
venturi	200-0	00000	02000	00100	20001	00000	11-10	00000	010
bicolor	300-0	00010	02111	11111	00201	00020	00100	00100	000
ruficru	300-0	00010	00111	11111	00201	00020	00000	00100	000
ponti	300-0	01010	00111	11111	00201	00000	00-00	00100	000
bulgari	300-0	01010	01111	11111	00201	00000	00000	00100	000
fulvipa	300-0	00010	01111	11111	00201	00000	00000	00100	000
viatica	300-0	00010	02111	11111	00201	00000	00000	00100	000
bezzian	500-0	00011	01---	-----	---01	01-00	00000	00000	000
verneri	500-0	00011	01000	11111	00001	01-00	00000	00000	000
stigi	-00-0	0----	--000	01111	00001	01101	10010	00000	000
contemp	400-0	00011	01000	11111	00001	01101	00010	00000	000
vagabun	400-0	01011	01000	11111	00001	01101	00010	00000	000
amentar	600-0	01020	00000	10110	00001	00010	01010	00000	010
atramen	600-0	0-0-0	00000	10110	00101	00010	01010	00000	010
vera	600-0	01020	00000	10110	00001	00010	01010	00000	0-0
leclerc	600-0	01020	10000	10110	00001	00010	11010	00001	010
haereti	700-0	01000	10000	10110	00011	00000	11-10	0000-	000
ibalia	700-0	01000	10---	-----	--011	00000	11-10	00000	000
morinia	001--	00031	00000	00000	02000	10030	111-1	00010	1-1
melanod	900--	---30	0-1--	-----	--000	10000	--111	00010	100
outgrou	-0--0	0-000	00000	00-00	00000	00000	--0--	00000	000

Appendix 4. - Character transformations read from cladogram in Fig. 11. Weight (as shown by the *cc* command) as calculated after 4 rounds of the command sequence *mh**; *bb**; *xs w*; *cc*; (after which stable weights were obtained). + additive (ordered), - non-additive (unordered) characters. Note that characters 3, 5, 13-14, 16, 18-19, 23-27, 29, 35 and 38-40, which have been deleted from the table below, all show the single-step transformation 0→1 and have weight 10+.

Character	State transformation(s)	Steps	Weight	Character	State transformation(s)	Steps	Weight
0	0→1, 0→2, 0→3, 0→5, 0→6, 0→7, 0→9, 5→4	8	10-	20	0→1, 0→2, 0→3	4	6-
1	0→1, 1→0	2	4+	21	0→1, 0→2	2	10-
2	0→1, 1→0	3	2+	22	0→1, 0→2	4	3-
4	0→1	3	2+	28	0→1, 0→2, 0→3	3	10+
6	0→1 (also 1→0 under some optimizations)	8	0+	30	1→0, 0→1 (Only 0→1 under another optimization)	7	0+
7	0→1	2	3+	31	1→0, 0→1 (only 1→0 under another optimization)	3	2+
8	0→1, 0→2, 0→3	4	6-	32	0→1	4	1+
9	0→1	4	1+	33	1→0, 0→1	4	1+
10	0→1	2	2+	34	0→1 (1→0 under another optimization)	1	10+
11	0→1, 0→2 (also 1→0, 1→2, 2→0 under some optimizations)	7	2-	36	0→1, 1→0	4	1+
12	0→1	2	4+	37	0→1	2	4+
15	0→1, 1→0	2	4+	41	0→1	5	0+
17	0→1	3	2+	42	0→1	2	2+

Appendix 5. - Synapomorphies of the nodes of the strict consensus cladogram shown in Fig. 11.

Node	Synapomorphies	Name	Node	Synapomorphies	Name
38	4(1)		53	11(1)	<i>semicinerea</i> + <i>grisetomentosa</i> group
39	0(4)		54	0(1), 3(1), 4(1), 5(1) 36(1)	<i>tenuiforceps</i> group
40	36(1)		55	8(1), 16(1), 19(1), 31(0), 33(0)	<i>viatica</i> + <i>vagabunda</i> group
41	33(0)		56	0(6), 6(1), 8(2), 28(1) 41(1)	<i>amentaria</i> group
42	20(1)		57	0(7), 6(1), 10(1), 23(1)	<i>haeretica</i> group
43	28(2)		58	21(1)	<i>rudis</i> + <i>labialis</i> group
44	0(4), 29(1), 33(1)		59	31(0), 35(1)	
45	7(1)		60	15(1), 18(1)	
46	17(1)	<i>semicinerea</i> group	61	1(1), 2(1)	
47	8(1), 22(1), 32(1), 42(1)	<i>grisetomentosa</i> group	62	17(1)	
48	20(3)		63	(24(1))	<i>Pollenia</i>
49	0(3), 12(1), 13(1), 14(1) 22(2), 37(1)	<i>viatica</i> group	64	8(3), 25(1), 32(1), 34(1) 38(1), 40(1), 42(1)	<i>Morinia</i> + <i>Melano-</i> <i>dexia</i>
50	0(5), 9(1), 11(1), 27(1)	<i>vagabunda</i> group			
51	17(1), 20(1), 31(0), 37(1)	<i>rudis</i> group			
52	(4(1))	<i>labialis</i> group			