

The taxonomy and phylogenetic relationships of the *Pollenia semicinerea* species-group (Diptera: Calliphoridae)

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ABSTRACT. Within *Pollenia* Robineau-Desvoidy, a *semicinerea* species-group is defined. It consists of the redescribed *P.semicinerea* Villeneuve, *P.grunini* sp.n., *P.mystica* sp.n. and *P.paragrunini* sp.n., and *P.pectinata* Grunin, for which some new characters are given. A key is provided and the known terminalia of both sexes are illustrated. A lectotype is designated for *P.semicinerea* Villeneuve. *P.semicinerea* is known from the Middle East (Israel, Syria, Lebanon), *P.grunini*, *P.mystica* and *P.paragrunini* from the Caucasus and neighbouring areas in the U.S.S.R. and *P.pectinata* from the temperate parts of the Palaearctic Region except west of Poland and U.S.S.R. It is argued that the *semicinerea*- and *rudis*-groups are monophyletic sister-groups. The *tenuiforceps*-group is most probably the monophyletic sister-group of the composite monophyletic group (*rudis*-group + *semicinerea*-group). The *intermedia*-group and the *griseotomentosa*-group are both monophyletic. The composite group (*rudis*-group + *semicinerea*-group + *tenuiforceps*-group + *intermedia*-group + *griseotomentosa*-group) is probably a monophyletic subgroup of *Pollenia*. A partly resolved synapomorphy diagram is provided, which is compared to trees generated by various computer programs in the Phylogeny Inference Package (PHYLIP) of Felsenstein. *Pollenia alajensis* Rodendorf (= *sytshevskajae* Grunin) is assigned to the *tenuiforceps* species-group on the basis of male and female genitalia.

Introduction

Members of the genus *Pollenia* Robineau-Desvoidy, 1830 are commonly known as cluster flies due to their habit of clustering in autumn in crevices and corners of dark parts of buildings such as attics, closets and window-frames. The genus is of general biological interest as members of one species-group (the *rudis*-group, see Rognes, 1987b), in the larval stages, are known to be parasites or predators of earthworms. The

genus as conceived at present has more than 100 members variously distributed in the Nearctic, Palaearctic, Oriental and Australian and New Zealand Regions (cf. Dear, 1986; Rognes, 1987b). Many of its species are extremely similar in external appearance and for this reason the genus is regarded by some authors as 'the most difficult genus of the Calliphoridae' (Mihályi, 1976; Dear, 1986).

In 1912 Villeneuve described *Pollenia semicinerea* from the Middle East (Villeneuve, 1912). Séguéy (1928a, b, 1934, 1941) keyed and illustrated various features of this species, apparently with specimens of the syntypic series

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at hand, and found the species to be recognizable in the male sex by a *rudis*-like distiphallus and very broad surstyli. The species was unknown to Zumpt (1956), who, on the basis of published data, left it to future workers to decide whether it was a good species or based 'auf abnorme Stücke von *rudis* bzw. einer der verwandten Arten . . .'. Further material was not known until Grunin (1966) listed and figured a species he identified as *semicinerea* from the U.S.S.R. Grunin's material showed very narrow surstyli in the male and he stated that Séguy ' . . . erroneously refers to very wide coxites [surstyli] in this species and even draws them as such . . .'. Lobanov (1976) described the ovipositor from Grunin's material. During examination of material of *Pollenia* from Israel in the collections of DZTAU (see below for abbreviations of museum depositories), additional material of what is evidently true *semicinerea* was discovered. Grunin, therefore, misidentified his material and did not realize that his '*semicinerea*' was a new species.

The purpose of the present paper is to define a *semicinerea* species-group within *Pollenia*; to redescribe Villeneuve's species and to designate a lectotype; to name and describe three species (one of them '*semicinerea*' of Grunin) as new to science; and to discuss the composition, monophyly and phylogenetic relationship of this and related species-groups within *Pollenia*.

Material and Methods

The study is primarily based on material in the following collections: British Museum (Natural History), London (BMNH); Zoologisches Institut, Christian Albrechts-Universität zu Kiel (ZIKIEL); Zoological Institute, Academy of Sciences, Leningrad (ZILEN); Muséum National d'Histoire Naturelle, Paris (MNHN); National Museum in Prague (NMP); Department of Zoology, Tel Aviv University, Tel Aviv (DZTAU); and the author's private collection (KR). National boundaries, and geographical names and spellings follow as far as possible the *Times Atlas of the World*, Comprehensive Edition, London, 1980. Names not found in this *Atlas* are spelled as on labels (transliterated in the case of Russian labels). Israel is defined as including areas under military administration as in the *Times Atlas*. The techniques used for dis-

section and making of microscopic slides of ovipositors are described in Rognes (1987a, b). For the evaluation of the phylogenetic reconstruction shown in Fig. 59 I have used the MIX, PENNY and BOOT parsimony method programs of the PHYLIP computer program package (version 3.0) written by Felsenstein (1984, 1985).

Genus *Pollenia* Robineau-Desvoidy

Pollenia Robineau-Desvoidy, 1830: 412. Type species: *Musca rudis* Fabricus, by original designation. For a list of generic synonyms, see Schumann (1986).

Diagnosis of the semicinerea species-group

The *semicinerea* species-group is characterized by the following combination of characters: (1) male frons very narrow, about 1–1.5× width of anterior ocellus, narrower than distance between posterior ocelli inclusive, parafrontals contiguous (frons thus narrower than all *rudis*-group members); (2) mouthedge well below line between large vibrissae; (3) palpi black, tip brownish; (4) facial carina usually conspicuous; (5) occiput with pale hairs, except for 3–4 irregular rows of black hairs below postocular row of cilia, no pale hairs invading posterior part of jowls; (6) outer *ph* present, on line with *prst* seta; (7) posterior thoracic spiracle yellow, though usually slightly darker than in the *rudis* species-group; (8) postalar wall with numerous yellow crinkly hairs, often mixed with black ones; (9) scutellum with 4–5 pairs of marginal setae; (10) t_1 with 1 or 2 *pv* setae; (11) t_2 with 2–4 *ad* setae; (12) t_3 with 2–6 *av* setae; (13) f_1 , f_2 and f_3 with black *pv* ground vestiture; (14) male with tarsi shorter than tibia, especially on hind leg; (15) basicosta black; (16) costa hairy below as far as junction with *sc*, bare below beyond this point; (17) node at base of r_{2+3} and r_{4+5} with hairs on both surfaces of wing; (18) abdomen with variable dusting, generally somewhat thinner than in the *rudis* species-group and with less conspicuous tessellations; (19) ventral abdominal vestiture in male quite normal and semidecumbent, no obvious difference from the one dorsally in length, density, quality or colour; (20) ST5 of male abdomen with normal vestiture; (21) male cerci very narrow, much nar-

rower than in *rudis* species-group; (22) male surstyli of variable shape and with variable vestiture; (23) distiphallus with midventral rounded projection ('lobe hypophallique médian' of Lehrer, 1963); (24) hypophallic lobes triangular, distally pointed and with central sclerotization; (25) paraphallic processes usually sclerotized to the tip, not appearing transversely truncated; (26) paraphallic processes distally armed with small tubercles or bare; (27) paraphallic processes usually proceeding distad more or less parallel with long axis of distiphallus, though curving towards midline in some species; (28) T7 and T8 in the female ovipositor middorsally without continuous stripe of microtrichiae from posterior to anterior margin; (29) marginal setae on T8 in ovipositor not absolutely marginal in position, sclerotization forming part of T8 always present behind them; (30) ST8 of ovipositor with dense cover of microtrichiae on posterior sixth to third; (31) membrane between T8 and ST8 on each side of ovipositor frequently devoid of microtrichiae proximally; (32) tip of ovipositor only with soft, slightly wavy and distally very thin hairs, no stiff blunt straight spines; (33) supraanal plate of ovipositor completely covered with microtrichiae; (34) cerci microtrichiose but with more or less extensive areas devoid of microtrichiae proximally; (35) lateral sacs of the female internal reproductive organs shaped as narrow tubes and most often sclerotized; (36) spermathecae almost circular, with apical papilla.

At present five species are included in this group: *P. semicinerea* Villeneuve, *P. pectinata* Grunin, *P. grunini* sp.n., *P. paragrugini* sp.n., and *P. mystica* sp.n. Almost nothing is known about their biology, and no immature stages are known.

Key to species of the *semicinerea*-group

Note. The key to females should be considered preliminary and used with utmost caution as it is based on a single dissected female of each species only (*grunini* and *pectinata* ovipositors are also figured by Lobanov, 1976, the former as '*semicinerea*'). Females should not be regarded as reliably recognizable without associated males. Note also that the female of *paragrugini* is unknown and not included in the key.

Males

- 1 Cerci straight, upper border almost rectilinear in profile view (Figs. 2, 14, 35) 2
- Cerci backwardly bent, upper border strongly curved in profile view (Figs. 26, 46); outer surface of surstyli clothed with densely-set short and regular vestiture in at least distal half; paraphallic processes armed; marginal setae of T5 normal, not bent over at tips; facial keel conspicuous; ST5 with normally shaped lobes 4
- 2 Surstyli strongly bent and sickle-shaped in profile view (Fig. 2), outer surface as seen from above distally bare but clothed with irregular rather long sparsely-set setae towards basal half; paraphallic process tips armed; marginal setae on T5 bent over at tips; facial keel conspicuous *grunini*
- Surstyli more or less straight in profile view, most of the outer surface as seen from above clothed with short, regular, densely-set vestiture; paraphallic process tips bare; marginal setae on T5 normal, tips not bent over 3
- 3 Surstyli distally expanded, long, club-shaped, weakly bent downwards (Fig. 35); apical parts not bent towards each other; tip bluntly rounded in profile view; lobes of ST5 normal (Fig. 42); head without *iv* setae; facial keel weak, i.e. just perceptible; *t*₃ with erect *a* and *av* ground vestiture on at least distal 2/3; 2 rows of strong setae on underside of hind tarsus as long as diameter of tarsus *pectinata*
- Surstyli not expanded but bent slightly downwards distally, not club-shaped, tip acute in profile view (Fig. 14); apical parts bent towards each other; lobes of ST5 of peculiar shape for a *Pollenia* (Fig. 21); head with *iv* setae weakly but clearly differentiated; facial keel conspicuous *mystica*
- 4 Surstyli constricted in middle part as seen in profile, distal part broad and almost transversely truncated (Fig. 46); paraphallic process tips narrow, not obliquely truncated *semicinerea*
- Surstyli not constricted in middle part, upper and lower border parallel as seen in profile, surstylus narrower and distally tapering more gradually and bent downwards (Fig. 26); paraphallic process tips broad as seen in frontal view, obliquely truncated *paragrugini*

Females

- 1 Lateral sacs not sclerotized; T6 with simple row of marginal setae; facial keel conspicuous or inconspicuous 2
- Lateral sacs sclerotized tubes; T6 heavily setose on posterior margin; facial keel conspicuous 3
- 2 Eyes of normal size, much higher than jowls as seen in exact profile view of head; cerci very elongate and narrow (Fig. 43); T6 subdivided along middle; strongly sclerotized parts of T7 less wide than area between them; ST6 with rather wide weakly sclerotized margin; ST7 also with rather wide weakly sclerotized areas laterally and posteriorly; pleural membrane 8 fully microtrichiose; facial keel

inconspicuous, i.e. just perceptible; abdominal dusting normal, rather dense and with conspicuous tessellations. *pectinata*

– Eyes very small as seen in profile, jowl in exact profile view of head about as high as eye; cerci normal, broad, blunt (Fig. 22); T6 undivided; strongly sclerotized halves of T7 broader than area between them; ST6 and ST7 almost fully sclerotized; pleural membrane 8 sparsely microtrichiose only in distal half; facial keel conspicuous; abdomen appearing black, dusting very weak, tessellations almost wholly absent from any view, dusting divided according to angle of view, one half appearing evenly but thinly dusted while other half appears shining black *mystica*

3 Lateral sacs strongly curved (Fig. 55); T6 and ST6 relatively short, a line through anterior pair of T6 spiracles passes near fore margin of tergite (Fig. 54); cerci microtrichiose except on proximal fourth

semicinerea

– Lateral sacs almost straight (Fig. 11); T6 and ST6 relatively elongate, a line through anterior pair of T6 spiracles passes through middle of tergite (Fig. 10); cerci without microtrichiae on proximal half

grunini

Pollenia grunini sp.n. (Figs. 1–12)

[*Pollenia semicinerea*: Grunin, 1966: 898, Figs. 11–13 (male genitalia), 899 (localities, comments); Lobanov, 1976: 35, Fig. 50 (female genitalia), 36 (key); Rognes, 1987b: 477; misidentifications, not Villeneuve, 1912.]

Diagnosis

♂♀. Facial carina conspicuous. Second antennal segment bright yellow, or at most weakly infuscated basally. Parafacial hairs about as long and fine as the longest arisal hairs. Thorax with very little dust dorsally except on anterior slope. Sternopleural vestiture long crinkly yellow, at most with very few black hairs. Pleura conspicuously dusted. R5 open. Lower squama brown. t_1 mostly with 2 *pv* setae. Abdomen yellowish to bluish white dusted with conspicuous tessellations, sometimes with a weak brassy sheen.

♂. Body length: 4.7–9.0 mm (mean 7.7 mm, $n=18$). Frons at narrowest point $0.013-0.032 \times$ head width (mean 0.022, $n=22$). Lower squama infuscated. Hind tibia and tarsi with decumbent ground vestiture. T5 with numerous long setae on disc, those on hindmost half long and bent fully over at tips. ST5 normal, as in Fig. 9. Genitalia as in Figs. 1–8. Cerci not curved

backwards as seen in profile view. Surstyli strongly curved and sickle-shaped, with outer surface clothed with sparsely-set rather long setae especially in basal half. Distiphallus with narrow hypophallic lobes, much longer than wide. Paraphallic processes sclerotized to tip and armed. The postgonite figured has a curved setae, the one on the other side of the dissected specimen is straight. A few sensillae are present distal to the seta. The phallapodeme figured is split distally, which appears to be an aberration.

♀. Body-length: 6.9–9.1 mm (mean 8.3 mm, $n=7$). Frons at vertex $0.304-0.331 \times$ head width (mean 0.318, $n=8$). Ovipositor as in Fig. 10. T6 and ST6 relatively long. A line across T6 between anterior pair of spiracles divides the tergite into anterior and posterior halves of about equal length. Cerci without microtrichiae in basal half. Lateral sacs (Fig. 11) rather straight, well sclerotized. Spermathecae as in Fig. 12.

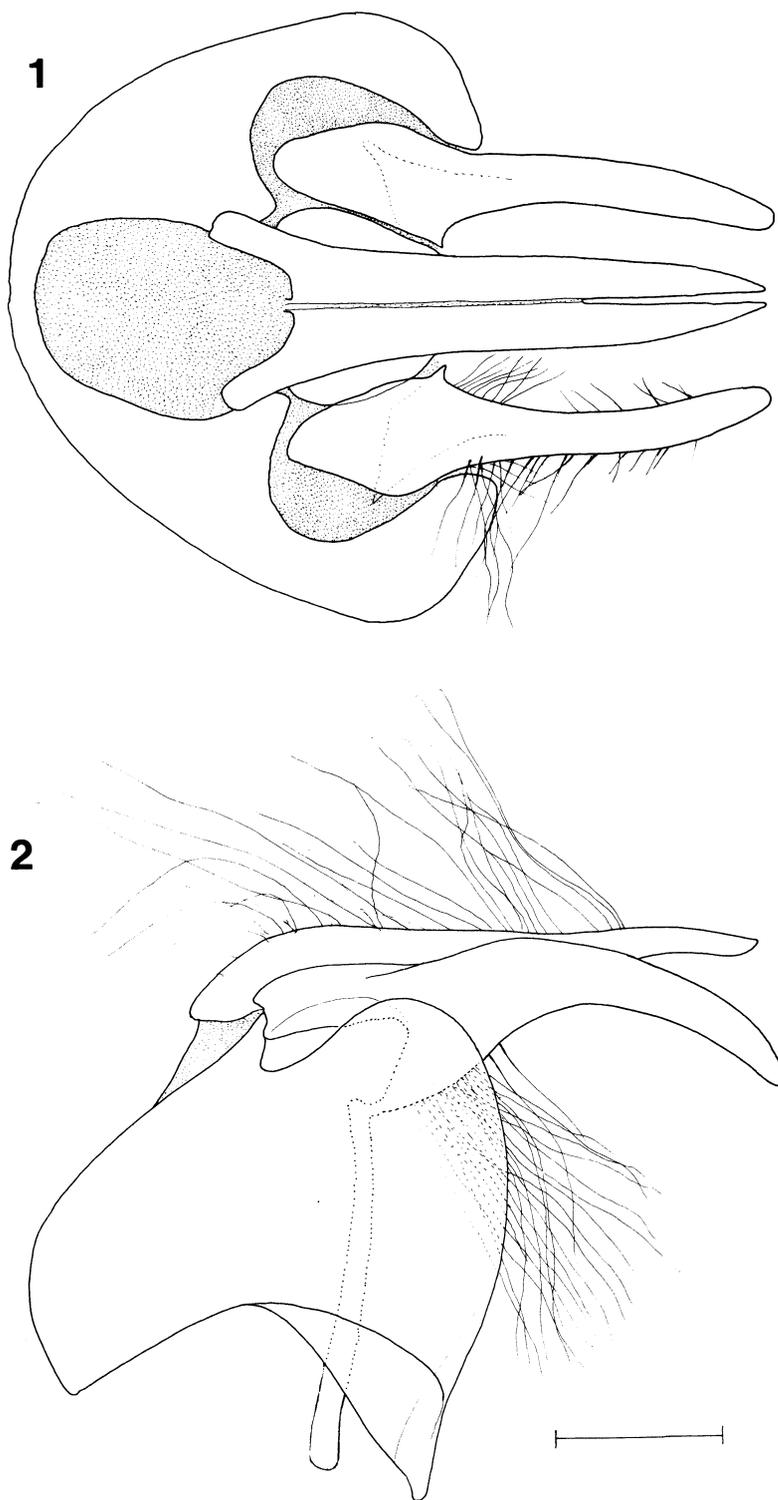
Biology

According to data labels this species has been captured on birch sap, on the dead body of *Apodemus silvaticus* (Linnaeus), on a dead mouse, in subalpine meadow, on a sunny wall, in larch forest, and by a heap of *Populus tremula* Linnaeus.

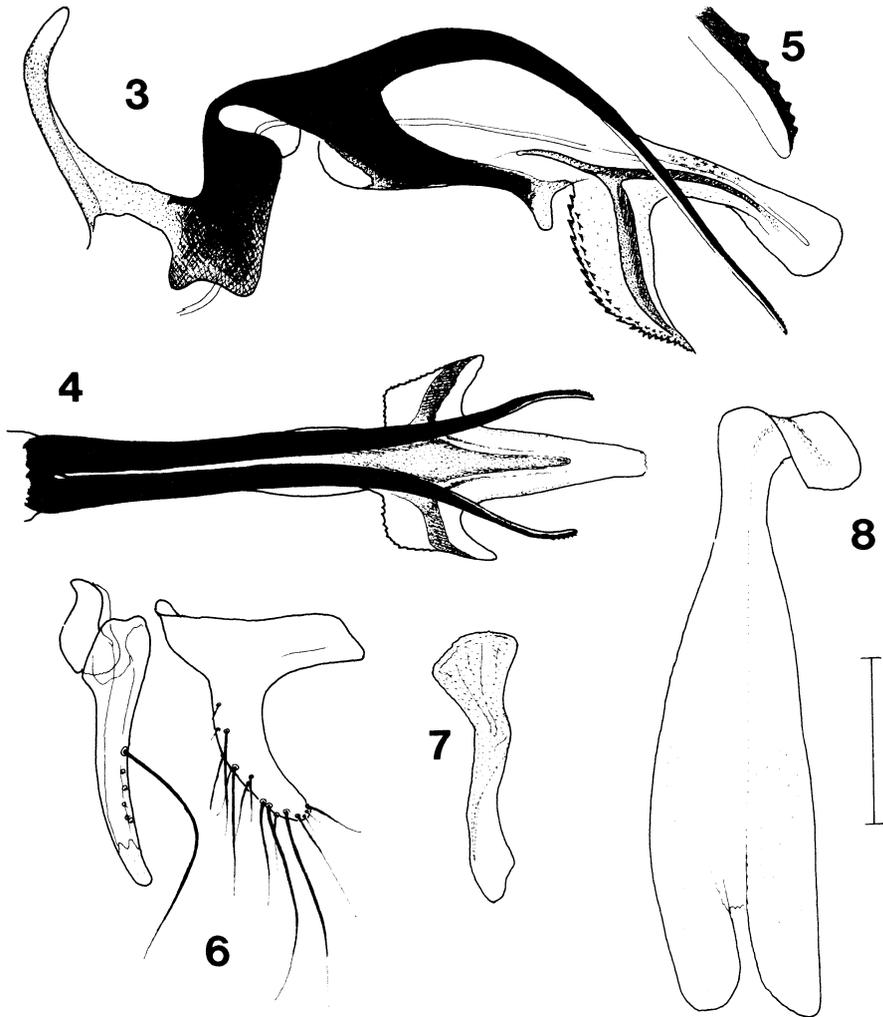
Type material

Holotype ♂, U.S.S.R. Russian S.F.S.R.: Stavropol' Kray, 5 km S Teberda, 17.iv.1964 (1400 m) (*Gorodkov*) (dissected, genitalia and ST1–5 in glycerol in glass micro-vial on pin, T1–5 glued to carton on pin) (ZILEN).

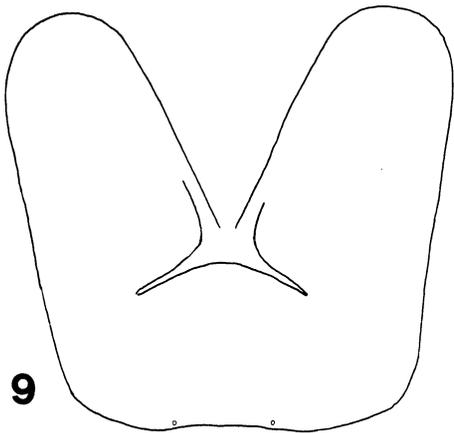
Paratypes, 21♂, 8♀, as follows. U.S.S.R.: Georgian S.S.R. (Gruziya), 1♂, Omalo (*Matushegiya*), 11.ix.1959 (*V. F. Zaitsev*) (ZILEN); Russian S.F.S.R., 1♂, Krasnodar Kray, Mt Oshten, Zhelob Pass, 6.vi.1903 (*Filipchenko*) (ZILEN); 19♂ 8♀, Stavropol' Kray, Teberda Reservation, Kurort, as follows: 1♂ 7.iv.1964; 1♂ 8.iv.1964; 8♂ 1♀ 13.iv.1964 (1♂ dissected); 1♂ 15.iv.1964; 1♂ 16.iv.1964; 1♂ 17.iv.1964; 2♂ 4♀ 3.v.1964 (1♀ dissected, T1–5 glued to carton on pin, uterus and spermathecae in glycerol in glass micro-vial on pin, ovipositor and ST1–5 on slide no. G.pr. 257); 1♀ 9.v.1964; 1♀ 11.v.1964; 1♂ 13.v.1964; 1♂ 19.v.1964; 1♀ 27.v.1964; 1♂ 31.v.1964; 1♂



FIGS. 1-2. *Pollenia grunini* (holotype), ♂ terminalia: 1, cerci, surstyli and epandrium, posterior view; 2, cerci, surstylus, epandrium and processus longus, lateral view. Scale 0.2 mm.



FIGS. 3–8. *Pollenia grunini* (holotype), ♂ terminalia: 3, phallosome, profile view; 4, distiphallus, dorsal view; 5, tip of paraphallic process; 6, pre- and postgonites; 7, ejaculatory sclerite; 8, phallapodeme. Scale 0.2 mm.



10.xi.1967 (1300–2050 m) (all *Gorodkov*) (ZILEN).

Remarks

All material of this species listed above was misidentified by Grunin and Lobanov as *semicinerea*. Grunin clearly observed that the genitalia differed from those published from *semicinerea* by Séguy, and suggested that Séguy

FIG. 9. *Pollenia grunini* (holotype), ♂ ST5. Scale 0.4 mm.

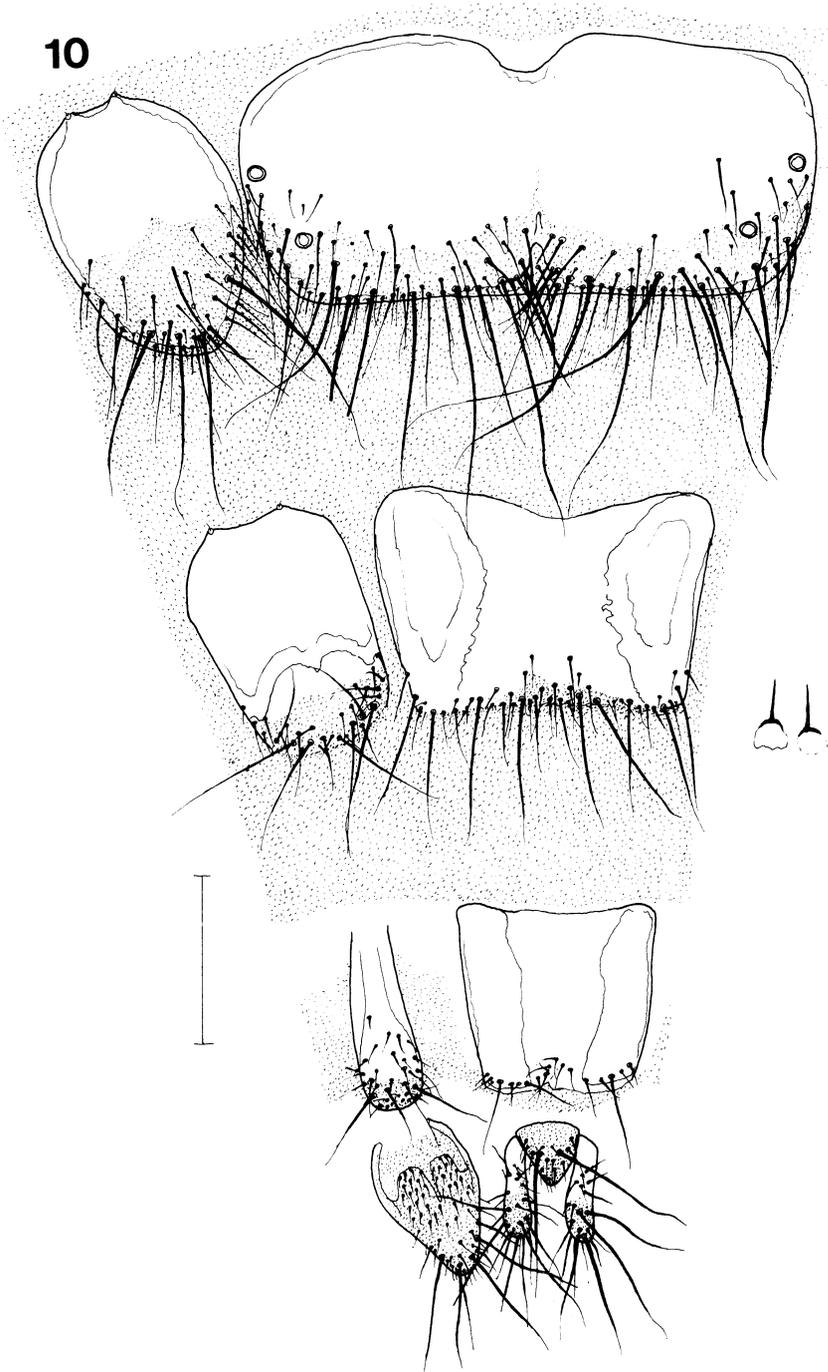
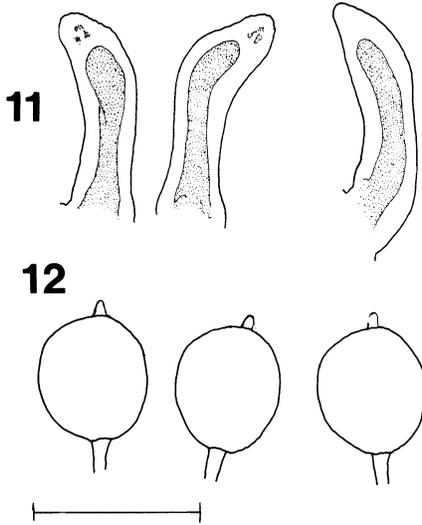


FIG. 10. *Pollenia grunini*, ♀ ovipositor (G.pr. 257). Stipple indicates extent of microtrichiae; inset: two microtrichiae enlarged. Scale 0.45 mm.



FIGS. 11–12. *Pollenia grunini*, ♀: 11, lateral sacs; 12, spermathecae. Scale 0.2 mm.

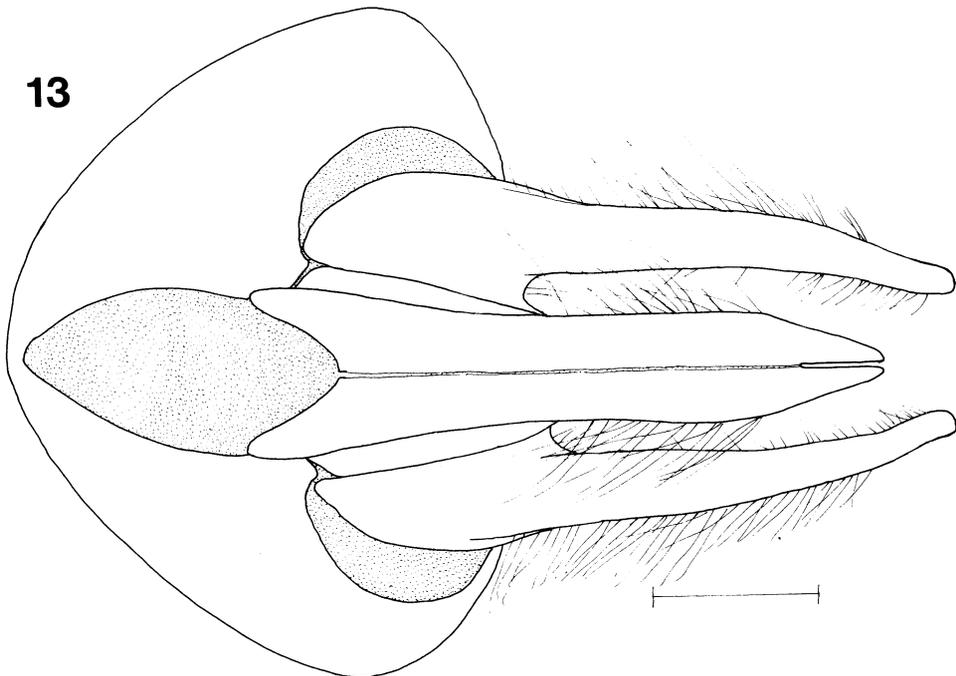
had made an error when making his drawings. It is a pleasure for me to name the species in Grunin's honour. Rognes (1987b) erroneously referred to the abdomen as shining black.

***Pollenia mystica* sp.n.** (Figs. 13–24)

Diagnosis

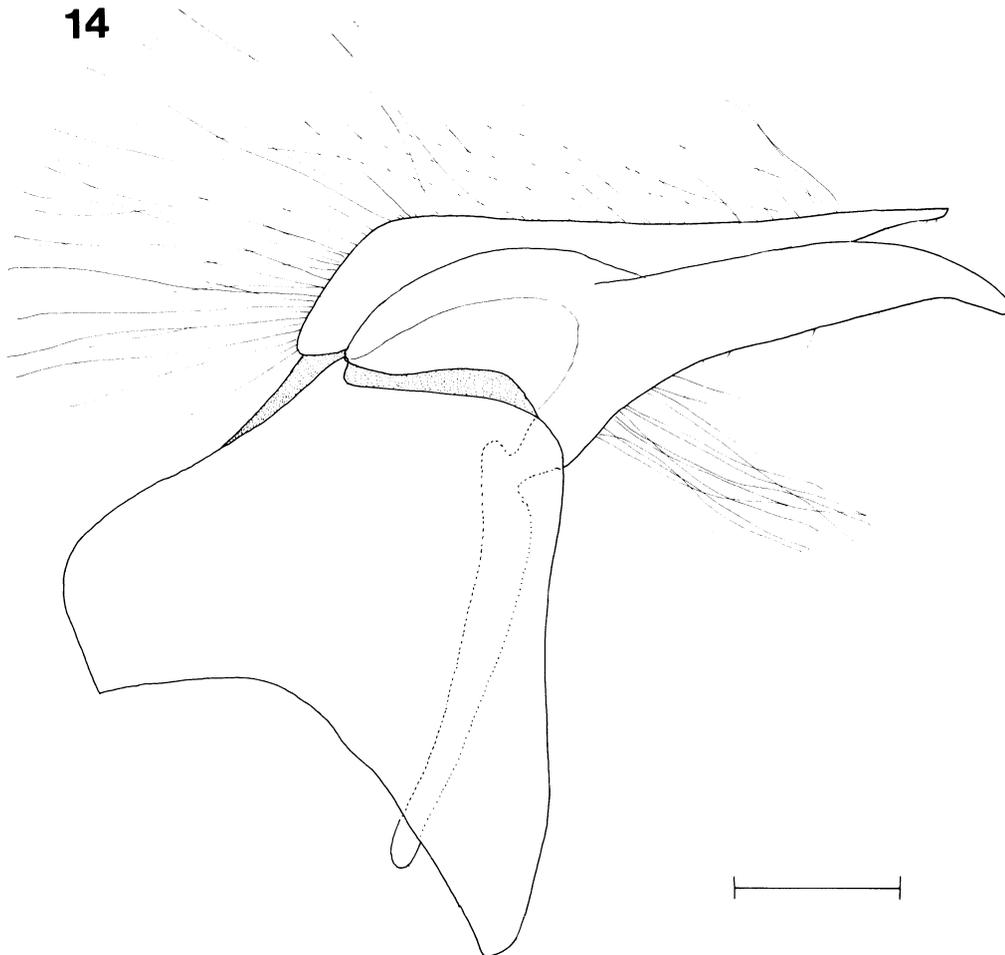
♂♀. Facial carina conspicuous. Second antennal segment dark, reddened only apically. Parafacial hairs inconspicuous, much shorter than longest arisal hairs. Thorax with very little dust dorsally, a weak layer on anterior slope. Sternopleural vestiture black. Pleura weakly dusted, shining black. t_1 with 1 ν . Abdomen very weakly dusted. R5 open (holotype) or closed (paratype).

♂. Body-length: 8.5 mm. Frons at narrowest point $0.016 \times$ head width. iv setae clearly differentiated, conspicuous, much stronger than postocular row of setae, though small. Hind tibia and tarsus with decumbent ground setulae. Pattern of dusting not known because specimen had most of the abdomen removed for dissection by Grunin. The pollinosity of the remaining T1–2 is very weak and disappears from certain directions of view. The recovered T5 (transferred from glycerol through ethanol and ethyl acetate and finally dried under the microscope lamp) shows no discal and marginal setae which are bent at tips. ST5 of very peculiar shape for a



FIGS. 13. *Pollenia mystica* (holotype), ♂ terminalia: cerci, surstyli and epandrium, posterior view. Scale 0.2 mm.

14



FIGS. 14. *Pollenia mystica* (holotype), ♂ terminalia: cerci, surstyli, epandrium and processus longus, lateral view. Scale 0.2 mm.

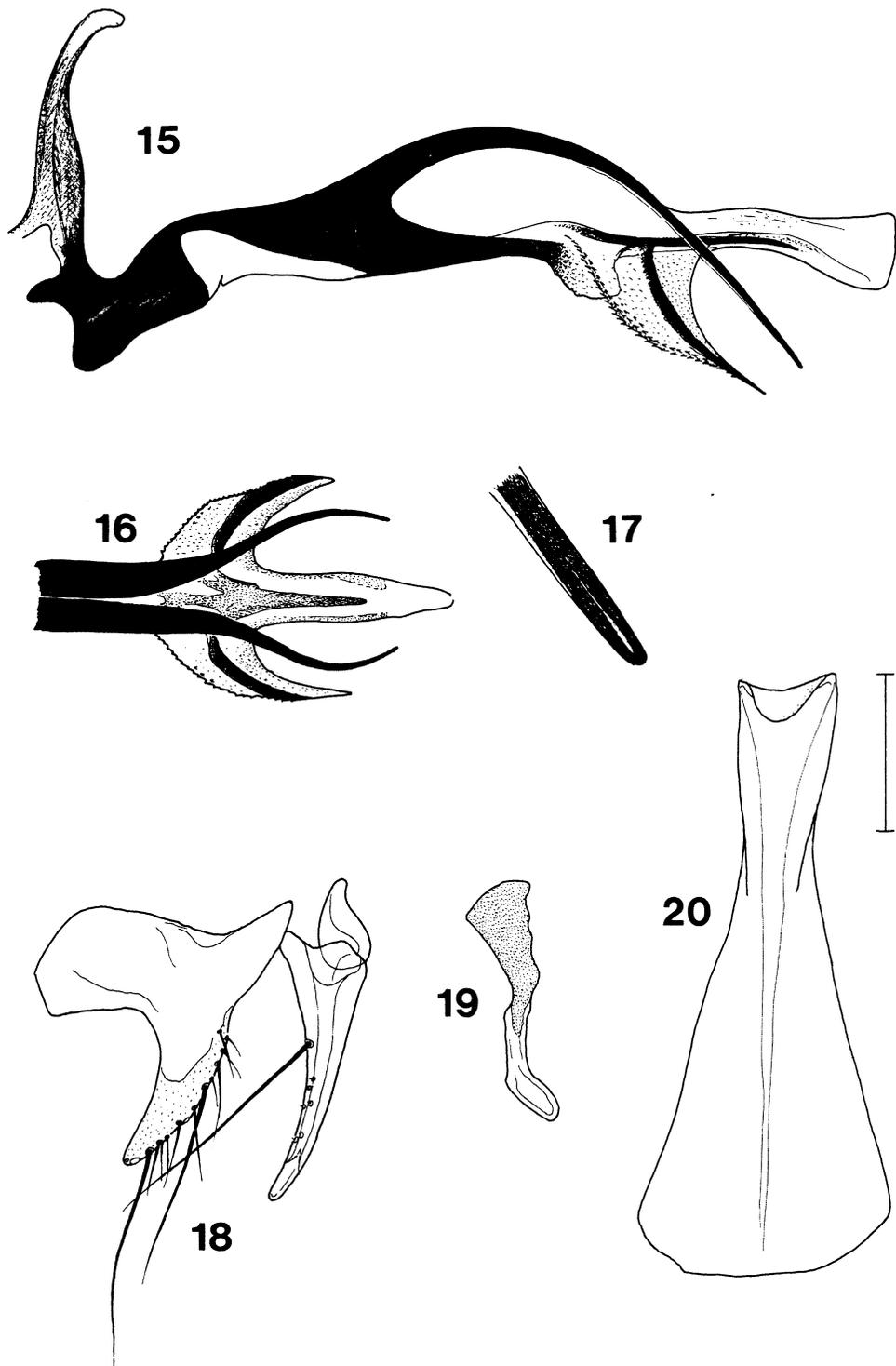
Pollenia (Fig. 21). Genitalia as in Figs. 13–20. Surstyli with parallel upper and lower borders, apex bent weakly downwards, rather acute as seen in profile; in dorsal view apices curved weakly towards each other. Hypophallic lobes with long acute distal prolongation, paraphallic processes fully sclerotized, unarmed and weakly curved towards mid axis of distiphallus.

♀. Body-length: 8 mm. Frons at vertex $0.363 \times$ head width, thus rather broad. Eyes very small as seen in profile. Jowl in exact profile view of head about as high as eye. Abdominal dusting very weak, tessellations almost wholly absent from any view, dusting divided lengthwise according to angle of view, one half appearing

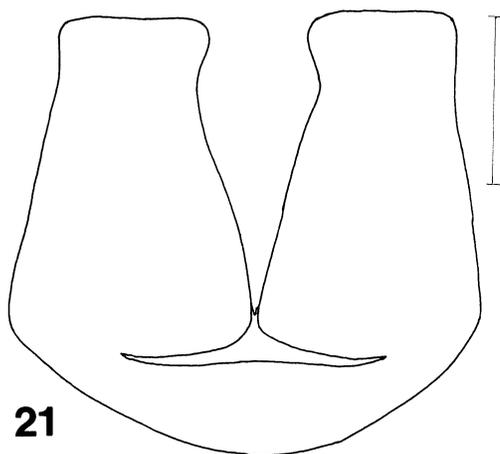
evenly but thinly dusted, while other half appears shining black. Ovipositor as in Fig. 22. ST6 and ST7 rather elongate. Strongly sclerotized halves of T7 much broader than weakly sclerotized area between them. Cerci devoid of microtrichiae in proximal half. Lateral sacs (Fig. 23) large and unsclerotized. Spermathecae as in Fig. 24.

Type material

Holotype ♂, U.S.S.R.: Georgian S.S.R. (Gruziya), Tskhra-tskaro, 2460 m, on stones, 13.v.1969 (*Gorodkov*) (dissected, T4–5 glued to bit of celluloid on pin, genitalia and other



FIGS. 15–20. *Pollenia mystica* (holotype), ♂ terminalia: 15, phallosome, lateral view; 16, distiphallus, dorsal view; 17, tip of paraphallic process (enlarged); 18, pre- and postgonites; 19, ejaculatory sclerite; 20, phallapodeme. Scale 0.2 mm.



21

FIG. 21. *Pollenia mystica* (holotype), ♂ ST5. Scale 0.4 mm.

abdominal parts in glycerol in glass micro-vial on pin) (ZILEN).

Paratype ♀, U.S.S.R.: Georgian S.S.R. (Gruziya), Bakuriani and above, upper levels of forest, 10.viii.1970 (*Rikhter*) (dissected, T1–5 glued to carton on pin, uterus and spermathecae in glycerol in glass micro-vial on pin, ST1–5 and ovipositor on slide no. G.pr. 259) (ZILEN).

Remarks

The material of this and the following species (and even 1♂ 1♀ *Pollenia amentaria* Scopoli=*P. vespillo*: auctt.=*P. nitens* (Zetterstedt)) was set aside in the ZILEN collection under a note by Grunin to the effect that he regarded it all as forming a new taxon ('*P. semicinerea* ssp.n. 1969'). *Pollenia mystica* has certain features which may lead to a suspicion that it may belong to the *intermedia* species group: unarmed, somewhat inwardly curved, fully sclerotized paraphallic processes; very prolonged distal process of the hypophallic lobes, and unsclerotized lateral sacs. However, the colour of the posterior thoracic spiracles, the narrow male cerci, the sparsely microtrichiose pleural membrane 8 in the ovipositor, the T8 of the ovipositor being prolonged behind the marginal setae (which thus are not exactly marginal), the basal half of the ♀ cerci being devoid of microtrichiae and the circular spermathecae clearly place the species in the *semicinerea* species-group.

Pollenia paragrugini sp.n. (Figs. 25–33)

Diagnosis

♂. Body-length: 9.4–10.2 mm ($n=2$). Frons at narrowest point $0.031\text{--}0.039\times$ head width (mean 0.034, $n=3$). Facial carina conspicuous. Second antennal segment bright yellow. Parafacial vestiture not conspicuous, hairs shorter than longest arisal hairs. Thorax with little dust dorsally except on anterior slope. Sternopleural vestiture mostly black, with a slight immixture of yellowish hairs. Pleura weakly and variably dusted, mostly shining black. t_1 with 1 *pv*. Hind tibia and tarsi with decumbent ground setulae. *h-sc* node on underside of wing sometimes with a few pale or black hairs. R5 open. Lower squama white. Discal and marginal setae of T5 not curved over at tip. ST5 normal (Fig. 33). Genitalia as in Figs. 25–32. Cerci bent backwards. Surstyli rather narrow and with parallel upper and lower borders, as seen in profile, no constrictions in middle part, evenly tapering and bent weakly downwards distally. In dorsal view the surstyli are straight and externally clothed with densely-set hairs. Paraphallic process tips armed, broad as seen from above, and appearing obliquely truncated.

♀. Unknown.

Type material

Holotype ♂, U.S.S.R.: Armenian S.S.R. (Armeniya), '8 km S Bigenak perevala' (=Bichenakskiy Pass), 27.vii.1970 (*Rikhter*) (dissected, postabdominal parts in glycerol in glass micro-vial on pin) (ZILEN).

Paratypes, 2♂ as follows: 1♂, same data as holotype (genitalia visible); 1♂, Armenian S.S.R. (Armeniya), 'okr. Ankavana', 13.vii.1965 (*Rikhter*) (dissected by Grunin (?), parts kept in glycerol on piece of celluloid on pin) (ZILEN).

Remarks

The material of this and the previous species (and even 1♂ 1♀ *Pollenia amentaria* Scopoli=*P. vespillo*: auctt.=*P. nitens* (Zetterstedt)) was set aside in the ZILEN collection with a note by Grunin to the effect that he regarded it all as forming a new taxon ('*P. semicinerea* ssp.n. 1969').

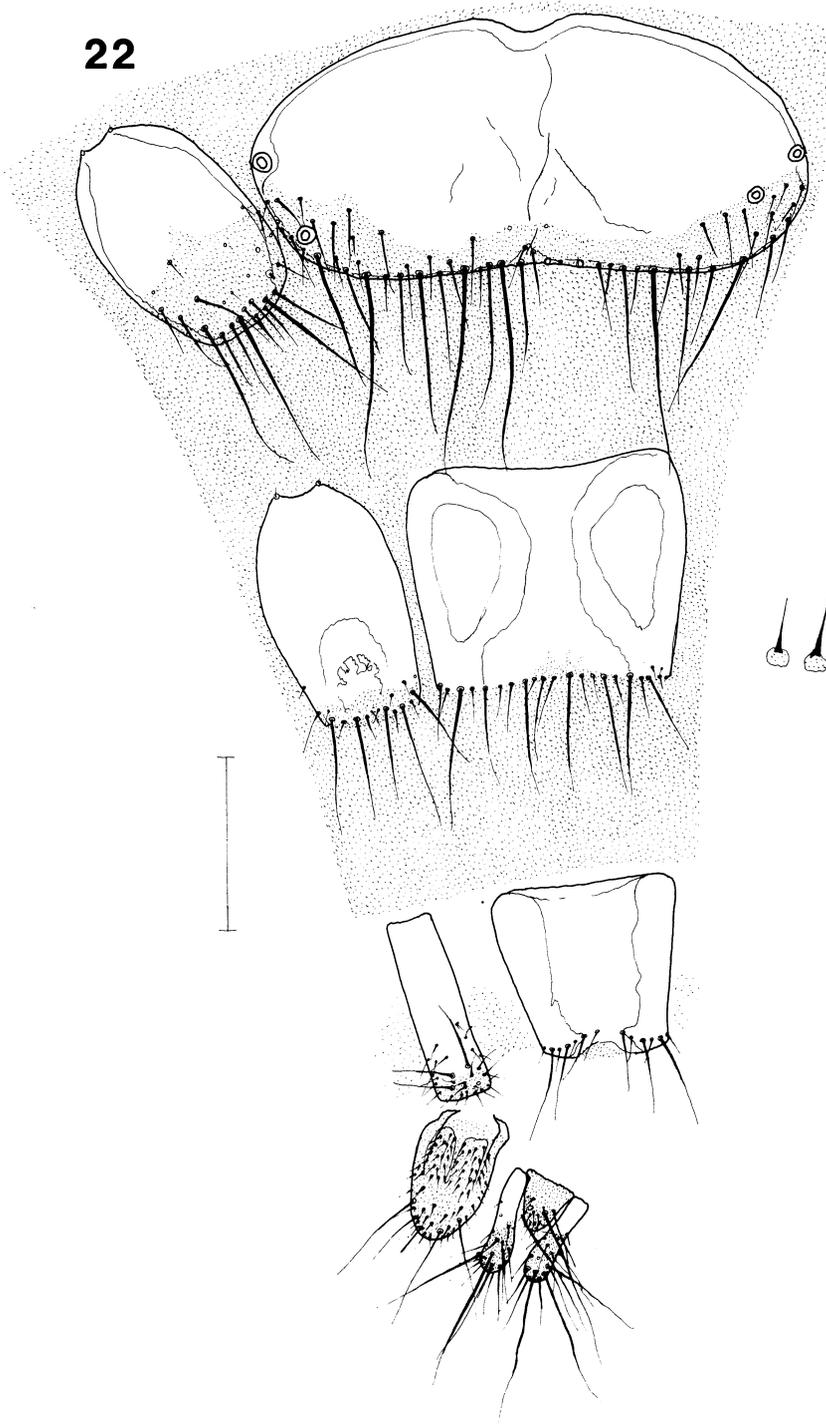


FIG. 22. *Pollenia mystica*, ♀ ovipositor (G.pr. 259). Stipple indicates extent of microtrichiae; inset: two microtrichiae enlarged. Scale 0.5 mm.

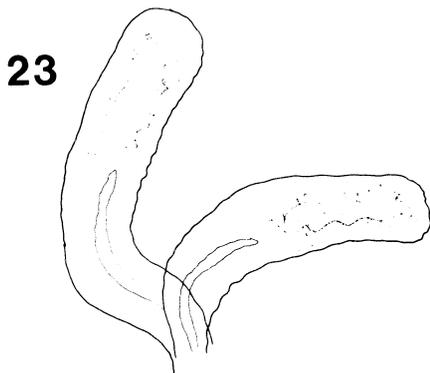
***Pollenia pectinata* Grunin** (Figs. 34–44)

Pollenia pectinata Grunin, 1966: 899. Holotype ♂, U.S.S.R. (ZILEN) (not examined).

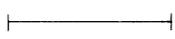
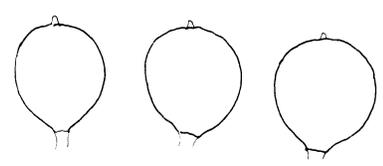
Diagnosis

♂♀. Facial keel inconspicuous, just perceptible. Second antennal segment bright yellow. Parafacialia with conspicuous dense and black vestiture, hairs stronger and longer than longest arisal hairs. Thorax with little dusting dorsally except on anterior slope. Sternopleural vestiture long, dense, crinkly and yellow. Pleurae strongly dusted. t_1 with 1 *pv*. R5 open. Lower squama weakly infuscated. Abdomen densely yellowish dusted with conspicuous tessellations.

♂. Body-length: 9.6–9.8 mm (mean 9.7 mm, $n=3$). Frons at narrowest point $0.014-0.026 \times$ head width (mean 0.021, $n=3$). Hind tibia with modified vestiture: 5–6 *av* setae each about twice as long as tibial diameter; numerous, long strong *ad* and *pd* setae interspersed with erect shorter setae, all these



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FIGS. 23–24. *Pollenia mystica*, ♀: 23, lateral sacs; 24, spermathecae. Scale 0.2 mm.

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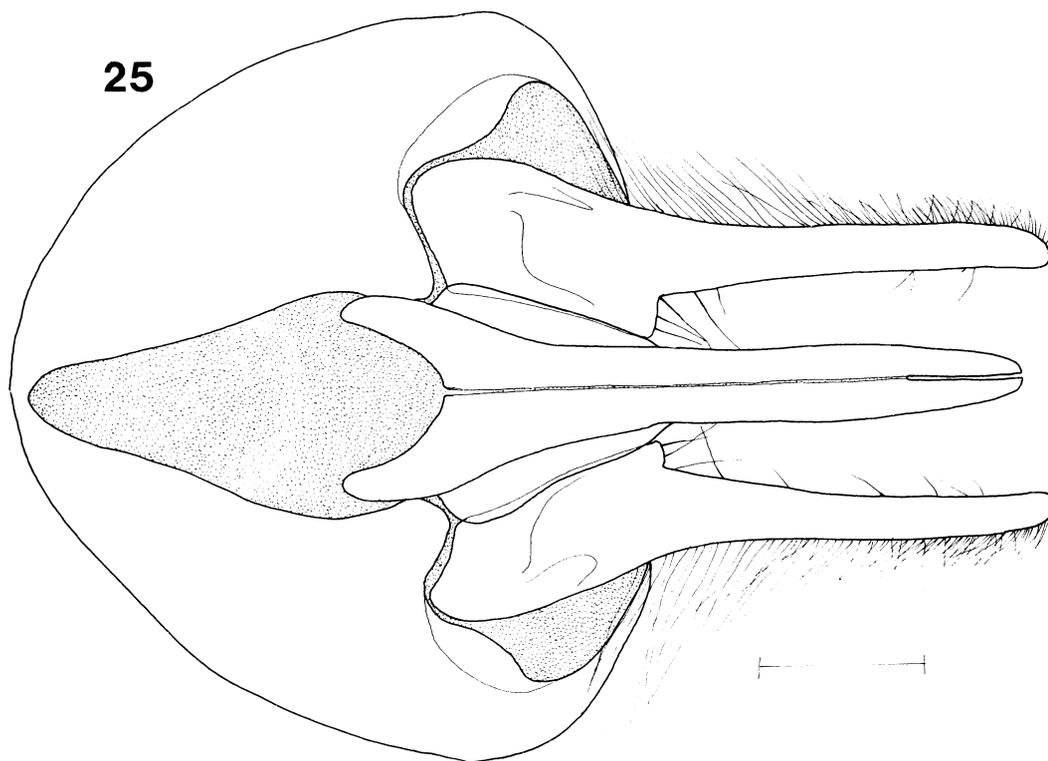


FIG. 25. *Pollenia paragrugini* (holotype), ♂ terminalia: cerci, surstyli and epandrium, posterior view. Scale 0.2 mm.

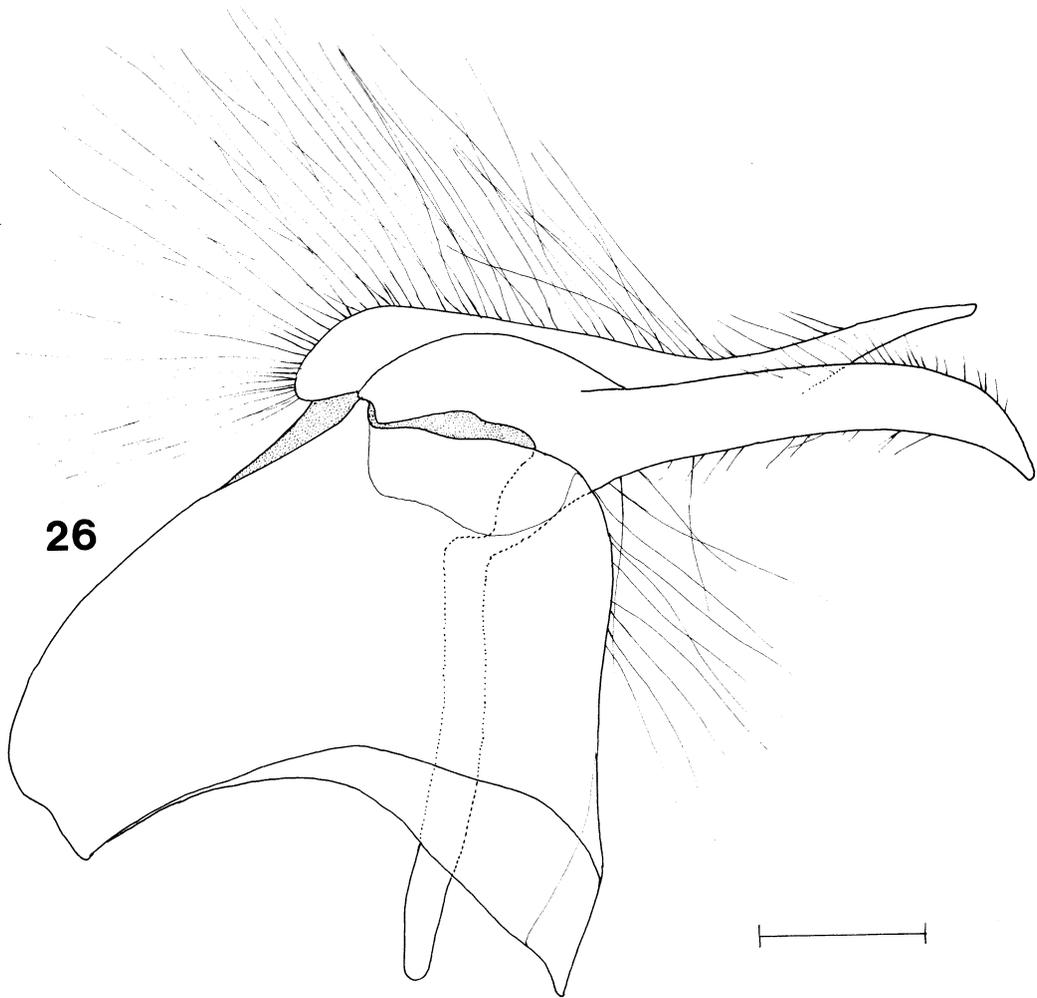
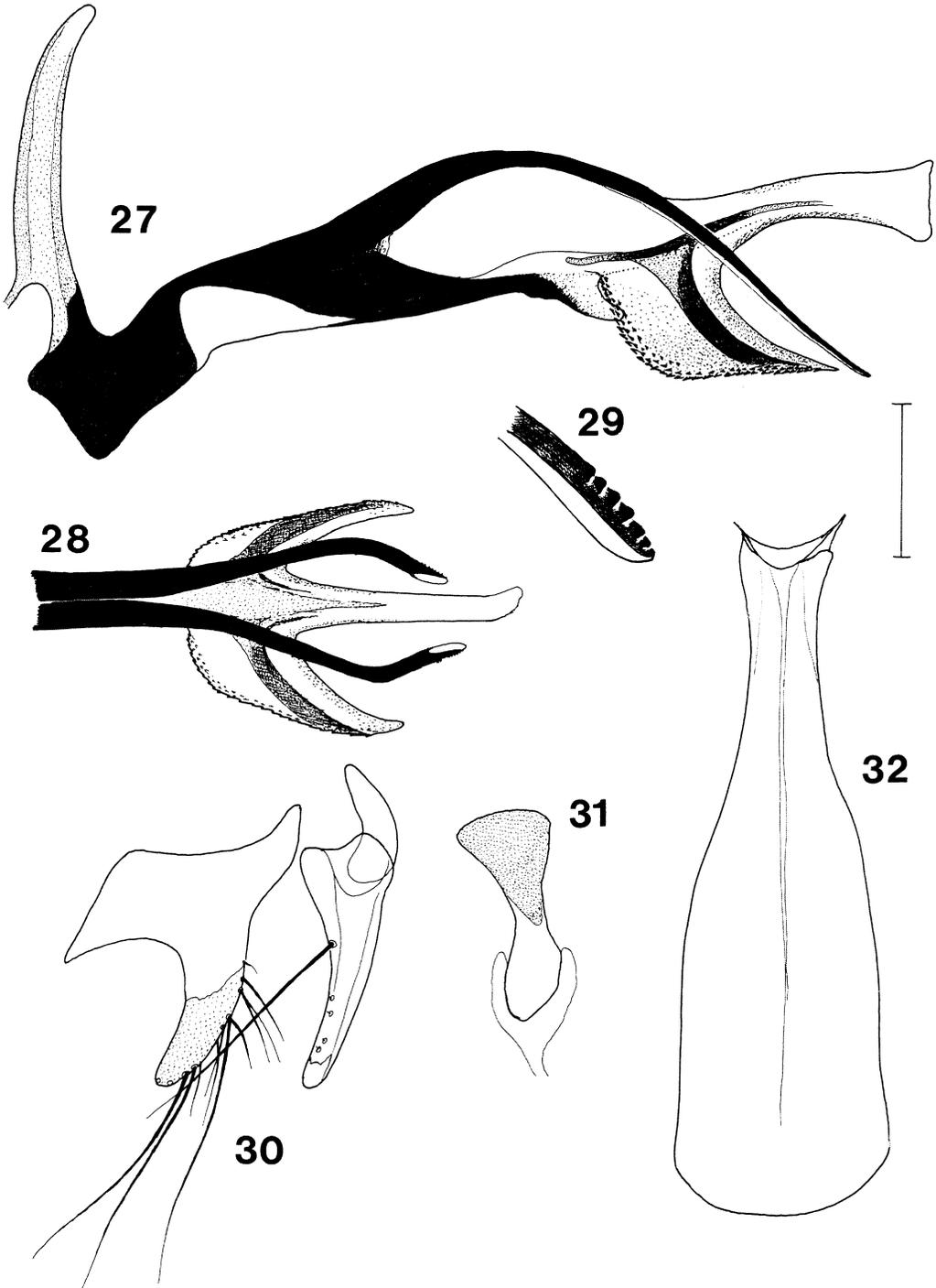


FIG. 26. *Pollenia paragrugini* (holotype), ♂ terminalia: cerci, surstyli, epandrium and processus longus, lateral view. Scale 0.2 mm.

appearing 'combed' backwards; both *av* and *a* surface with erect ground vestiture on distal two-thirds of its length. *d* preapical setae of hind tibia fully as long as hind metatarsus, which is short and thickened. Anterior and dorsal surface of the proximal segments of hind tarsus also with loose erect ground vestiture. Hind metatarsus with remarkably strong ventral spines in two rows, spines about as long as diameter of metatarsus. T5 with no setae bent over at tip. ST5 normal, as in Fig. 42. Genitalia, previously illustrated by Grunin (1966), as in Figs. 34–41. Cerci straight as seen in profile view. Surstyli long, rather narrow, club-shaped, distally expanded both in profile and dorsal view. Base

of surstyli lacking bundle of long setae internally. Paraphallic processes fully sclerotized distally and unarmed.

♀. Body-length: 8.0–9.8 mm (mean 9.1 mm, $n=3$). Frons at vertex $0.333\text{--}0.352\times$ head width (mean 0.345 , $n=4$). Hind tarsi as long as hind tibia, both with normal unmodified vestiture. Ovipositor, previously illustrated by Lobanov (1976), as in Fig. 43. T6 with line of weak sclerotization mid-dorsally. Strongly sclerotized halves of T7 much narrower than weakly sclerotized area between them. ST6 and ST7 with characteristic central area of strong sclerotization. Pleural membrane 8 fully covered with microtrichiae. Cerci very long and narrow,



FIGS. 27–32. *Pollenia paragrugini* (holotype), ♂ terminalia: 27, phallosome, lateral view; 28, distiphallus, dorsal view; 29, tip of paraphallic process; 30, pre- and postgonites; 31, ejaculatory sclerite; 32, phallopodeme. Scale 0.2 mm.

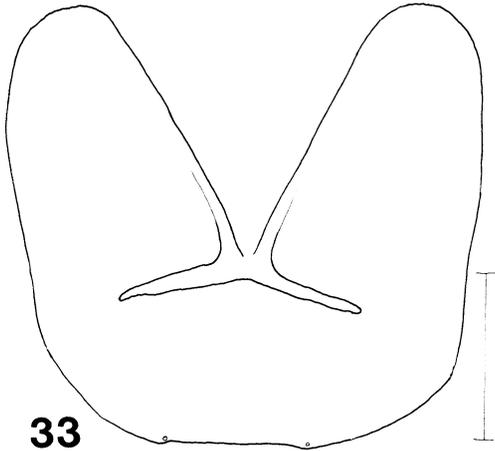


FIG. 33. *Pollenia paragrugini* (holotype), ♂ ST5. Scale 0.4 mm.

devoid of microtrichiae in basal third to quarter. Lateral sacs unsclerotized tubes. Spermathecae as in Fig. 44.

Material examined

MONGOLIA: 1 paratype ♂, southwest of the Khentei Range, Sutszukté pass. 30.viii.1924

(Kozlov); 2♂♂, Ara-Khangaikskii aimak, 15 km south Somona-Tsulut, 29.vii.1967 (Zaitsev). U.S.S.R.: Russian S.F.S.R., 1 paratype ♂, Krasnoyarskiy Kray, Minusinsk, ix.1897 (Tyutchev) (dissected); 1 paratype ♂, Primorskiy Kray, River Sankhobé valley, 11.v.1937 (Grunin); 1 paratype ♀, same data but 8.v.1937; 1♂, Primorskiy Kray, Kedrovaya reservation, 7.vii.1962 (Narchuk); 1♀, Primorskiy Kray, Sututinskii reservation, 27.v.1962 (Rasnitsyn & Sulimov) (dissected, ovipositor on slide no. G.pr. 258). (All ZILEN and identified as *pectinata* by Grunin.)

Remarks

This species is known from Poland, temperate parts of U.S.S.R. from the North European territory to the Far East, Mongolia and China (Grunin, 1966; Draber-Mořko, 1978; Schumann, 1986).

***Pollenia semicinerea* Villeneuve** (Figs. 45–56)

Pollenia semicinerea Villeneuve, 1912: 51; Séguy, 1928a: 374 (key). Séguy, 1928b: 171

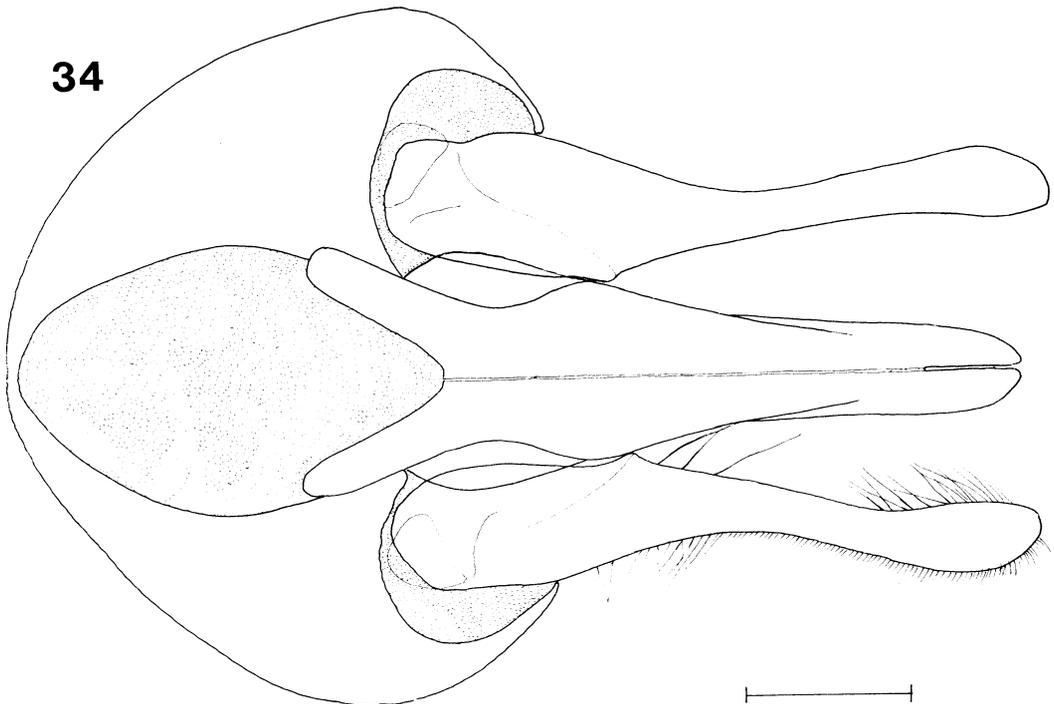


FIG. 34. *Pollenia pectinata*, ♂ terminalia: cerci, surstyli and epiandrium, posterior view. Scale 0.2 mm.

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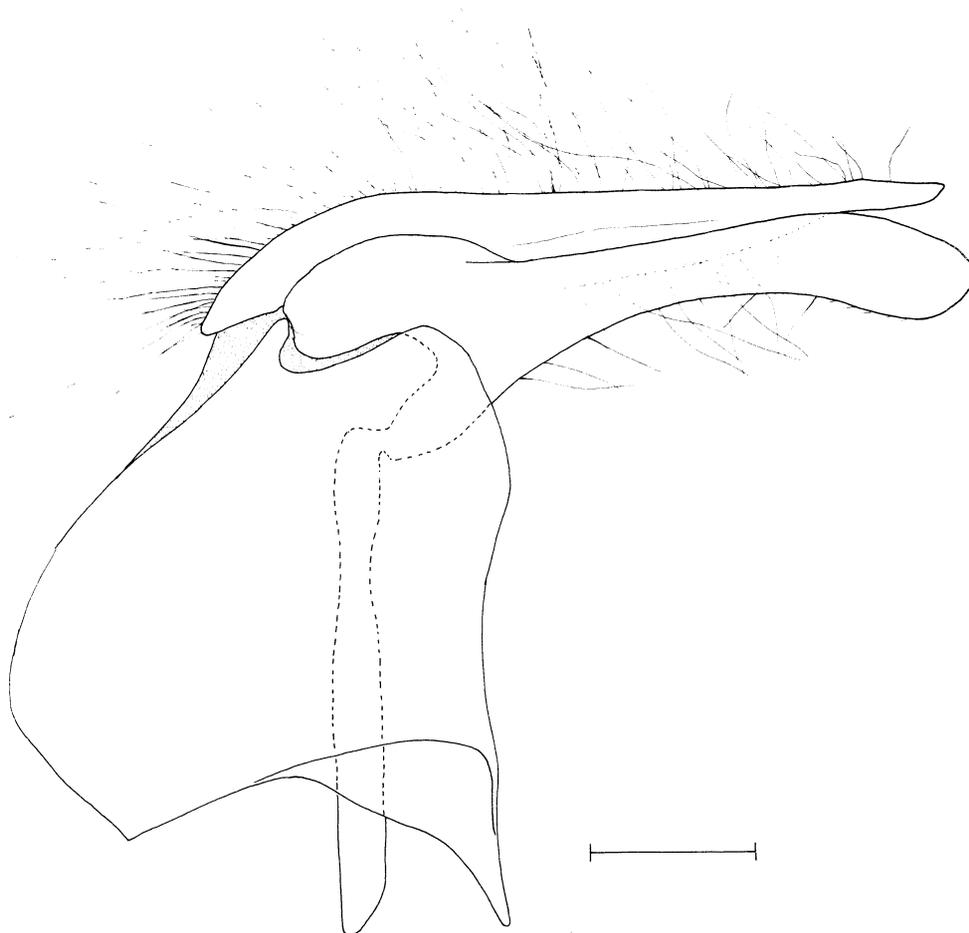


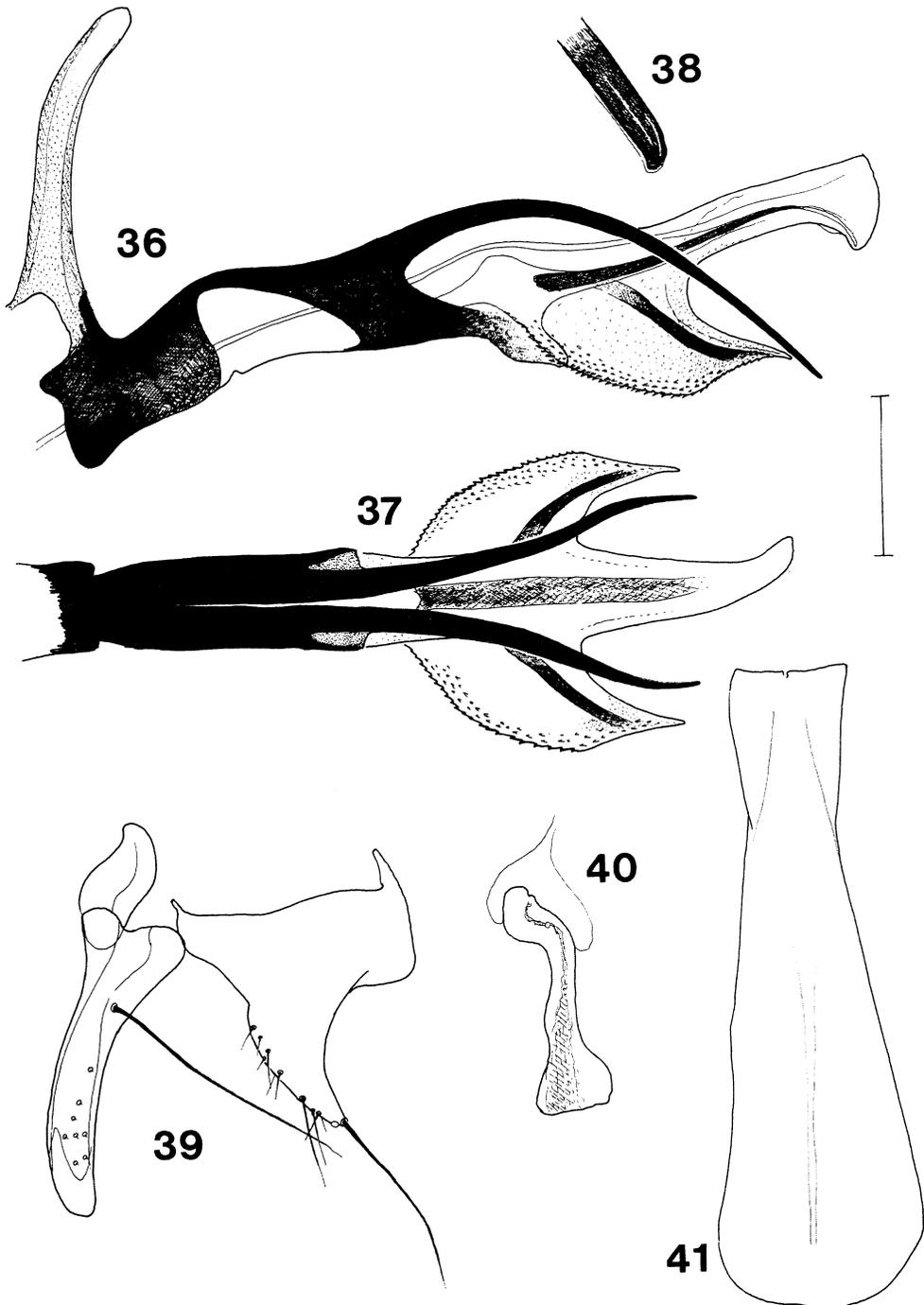
FIG. 35. *Pollenia pectinata*, ♂ terminalia: cerci, surstylus, epandrium and processus longus, lateral view. Scale 0.2 mm.

(key); 174, Fig. 223 (genital capsule in profile); 174, Fig. 224 (distiphallus in profile); 177–178 (description, mainly a transcript from Villeneuve). Séguy, 1934: 45, Fig. 6 (cercus and surstylus in profile, as '*Pollenia intermedia*'); 46 (key); 48 (text as follows: '[other species and *semicinerea*] . . . se distingueront immédiatement par la forme des forceps internes [cerci] (Fig. . . . 6)' [note: Fig. 6 is of surstylus in profile; legend says this figure is of *Pollenia intermedia*]); 49, Fig. 11 (distiphallus in profile); 50 (description, 'Système pénien du type *rudis*, mais différent par la forme des forceps externes dont les branches sont très épaisses'). Séguy, 1941: 22

(key); 23, Fig. 24 (cercus and surstylus in profile, as '*P. intermedia*' [identical with Séguy, 1934: 45, Fig. 6]); 24, Fig. 27 (distiphallus in profile). Lectotype ♂, here designated, SYRIA (MNHN) (examined).

Diagnosis

♂♀. Facial carina high and conspicuous, of variable width, from sharp edged to flattened on top. Second antennal segment bright yellow. Parafacial hairs about as long and fine as longest arisal hairs. Thorax black with very little dust dorsally except on anterior slope. Sternopleural vestiture predominantly black. Pleura weakly



FIGS. 36–41. *Pollenia pectinata*, ♂ terminalia: 36, phallosome, lateral view; 37, distiphallus, dorsal view; 38, tip of paraphallic process (enlarged); 39, pre- and postgonites; 40, ejaculatory sclerite; 41, phallopodeme. Scale 0.2 mm.

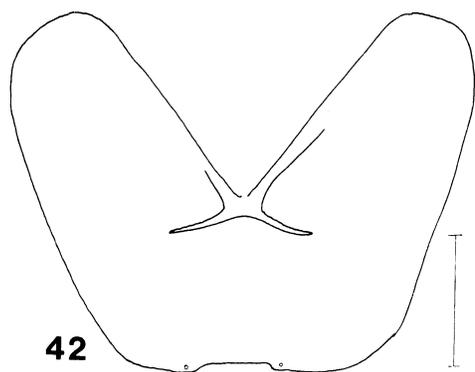


FIG. 42. *Pollenia pectinata*, ♂ ST5. Scale 0.4 mm.

dusted, almost shining black. *h-sc* node on underside of wing sometimes with a few pale or black hairs. R5 open. Lower squama white or weakly infuscated. t_1 with 1(-2) *pv*. Abdomen yellowish to bluish, most often rather thinly dusted; tessellations conspicuous.

♂. Body-length: 6.9–10.0 mm (mean 8.9 mm, $n=7$). Frons at narrowest 0.020–0.050×head width (mean 0.036, $n=9$). t_3 with normal decumbent ground setulae on *a* and *av* surface. Hind tarsus with decumbent ground vestiture on anterior and dorsal surface. T5 marginal setae not curved over at tip. ST5 normal, as in Fig. 53. Genitalia as in Figs. 45–52. Cerci bent backwards. Surstylus with outer surface clothed with densely set, short and regular vestiture on distal part, in profile view strikingly broad, somewhat constricted in middle, distally almost transversely truncated with a sharp lower corner; paraphallic processes narrow and armed.

♀. Body-length: 6.1–9.8 mm (mean 8.7 mm, $n=9$). Frons at vertex 0.314–0.343×head width (mean 0.328, $n=11$). Ovipositor as in Fig. 54. T6 and ST6 relatively short. A line through anterior spiracles of T6 passes near its fore margin. Cerci without microtrichiae on basal fourth. Lateral sacs (Fig. 55) strongly curved and sclerotized. Spermathecae as in Fig. 56.

Type material

Lectotype ♂, SYRIA: between Homs and Bahret Homs, 19.v.1908 (*Gadeau de Kerville*) (dissected, T1–5 glued to carton on pin, ST1–5 and postabdomen in glycerol in glass micro-vial on pin) (MNHN).

Paralectotypes, 2♂ 2♀ as follows: 1♂, 1♀,

same data as lectotype (MNHN); 1♂, same data as lectotype (dissected) (ZIKIEL); 1♀, LEBANON: near Ba'albek, last week of v.1908 (*Gadeau de Kerville*) (MNHN).

Note on type material

Pollenia semicinerea was described from an unspecified number of males and females. No syntypes have been found in Villeneuve's collection in Brussels or Mesnil's collection in Ottawa. Likewise, the specimen(s) dissected by Séguy have not been traced, but a slide with genitalia is in MNHN. The lectotype carries a red label reading 'TYPE' (printed) and a white label reading 'Pollenia semicinera Villen.' (black ink hand). I have labelled the recovered syntypes as lectotype and paralectotypes.

Other material examined

ISRAEL: 1♀, ?loc. (illegible), 11.v.1957 (?); 1♀, Dovrat, 14.v.1974 (*Kaplan*); 1♀, Golan, Qatzrin, 30.v.1981 (*Kaplan*); 1♂, Merom Golan, 14.iii.1975 (*Kaplan*); 1♀, Merom Golan, 15.iii.1975 (*Kaplan*); 1♀, Monfort, 10.iii.1981 (*Furman*) (dissected, ovipositor on slide no. G.pr. 234); 1♀, Mt Hermon (1500 m), 22.iv.1969 (*Kugler*); 1♂, Mt Hermon (1600 m), 9.vi.1975 (*Kaplan*); 1♀, Mt Hermon (1650 m), 22.vi.1973 (*Freidberg*); 1♂ 1♀, Mt Hermon (2000 m), 8.vi.1975 (*Kaplan*); 1♀, Mt Hermon (2000 m), 1.x.1975 (*Kaplan*); 2♂, N. Bezet, 22.iii.1974 (*Furth*) (1♂ dissected); 1♂, Nafech, 15.iii.1975 (*Kaplan*) (all DZTAU, some duplicates in KR).

Remarks

There is confusion in Séguy's publications as to the identity of Fig. 6 in Séguy (1934). To my knowledge there is no *Pollenia* with a distiphallus as in Séguy, 1934: Fig. 18 (*intermedia* correctly figured) in combination with a surstylus as in Fig. 6 (*semicinerea* correctly figured – although not particularly narrowed in middle – but wrongly labelled as *intermedia*).

Phylogenetic relationships of the *semicinerea*-group and related species-groups within *Pollenia*

In the treatment to follow I will consider the following species-groups within *Pollenia* which

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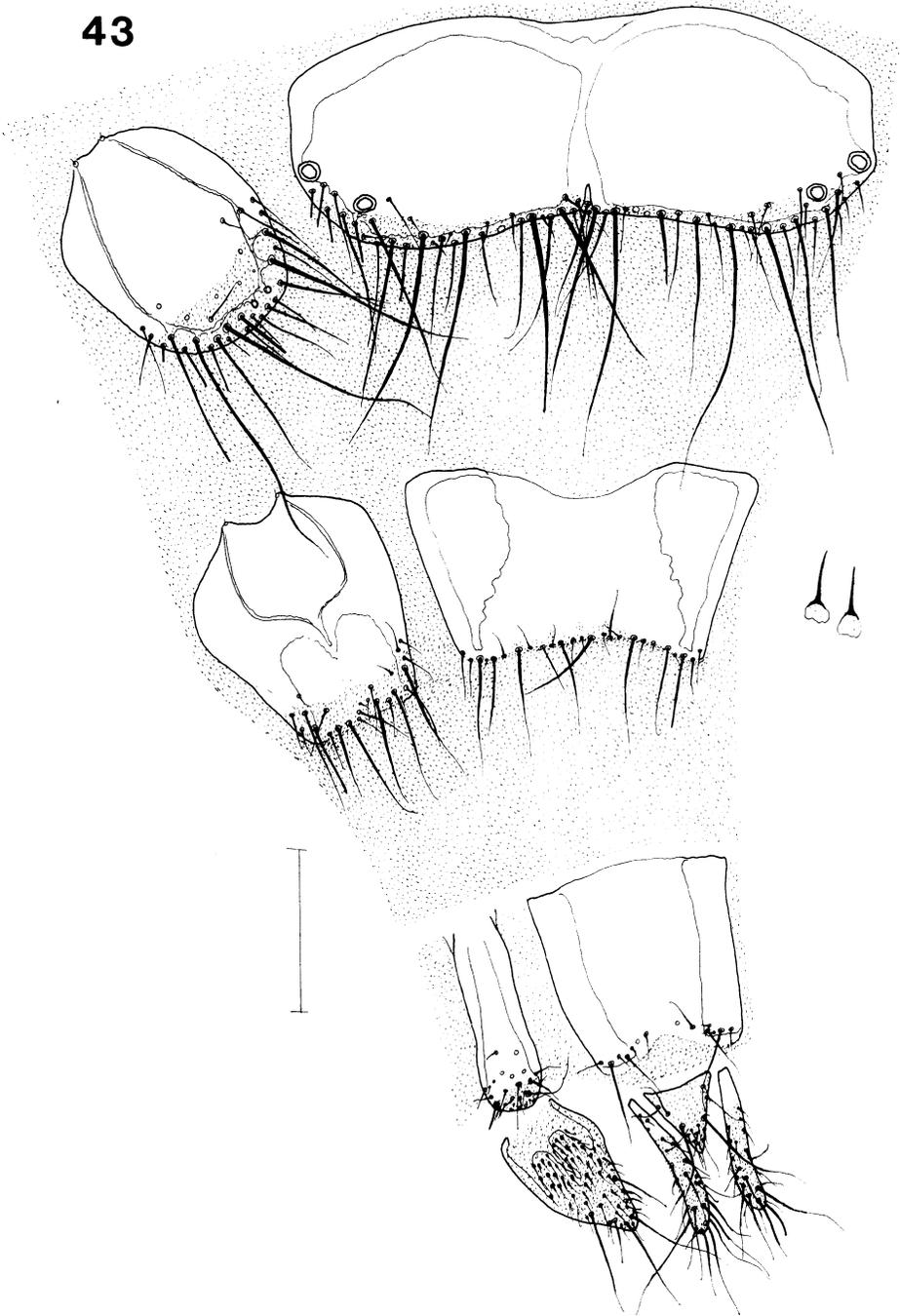


FIG. 43. *Pollenia pectinata*, ♀ ovipositor (G.pr. 258). Stipple indicates extent of microtrichiae; inset: 2 microtrichiae enlarged. Scale 0.43 mm.

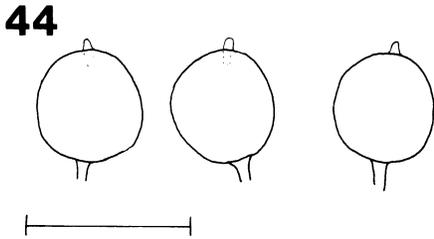


FIG. 44. *Pollenia pectinata*, ♀ spermathecae. Scale 0.2 mm.

taken together probably form a monophyletic subgroup of the genus:

griseotomentosa-group:

Pollenia griseotomentosa (Jacentkovský, 1944)

Pollenia mayeri Jacentkovský, 1941a

intermedia-group:

Pollenia intermedia Macquart, 1835

Pollenia pseudintermedia Rognes, 1987a

tenuiforceps-group:

Pollenia alajensis Rodendorf, 1926

= *Pollenia syshevskajae* Grunin, 1970a

Pollenia dasypoda Portschinsky, 1881

Pollenia similis Jacentkovský, 1941b

Pollenia tenuiforceps Séguy, 1928a

(Note: male holotype (in NMP) of *similis* has been available for study, safely identified females of *tenuiforceps* and *similis* have not.)

semicinerea-group:

Pollenia grunini sp. n.

Pollenia mystica sp. n.

Pollenia paragrugini sp. n.

Pollenia pectinata Grunin, 1966

Pollenia semicinerea Villeneuve, 1912

rudis-group:

Pollenia angustigena Wainwright, 1940

Pollenia hungarica Rognes, 1987b

Pollenia longitheca Rognes, 1987b

Pollenia luteovillosa Rognes, 1987b

Pollenia pseudorudis Rognes, 1987b

Pollenia rudis (Fabricius, 1794)

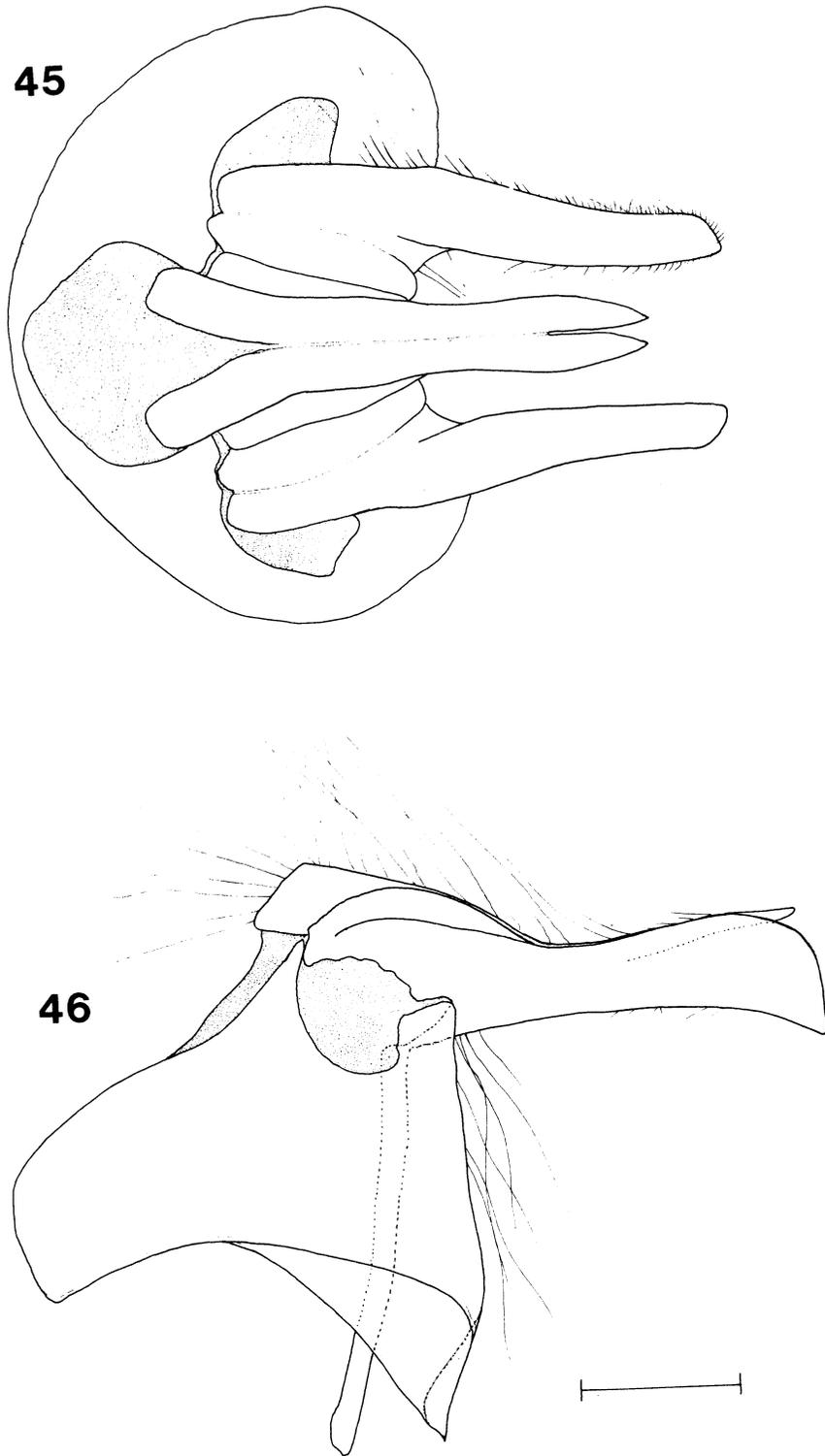
Unknown species no. 1 (see Rognes, 1987b)

The composition of some of these species-groups has been discussed in previous papers (Rognes, 1987a, b). Re-examination of the male and female genitalia of *Pollenia alajensis* (= *P. syshevskajae*) has revealed that it clearly

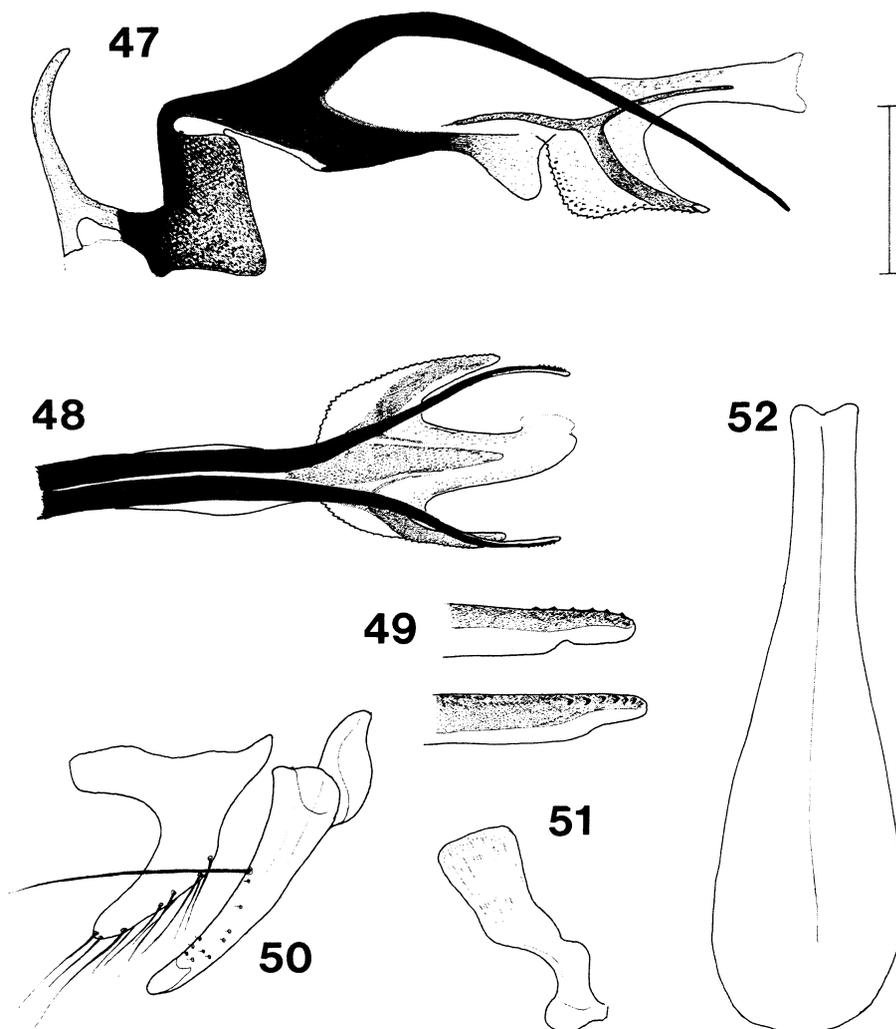
belongs in the *tenuiforceps*-group. I argue below that all the groups are monophyletic. The synapomorphy diagram in Fig. 59 illustrates an attempt at reconstructing their phylogenetic interrelationships. Other species of *Pollenia* are treated as the out-group. The diagram is based on twenty-two cladogenetic trends which I have found relevant for group comparisons and on which I have found it possible to have an opinion concerning polarity. In the Appendix below I give some data on the results generated by the MIX and PENNY algorithms of Felsenstein's PHYLIP (Phylogeny Inference Package) computer program on the basis of the same trends, and their confidence levels given by the BOOT program of the same package (see Felsenstein, 1985). Cladogenetic analysis begins in principle with the lowest taxonomic levels (species, species-groups) and gradually, through search for the sister-group (Hennig's principle), establishes larger groups at higher taxonomic levels. This means that the discussion in principle should start from the top of the diagram and that the trends should be numbered accordingly: trend 22 as no. 1, etc. However, as it is easier to discuss and understand the larger groupings first, I have, for practical reasons, not followed this principle. The trends are as follows (a – apomorphies, p – plesiomorphies):

- (1) Presence of a median hypophallic lobe (a), its absence (p)

The apomorphous character alternative is present in all members of all the species-groups considered here (cf. also figures in Lehrer, 1972; Mihályi, 1976, 1979; Rognes, 1987a, b) except in one member (*griseotomentosa*) of the *griseotomentosa*-group. Its absence here may be due to secondary reduction (cf. diagram). Alternatively, it is present in the other member of this group (*mayeri*) because of underlying synapomorphy (cf. Sæther, 1979, 1983, 1986) affecting the *griseotomentosa*-group. This trend is unique within Calliphoridae and apparently also within the Calliphoroidea of Hennig (cf. also figures in Tschorsnig, 1985a, b; Pape, 1986), and like trend (2) seems to satisfy the minimum criteria for synapomorphy given by Sæther (1979, 1983). Lehrer (1970, 1972) maintains that a median hypophallic lobe is present in *Phormia regina* (Meigen). This is an error. Nothing like it is present in the *regina* distiphallus, which is quite obvious when this organ is examined from



FIGS. 45-46. *Pollenia semicinerea*, ♂ terminalia: 45, cerci, surstyli, and epandrium, posterior view; 46, cerci, surstylus, epandium and processus longus, lateral view. Scale 0.2 mm.



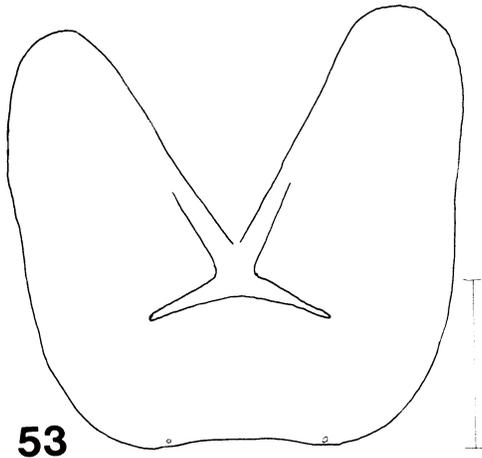
FIGS. 47–52. *Pollenia semicinerea*, ♂ terminalia: 47, phallosome, lateral view; 48, distiphallus, dorsal view; 49, tip of paraphallic process (enlarged); 50, pre- and postgonites; 51, ejaculatory sclerite; 52, phallopodeme. Scale 0.2 mm.

various angles of view. However, basal folds in the hypophallic lobes on each side mimic a 'lobe hypophallique médian', when the distiphallus is examined in exact profile view. Hennig (1976: XLVII) homologizes the median hypophallic lobe (. . . 'ein solches Gebilde' . . .) with one found here and there in Scathophagidae and Anthomyiidae. I find this homologization unsubstantiated. Most probably the 'lobe hypophallique médian' is an independent acquisition in *Pollenia*.

(2) Presence of central sclerotization in the

hypophallic lobes (a), absence of such strengthening (p).

The apomorphic character alternative is present in all members of all the species-groups considered here, except in one member (*mayeri*) of the *griseotomentosa*-group. In *griseotomentosa* it is only developed distally (see figure in Mihályi, 1976). Its absence in *mayeri* may be due to secondary reduction (see diagram). Alternatively, it is present in *griseotomentosa* because of underlying synapomorphy (see Sæther, 1979, 1983, 1986) affecting the *griseotomentosa*-



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FIG. 53. *Pollenia semicinerea*, ♂ ST5. Scale 0.4 mm.

group. Presence of a central sclerotization is a unique feature within Calliphoridae, and apparently also within the Calliphoroidea of Hennig (1958, 1973, 1976) (=Tachinidae s.lat. of Griffiths, 1972) (=Oestroidea of McAlpine *et al.*, 1981) (see also figures in Tschorsnig, 1985a, b; Pape, 1986). Thus, like trend (1) it seems to satisfy the minimum criteria for synapomorphy given by Sæther (1979, 1983). (Note: A somewhat similar, but probably not homologous structure is present in *Morinia melanoptera* (Fallén) (see Rognes, 1986).)

Trends (1) and (2) establish the monophyly of a subgroup of *Pollenia* consisting of all the five species-groups considered here. No name has been in use for this assemblage.

- (3) Facial carina absent or faint (a), well developed, conspicuous and usually rather narrow (p)

A well-developed facial keel is present in most species of *Pollenia* and therefore assumed to be plesiomorphous for the groups under consideration here. In the *intermedia*-group the facial keel is almost absent in *intermedia*, but distinct and rather sharp in *pseudintermedia*. It may therefore be a credible assumption that the *intermedia*-group form a monophyletic assemblage with the *griseotomentosa*-group, sharing with it a reduced facial carina or a tendency to reduce it. Note that trend (3) conflicts with trend (4), discussed below, and that the diagram is unresolved on this point. The faint carina in *Pollenia pectinata* (see above) is interpreted as a secondary

reduction within the *semicinerea*-group. In three *rudis*-group members the carina is very broad and *pallida*-like (cf. Rognes, 1987b). This is also best interpreted as a secondary change.

- (4) Tendency in males to develop a peculiar, erect, thin, often dense and sometimes even separately coloured ventral vestiture (the hairs may be curly at tips) on abdominal tergites, being quite different from the one dorsally (a), ventral vestiture semidecumbent and similar to the dorsal one (p).

Erect and rather thin, but not particularly dense ventral vestiture is present in both members of the *intermedia*-group. In *similis* of the *tenuiforceps*-group the hairs are erect, thin and curly at tips, but the plesiomorphous character alternative is present in the other members. No members of the *semicinerea*-group show the apomorphous feature. The apomorphous alternative is very strongly developed in *hungarica*, *luteovillosa*, *rudis* and Unknown species No. 1 in the *rudis*-group. I know of no other *Pollenias* where the apomorphous character alternative is developed. The trend may be interpreted as an underlying synapomorphy in the sense of Sæther (1979, 1983, 1986) establishing the monophyly of the group (*intermedia*-group + *tenuiforceps*-group + *semicinerea*-group + *rudis*-group). Lehrer (1963, 1970, 1972) reserved the name *Pollenia* R.-D. (s.str.) for this assemblage and transferred *Pollenias* without a median hypophallic lobe (and also *mayeri*) to *Nitellia* Robineau-Desvoidy. I do not recommend this restriction of the name *Pollenia*. Note that this interpretation of trend (4) conflicts with trend (3), discussed above and that the diagram is unresolved at this point.

- (5) Outer *ph* most often absent (a), present (p).

The outer *ph* seta is almost always absent in *griseotomentosa* (more than a hundred specimens examined), and usually (but not always) so in *mayeri* (5♂ 3♀ examined). Among the species-groups under consideration I only know of a single species in the *rudis*-group (*luteovillosa*) which constantly lacks this seta.

- (6) Small size (4–6 mm) (a), normal size (5–11 mm) (p).

P.mayeri and *griseotomentosa* are both very small for *Pollenias*, and seem to be the only species which regularly are so small.

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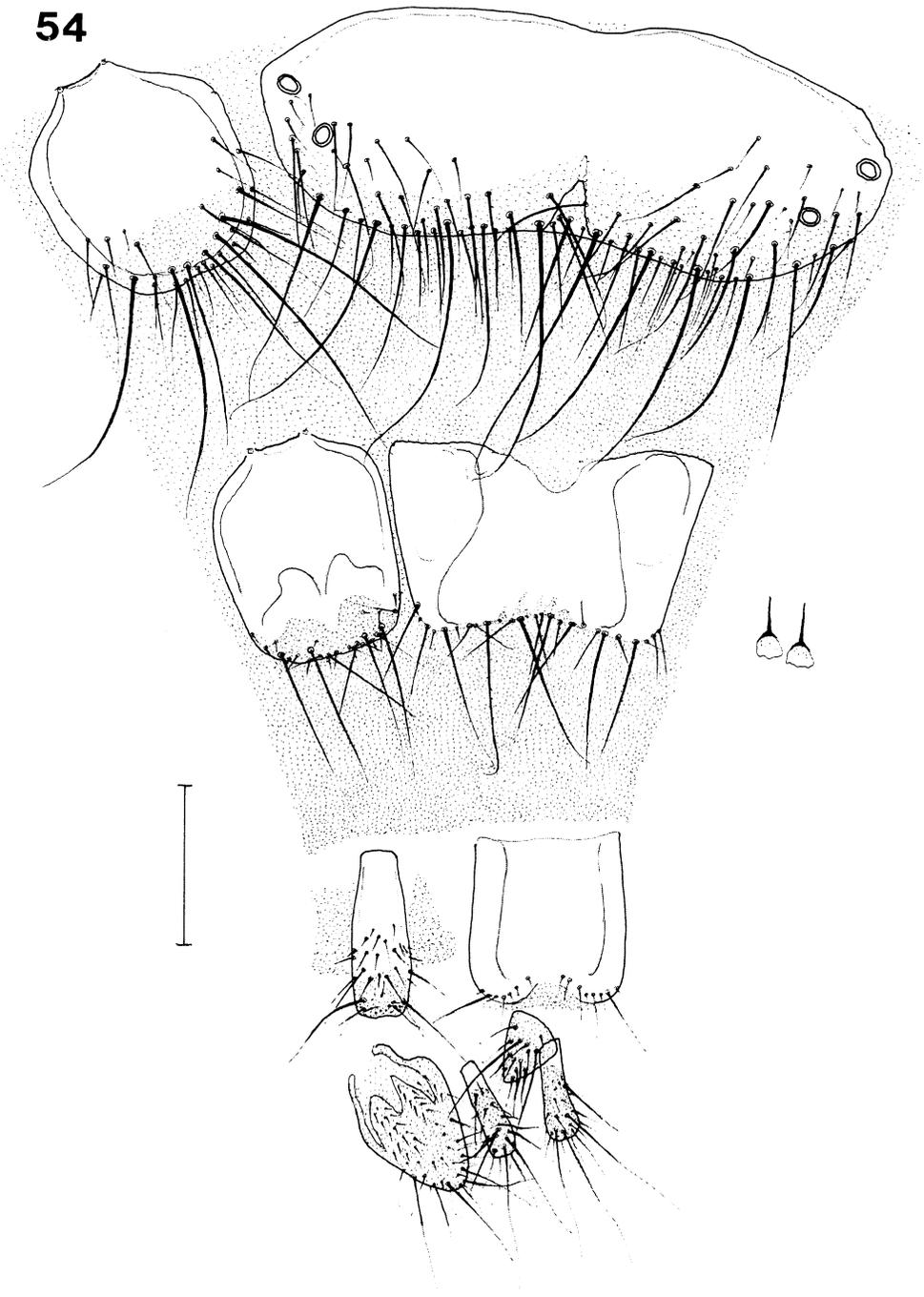
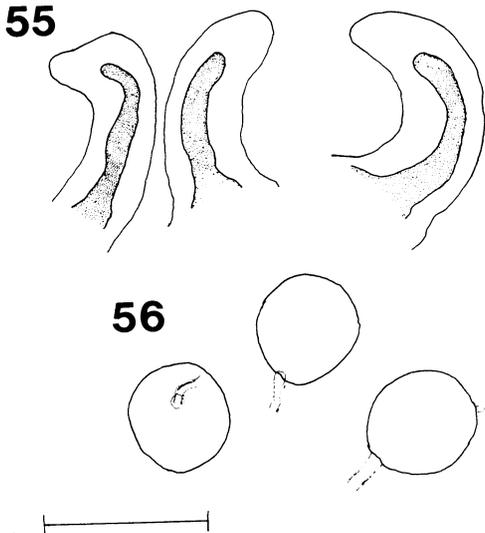


FIG. 54. *Pollenia semicinerea*, ♀ ovipositor (G.pr. 234). Stipple indicates extent of microtrichiae; inset: two microtrichiae enlarged. Scale 0.4 mm.



FIGS. 55–56. *Pollenia semicinerea*, ♀: 55, lateral sacs; 56, spermathecae. Scale 0.2 mm.

- (7) Abdomen not with typical rectangular tessellations, pattern of abdominal dusting rather forming dark blackish longitudinal band occupying central half or broad blackish anteriorly narrowing triangles (cf. Mihályi, 1976; 1979; Emden, 1954, under 'varia') (a), typical square tessellations (p).

The apomorphous alternative is present in *griseotomentosa* and *mayeri* only.

Trends (5), (6) and (7) (together with trends (18) and (19), see below) establish the monophyly of the *griseotomentosa*-group. The genus group names *Polleniella* Jäcentkovský, 1941b (type species: *Polleniella distincta* Jäcentkovský, 1941b = *Pollenia mayeri* Jäcentkovský, 1941a) and *Jäcentkovskiyomyia* Lehrer, 1963 (type-species: *Polleniella griseotomentosa* Jäcentkovský, 1944) are not available for this assemblage. I do not propose to revive any of these names.

- (8) Very dark brown lappets of the metathoracic spiracles (a), yellow lappets (p).

The presence of the apomorphous character alternative in the *intermedia*-group is unique among *Pollenias* with a median hypophallic lobe. In the out-group both alternatives occur, but I find that in out-group species with dark spiracle colour the hue nevertheless is different

from the one in the *intermedia*-group. The trend establishes the monophyly of the *intermedia*-group. The genus-group name *Polleniomyia* Jäcentkovský, 1942 is available for it. I do not propose to revive this name.

- (9) More or less inwardly curved, not always fully sclerotized paraphallic processes which do not appear apically thickened in any view (cf. figures in Rognes, 1987a) (a), paraphallic processes proceeding distad more or less parallel with axis of distiphallus (p).

This trend appears not to be homologous with trend (13), see discussion below. Its presence in the *intermedia*-group is almost unique among *Pollenias* with a median hypophallic lobe (*P. paragrugini* and *P. mystica* appear to be the only exceptions) and corroborates the monophyly of the *intermedia*-group established by trend (8).

- (10) Inner wall of the lateral sacs of the female internal reproductive system sclerotized so that tubes or discs are formed (a), unsclerotized lateral sacs tubes (p).

Sclerotized lateral sacs were found in all of the female members of the *tenuiforceps*-group examined, in all *rudis*-group members (Rognes, 1987b), and in *semicinerea* and *grugini* in the *semicinerea*-group. Note, however, that the lateral sacs are differently shaped in the *tenuiforceps*-group and the *rudis*-group; see discussion of trend (15), below. Apart from a single aberrant specimen of *Pollenia intermedia* (reported in Rognes, 1987b), I have not seen sclerotized lateral sacs in other species of *Pollenia*. I interpret the apomorphous alternative as a synapomorphy satisfying Sæther's (1983) minimum criteria, but which shows secondary reduction in some members of the *semicinerea*-group. The synapomorphy establishes the monophyly of the composite group (*tenuiforceps*-group + *semicinerea*-group + *rudis*-group). No name has ever been used for this assemblage.

- (11) Tendency for male members to develop a peculiar vestiture (e.g. elongated setae, high number of setae, erect, dense and elongated ground vestiture, ventral spines on the metatarsi) on the hind legs, especially affecting the hind tibia and metatarsi (a), quite normal vestiture with a moderate number of setae on the tibiae,

decumbent ground vestiture on tibiae and tarsi, and no ventral spines on the metatarsi (p).

The apomorphous character alternative is present in at least two members of the *tenuiforceps*-group (*dasyпода* and *similis*, and also in occasional specimens of *alajensis*), in one member of the *semicinerea*-group (*pectinata*), and to at least some extent in five of seven members of the *rudis*-group (*angustigena*, *hungarica*, *luteovillosa*, *rudis*, and Unknown species No. 1) (see Rognes, 1987b). I know of no other *Pollenias* with similarly modified hind legs. The apomorphous alternative appears to be a typical underlying synapomorphy in the sense of Sæther (1979, 1983, 1986). It corroborates the monophyly established by trend (10).

- (12) Median hypophallic lobe fully sclerotized (a), strongly sclerotized in posterior part only, apical and distal parts translucent and pale (p).

Figures illustrating this character are found in Lehrer (1972) and Rognes (1987a,b). The apomorphous alternative is found only in the *tenuiforceps*-group.

- (13) Inwardly curved paraphallic processes (Fig. 57), in some views appearing apically thickened (a), paraphallic processes proceeding distad more or less parallel with long axis of distiphallus (p).

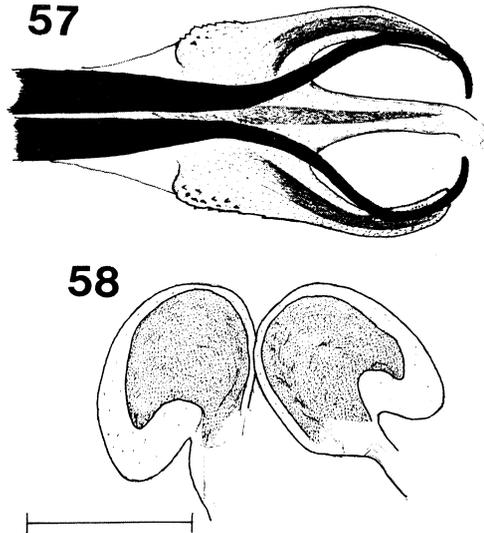
This trend occurs uniquely and uniformly in the *tenuiforceps*-group. It is absolutely correlated with trend (12), (14) and (15). For this reason it is not regarded homologous with trend (9) (empty spaces in corresponding positions of diagram of Fig. 59).

- (14) Blunt apex of hypophallic lobes (a), pointed apex of hypophallic lobes (p).

The apomorphous alternative occurs only in the *tenuiforceps*-group. Good figures illustrating this point are published by Lehrer (1972: Fig. 55), Grunin (1970b) and Mihályi (1979) for *dasyпода*, by Rodendorf (1926) and Grunin (1970a) for *alajensis*, by Zumpt (1956) and Mihályi (1979) for *tenuiforceps*. See also Fig. 57.

- (15) Lateral sacs present in the form of short sclerotized flattened discs (Fig. 58) (a), elongate sclerotized tubes (p).

The transformation series is hypothesized to



FIGS. 57–58. *Pollenia dasyпода*, 57, ♂ distiphallus, dorsal view; 58, ♀ lateral sacs. Scale 0.2 mm.

have been as follows: unsclerotized tubes → sclerotized tubes (cf. trend (10)) → sclerotized discs. The peculiar shape of the lateral sacs of the *tenuiforceps*-group females beautifully parallels the structure of apical part of the male distiphallus, particularly the inwardly curved apex of the paraphallic processes and the blunt hypophallic lobes (cf. trends (13) and (14), above). No better proof could be found for the assumption of Graham-Smith (1938) that the paraphallic processes are inserted into the lateral sacs during copulation.

Trends (12), (13), (14) and (15) establish the monophyly of the *tenuiforceps*-group. The genus group name *Dasypollenia* was proposed by Jacentkovský (1941b: 22; 1941c: 31; 1942: 210) on various occasions for this assemblage. However, it was put forth either without taxonomic characters or without fixation of type-species or both. The name is therefore technically a nomen nudum and thus unavailable. The genus-group name *Parapollenia* Lehrer, 1963: 290 (type-species: *Pollenia dasyпода* Portschinsky) is available for this species-group, but I do not propose to revive this name.

- (16) T8 marginal setae in ovipositor not quite marginal, always a sclerotized part of T8 behind them (a), exactly marginal (p) (see also figures in Rognes, 1987a,b).

The apomorphic alternative occurs uniformly in the *semicinera*-group and in the *rudis*-group. In species of *Pollenia* outside all the species-groups under consideration here (the outgroup) the apomorphic alternative is most common. It may therefore be a ground-plan feature of the genus *Pollenia* since exactly marginal T8 setae is the rule in Calliphoridae outside *Pollenia*. Thus it is possible to interpret the trend to go in the opposite direction (exactly marginal setae apomorphic, i.e. pseudoplesiomorphy, reversal) at this level within the genus. Trend (16) may then become a possible synapomorphy for a composite group consisting of the *griseotomentosa*-group + *intermedia*-group + *tenuiforceps*-group. Trend (16) interpreted in this manner conflicts with trends (10) and (11), both of which I find very persuasive. For the time being I reject this interpretation and consider trend (16) to establish the monophyly of the group (*semicinera*-group + *rudis*-group). No name has ever been used for this assemblage.

- (17) Tips of paraphallic processes armed with small to minute tubercles (a), unarmed (p).

The apomorphic trait is present in three of the five members of the *semicinera*-species-group and in four of seven members of the *rudis*-group. All other species in the groups under consideration here have unarmed processes. Both alternatives occur here and there elsewhere in the genus. The trend may be interpreted as an underlying synapomorphy (Sæther, 1979, 1983, 1986) (showing outside parallelism) corroborating the monophyly established by trend (16).

- (18) male cerci very narrow (a), moderately broad (cf. figures in Rognes, 1987a, b) (p).

Narrow male cerci are uniformly present in the *semicinera* and *griseotomentosa*-group, but are interpreted as independent acquisitions.

- (19) Hind tarsi in the male shorter than hind tibia (a), as long as or longer than hind tibia (p).

Short hind tarsi are present in the *semicinera*-group, the *tenuiforceps*-group (cf. Rognes, 1987a, b) and the *griseotomentosa*-group (Rognes, 1987b), but are interpreted as independent acquisitions.

Trends (18) and (19) establish the monophyly of the *semicinera*-group.

- (20) Basicosta yellow (a), basicosta black (p).

Yellow basicosta is the rule in the *rudis*-group (with occasional individual exceptions in some of the species) (Rognes, 1987b). In all the other groups under consideration here, the basicosta is black.

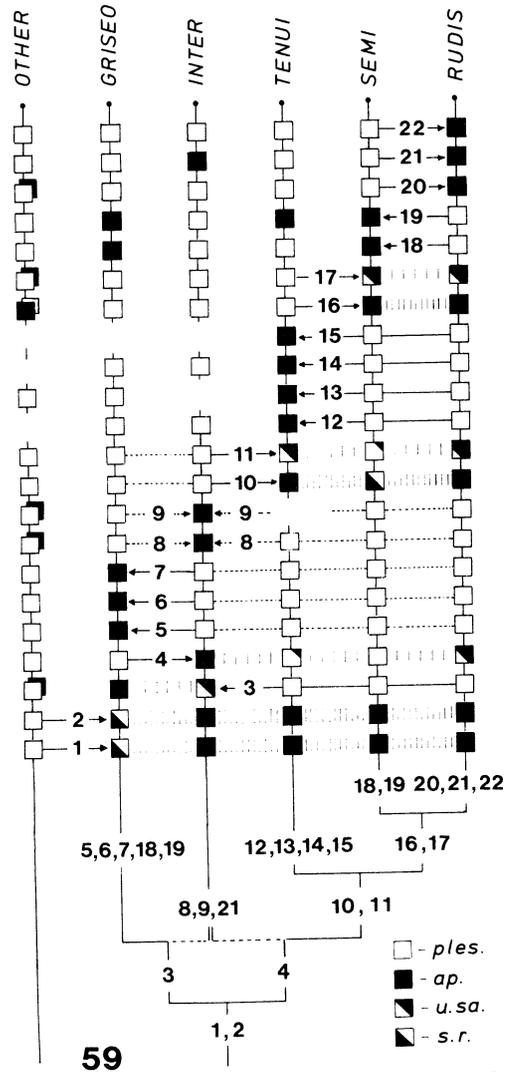


FIG. 59. Scheme of argumentation illustrating the relationship of species-groups in *Pollenia*. Abbreviations: OTHER=other members of the genus *Pollenia* (out-group); GRISEO = *griseotomentosa*-group; INTER = *intermedia*-group; TENUI = *tenuiforceps*-group; SEMI = *semicinera*-group; RUDIS = *rudis*-group; ap. = apomorphies; ples. = plesiomorphies; s.r. = secondary reductions; u.sa. = underlying synapomorphies. See text for discussion.

(21) Spermathecae elongate (a), circular (p).

Elongate spermathecae are present uniformly in the *rudis*- and *intermedia*-group (Rognes, 1987a, b), but are interpreted here as independent acquisitions.

(22) Tip of paraphallic processes appearing transversely truncated in certain views (a), processes rather evenly sclerotized to tip, not appearing truncated (p).

This feature is present in all species of the *rudis*-group except *longitheca* (Rognes, 1987b).

Trends (20), (21) and (22) establish the monophyly of the *rudis*-group.

From the above discussion it is a credible assumption that the *semicinerea*-group and the *rudis*-group are sister-groups. The former is distributed in the Middle East–Caucasus area of the Palaeartic and the temperate parts of the East Palaeartic (east of and including Poland and the North European territory of the U.S.S.R. to

China and Mongolia). The latter is known mainly from the Nearctic and West Palaeartic. Thus they roughly show a vicariant pattern of distribution with overlap in East Europe, the European territory of the U.S.S.R. and the Middle East–Caucasus area.

Appendix

The data presented in Fig. 59 were run through the MIX and PENNY parsimony method programs of PHYLIP (version 3.0) (see Felsenstein 1984, 1985). Data were coded as follows:

A	00000000000000000000
rudis	1101000001100001100111
semi	1101000001100001111000
tenui	1101000001111110001000
inter	1111000110000000000010
griseo	1110111000000000011000
other	0000000000000001000000

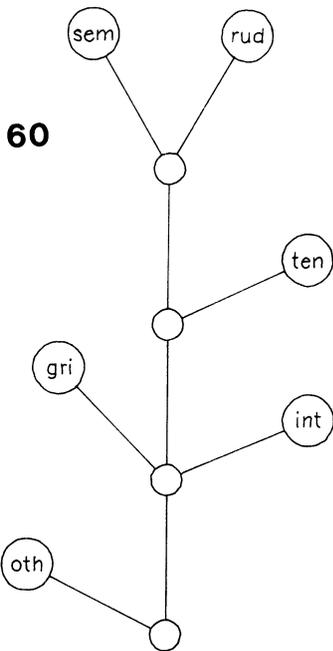


FIG. 60. The three most parsimonious trees generated by the MIX and PENNY algorithms of the PHYLIP program package (Felsenstein, 1984, 1985) from the data presented in Fig. 59. Phylogenies are evaluated by the Wagner parsimony criterion. The three trees can be generated by resolving the trifurcation into the three possible bifurcations. All abbreviations are the three first letters of the ones used in Fig. 59. See text for further explanation.

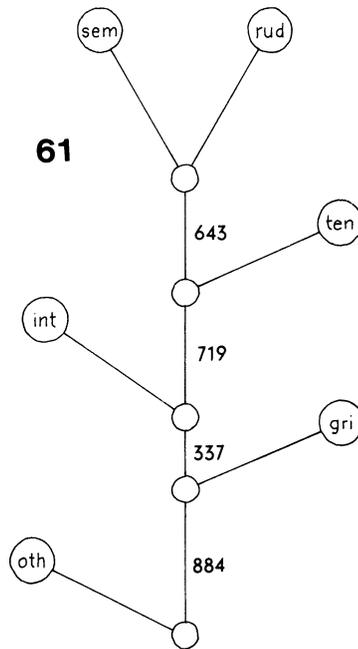


FIG. 61. A majority-rule consensus tree generated by the BOOT bootstrap procedure of PHYLIP program package (Felsenstein, 1984, 1985) from the data presented in Fig. 59. Phylogenies are evaluated by the Wagner parsimony criterion. 1000 bootstrap samples were analysed. Next to each branch is shown the number of times that the monophyletic group it defines occurred among the bootstrap replicates. All abbreviations are the three first letters of the ones used in Fig. 59. See text for further explanation.

The twenty-two numbers for each species-group represent the trends (the leftmost number trend (1), etc.) coded in binary form, 0 for the plesiomorphies, 1 for the apomorphies, underlying synapomorphies and secondary reductions. 'A' represents the ancestral states. Note that trend 4 for the *semicinerea*-group is coded as 1 (underlying synapomorphy, see discussion above) even though it is actually present in the plesiomorphous form.

MIX (version 3.01) parsimony algorithm (Wagner method) found three minimal length trees, each requiring twenty-eight steps, as shown in Fig. 60. The two diagrams shown in Fig. 59 are both represented among these. If trend 4 in the *semicinerea*-group was coded as 0 (plesiomorphy), the same three trees were generated, each requiring twenty-nine steps. The PENNY (version 3.0) algorithm which finds all most parsimonious trees (Wagner method) gave the same result. The BOOT (version 3.01) bootstrap procedure (Felsenstein, 1985) was run on the above data set with 1000 replicates. The result is shown as a majority-rule consensus tree (Fig. 61). This is compatible with the ones in Fig. 59, but note that the confidence level for the composite groups is always below 95% (the limit of statistical significance, see Felsenstein, 1985).

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