AN ANNOTATED KEY TO DROSOPHILID GENERA WITH BARE OR MICROPUBESCENT ARISTAE AND A REVISION OF *PARACACOXENUS* (DIPTERA: DROSOPHILIDAE)

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The world genera (15 in all) of Drosophilidae with bare (i.e., non-plumose) aristae are brought together, and a key is provided for identifying them. Notes are provided in the key on type species, synonymy, numbers and distributions of included species, and pertinent literature. The genus *Paracacoxenus* Hardy is revised to include not only its one Nearctic species, *guttatus* Hardy and Wheeler, but also three European species that were originally assigned to *Cacoxenus* Loew, i.e., *argyreator* (Frey), *exiguus* (Duda), and *inquilinus* (Hendel). Lectotypes are designated for *Cacoxenus punctatus* Duda (a junior synonym of *Gitonides perspicax* Knab), for *Gitona vlasovi* Duda, for *Paracacoxenus argyreator* (Frey), and for *P. exiguus* (Duda). The paper includes 30 figures.

Introduction

This study arose from requests to identify a peculiar drosophilid that Mr. J. M. Powell, Forest Entomology and Pathology Laboratory, Calgary, Alta., reared from bolts of lodgepole pine (*Pinus contorta* Dougl.) infested with stem rust (*Cronartium commandrae* Pk.). It was established with difficulty that the flies involved belong to *Paracacoxenus guttatus* Hardy and Wheeler, a species described from Washington and Oregon (Hardy and Wheeler 1960) but, until now, otherwise unknown. Mr. Powell's collections constitute the first record of the species in Canada and provide the only known information on its biology.

It is difficult to identify *P. guttatus* because neither the genus nor the species is included in published keys. The same is true for a number of other more or less similar drosophilids from various parts of the world, and this situation increases the difficulty of distinguishing any of these groups from their relatives. The purpose of this paper is to provide a key to all of these relatively poorly known genera and to revise the genus *Paracacoxenus* Hardy. A companion paper in preparation by Mr. Powell will deal with the biology of *P. guttatus*, and its possible role in the etiology of stem rust in pines.

Systematic Relationships

Paracacoxenus Hardy (*in* Hardy and Wheeler 1960) is one of a relatively few genera of Drosophilidae with a bare or micropubescent arista (i.e., a non-plumose arista) (Figs. 1, 3, 5, 7). The same character occurs in *Acletotoxenus* v. Frauenfeld (1868), in some *Baeodrosophila* Wheeler and Takada (1964), and in *Cacoxenus* Loew (1858), *Colocasiomyia* de Meijere (1914), *Drosophilella* Duda (1923), *Erima* Kertesz (1899), *Gitona* Meigen (1830), *Gitonides* Knab (1914), *Hyalistata* Wheeler (1960*a*), *Luzonimyia* Malloch (1926), *Mayaguesa* Wheeler (1960*b*), *Pseudocacoxenus* Duda (1925), *Pseudiastata* Coquillett (1908), and *Sinophthalmus* Coquillett (1904). All other taxa with "bare" arista that at one time or another were assigned to the Drosophilidae appear to belong to other families. For example, *Aulacigaster* Macquart (1835) is now placed in a separate family, the Aulacigastridae (Duda 1924), *Blaesochaetophora* Czerny (1904) (treated as drosophilid by Sturtevant 1921) belongs to the Heleomyzidae (Malloch 1933), *Cinderella* Steyskal (1949) belongs in the Heleomyzoidea (Hennig, personal communication) (new placement), and *Cacoxenus semiluteus*

Loew (1869) [now called *Paratissa semilutea* (Loew)] belongs in the Ephydridae (Wirth 1965).

A bare or micropubescent arista is so distinctive in the Drosophilidae that it is frequently employed in the opening couplets of keys to remove quickly the known groups that possess it. However, the 15 drosophilid genera brought together here because they have this character do not comprise a strictly natural group. To be sure, some of them, e.g., *Gitonides* (Figs. 16, 26, 27), *Cacoxenus* (Figs. 10, 17, 18, 24, 25) and *Paracacoxenus* (Figs. 1, 2, 4, 8, 9, 11, 12, 13, 14, 19, 20, 21, 22, 23) are more closely related to each other than they are to genera with plumose aristae, but the assemblage as a whole is not monophyletic. Actually, the genera mentioned include representatives of both of the two main subfamilies commonly recognized in the Drosophilidae, i.e., Steganinae and Drosophilinae, and some excluded genera (with plumose aristae) are almost certainly more closely related to one or other of the included genera, than some of the latter are to each other. For example, *Leucophenga* Mik., *Rhinoleucophenga* Hendel, and *Amiota* Loew (Steganinae with plumose aristae) are probably much more closely related to *Gitona* (Fig. 3), *Pseudiastata* (Fig. 6), *Erima*, and *Sinophthalmus* (Steganinae with bare aristae), than the latter are to such genera as *Baeodrosophila*, *Colocasiomyia*, and *Drosophilella* (Drosophilinae with bare aristae). In short, most, though not all, of the drosophilid genera with a non-plumose arista belong in the *Phortica–Leucophenga* assemblage, but a bare arista by itself does not serve to define this assemblage and is not restricted to it. It is simply a convenient key character to separate a number of rather peculiar and poorly known genera from the remainder of the family.

Paracacoxenus belongs to the subfamily Steganinae Duda (1934), *sensu* Wheeler (1965) (= Steganinae + Amiotinae of Brues and Melander 1932, and of Brues, Melander, and Carpenter 1954), a group which is believed to include the most primitive genera of Drosophilidae (Sturtevant 1942, p. 26; Wheeler 1952*a*, p. 164; Hardy 1965, p. 33). This subfamily has never been satisfactorily defined and its taxonomic limits are still uncertain. Although it is beyond the scope of this paper to attempt such a definition, it seems useful to list some of its most important characteristics. These are as follows: prescutellar acrostical bristles present (Fig. 2); scutellum relatively large, dorsally convex, and with divergent basal bristles (Fig. 2); lower reclinate frontal bristles strong, that is, about equal in size to the proclinate frontal bristles (Fig. 1); upper reclinate frontal bristles situated high on the frons, that is, about in line with the posterior ocelli (Fig. 1). In addition many Steganinae have bare or micropubescent aristae, and wing cell 1st M_2 (first basal cell) is frequently separated from 2nd cell M_2 (discal cell) by a crossvein (Fig. 4). Furthermore the surstylus of the male genitalia is usually present as a moveable lobe, that is, it is not solidly fused with the margin of the epandrium (Figs. 19, 20, 21, 24, 25). *Paracacoxenus* has all these characters.

Within the subfamily Steganiinae the closest relatives of *Paracacoxenus* are *Cacoxenus* and *Gitonides*. Before the species *guttatus* (type species of *Paracacoxenus*) was formally described, it was referred to the genus *Cacoxenus* (Wheeler 1952*a*), but subsequent comparison of *guttatus* with *indagator* Loew (type species of *Cacoxenus*) showed that they are generically distinct (Hardy and Wheeler 1960). Consequently, the genus *Paracacoxenus* Hardy (*in* Hardy and Wheeler 1960) was erected for *guttatus*; at the same time many details of both genera were compared.

Wheeler (1952*b*) considered *Gitonides* as doubtfully distinct from *Cacoxenus*, but the same year he (Wheeler 1952*a*) referred the species *perspicax* Knab (type species of *Gitonides*) to *Cacoxenus*, along with the undescribed Nearctic species that was later to become *P. guttatus*. Later, however, Hardy and Wheeler (1960) recognized *Gitonides* as a valid genus allied to *Paracacoxenus*. Hardy (1965) listed some of the main differences between all three genera.

The following key separates these genera and all other drosophilid genera with bare aristae and helps to clarify their systematic relationships.

Key to Drosophilid Genera with Bare or Micropubescent Aristae

1. Arista bare or micropubescent, main stem never with undulations and never bifurcate at apex (Figs. 1, 3, 5, 7) 2
   Arista with one or more rays; main stem usually with noticeable undulations and usually bifurcate at apex ..... most Drosophilidae
2. Ocellar bristles absent (*Luzonimyia* Malloch apparently has tiny hairs laterad of anterior ocellus) (Fig. 7) 3
   Ocellar bristles present (Figs. 1, 3, 5) 5
3. Face with a nose-like carina (Fig. 3). Cheek moderately broad. Anterior reclinate orbital distinctly shorter than the proclinate orbital; posterior reclinate orbital arising nearer to proclinate orbital than to inner vertical bristle. Preapical dorsal tibial bristle weakly developed on mid tibia (Fig. 9) ..... *Colocasiomyia* de Meijere (1914)
   [Type and only known species, *C. cristata* de Meijere (*loc. cit.*), by monotypy, from Java.]
   Face not carinate (Figs. 5, 7). Cheek extremely narrow (Fig. 7). Anterior reclinate orbital as strong as proclinate orbital (Fig. 7). Preapical dorsal tibial bristles not evident (Figs. 10, 11) 4
4. With one obvious pair of dorsocentral bristles, an anterior pair not or scarcely distinguishable. Humeral bristle moderately strong (Fig. 2). Disc of scutellum strongly convex. Frons without a pair of tiny hairs in transverse line with anterior ocellus ..... *Acletotoxenus* v. Frauenfeld (1868)
   [Type and only known species, *Gitona formosus* Loew (1864) (= *A. syrphoides* v. Frauenfeld, *loc. cit.*), by monotypy, from Europe and Canary Islands. For detailed description see Duda 1934. Head (Fig. 7) and male genitalia (Figs. 28, 29, 30) illustrated below.]
   With two obvious pairs of dorsocentral bristles, the anterior pair moderately strong. Without humeral bristle. Disc of scutellum flattened. Frons with a pair of tiny hairs in transverse line with anterior ocellus ..... *Luzonimyia* Malloch (1926)
   [Type and only known species, *L. nigropuncta* Malloch (*loc. cit.*), by monotypy, from Luzon, Philippine Islands.]
5. Wings with three or more dark spots or clouds, posterior crossvein always clouded (Fig. 6) 6
   Wings usually wholly hyaline, posterior crossvein never clouded (Fig. 4). (In *Gitona distigma* Mg. and *G. beckeri* Duda there is a spot at apex of r_1) 8
6. Tibiae with three white and three black bands. Face with a strong nose-like carina; prelabrum (tormae) (Fig. 1) about as long as width of third antennal segment; proclinate orbital bristles arising on upper half of forns; anterior reclinate orbital not half as long as proclinate orbital; first basal and discal cells separated by a crossvein (Fig. 4) ..... *Sinophthalmus* Coquillett (1904)
   [Type and only known species, *S. pictus* Coq. (*loc. cit.*), by original designation, from southwestern United States and Mexico. For detailed description see Wheeler 1952*a*.]
   Tibia usually not banded, at most with a single band near base; face without a nose-like carina (Figs. 5, 6), prelabrum not more than half as long as width of third antennal segment; proclinate orbital arising on lower half of frons; anterior reclinate orbital about equal in size to proclinate orbital; first basal and discal cells confluent (Fig. 6) 7
7. Anterior pair of orbitals cruciate and arising closer to lunule than to lower reclinate orbitals; ocellar bristles large, directed anterolaterally ..... *Pseudiastata* Coquillett (1908)
   [Type, *P. nebulosa* Coquillett (*loc. cit.*), by monotypy. The genus contains five described species in southern United States, Central and South America. For review see Hardy 1959.]

Anterior pair of orbitals proclinate and arising closer to lower reclinate orbital than to lunule (Figs. 1, 3, 5, 7); ocellar bristles very small, upright, and cruciate (Fig. 5) ..... *Mayaguesa* Wheeler (1960*b*)
[Type and only known species, *M. argentifera* Wheeler (*loc. cit.*), by original designation, from Puerto Rico.]

8. Prescutellar acrostical bristles absent; anterior dorsocentral bristles arising far forward, that is, as far from the posterior dorsocentrals as from each other; second segment of fore tarsus with toothed protuberance ..... *Drosophilella* Duda (1923)
[Type and only known species, *D. seminigra* Duda (*loc. cit.*), by monotypy, from New Guinea.]

Prescutellar acrostical bristles present (Fig. 2); anterior dorsocentral bristle arising near posterior dorsocentrals (Fig. 2); second segment of fore tarsus simple 9

9. Head, thorax, and abdomen shining black; halteres black; first basal and discal cells confluent (Fig. 6); facial carina broad and nose-like; interfrontal setulae (Fig. 1) absent or very sparse ..... *Pseudocacoxenus* Duda (1925)
[Type and only known species, *P. lineatifrons* Duda (*loc. cit.*), by monotypy, from Costa Rica.]

Head, thorax, and abdomen not shining black; halteres pale 10

10. First basal and discal cells separated (Fig. 4) 11

First basal and discal cells confluent (Fig. 6) 15

11. Femora and tibiae usually with alternating pale and dark bands; ocelli on a pronounced mound; all orbital bristles arising in upper half of frons, and frequently flattened; preapical tibial bristles undeveloped ..... *Erima* Kertesz (1899)
[Type, *E. fasciata* Kertesz[1] (*loc. cit.*), by monotypy, from New Guinea. Four additional species known, three in Africa (Hackman 1960, 1963) and one *E. lepidothrix* (Wheeler and Takada) (new combination), from the Caroline Is. (Wheeler and Takada 1964).]

Legs not banded; ocelli not on a pronounced mound; lowermost orbital bristles arising on lower third of frons, and not flattened; preapical tibial bristles present or absent 12

12. Compound eye with a horizontal band, thorax with a pleural stripe, preapical dorsal tibial bristles (Figs. 8, 9) present, though small, on all tibiae ..... *Gitonides* Knab (1914)
[Type and only known species,[2] *G. perspicax* Knab[3] (*loc. cit.*), by monotypy, from Oriental Region. For detailed description see Hardy 1965.]

Compound eye without a band; preapical dorsal tibial bristles present or absent ... 13

13. Facial carina moderately prominent, rather broad and somewhat nose-like in profile (Fig. 3); yellowish- or reddish-brown species with yellow legs ..... *Gitona* Meigen (1830)
[Type, *G. distigma* Meigen (*loc. cit.*), by monotypy, from Central Eurasia. Three additional Palearctic species, *beckeri* Duda, *canariensis* Duda, and *vlasovi* Duda,[4] are known (Duda 1934); three African species, *G. gossypii* Séguy (1933*a*), *G. inornata* Séguy (1933*b*), and *G. paolii* Séguy (1933*b*) (see also Séguy 1934) may belong here. For Nearctic species assigned to *Gitona*, see couplets 12 and 16.]

Facial carina low and more or less linear, not at all nose-like in profile (Fig. 1); dark-brown species with brown legs 14

14. Acrostical setulae in about 15–20 irregular rows; mid coxa with two strong bristles on anterodorsal surface; preapical dorsal tibial bristles undeveloped on all tibiae (Figs.

[1]Dr. F. Mihalyi, Zoological Department of the Hungarian National History Museum, Budapest, kindly informed me (*in lit.*) that the types of *E. fasciata* ("2 ex. N. Guinea Biro 1896, *Erima* Astrolabe B.; *Erima fasciata* Kert. det. Kertesz, typus" according to Duda 1923) are no longer in the Budapest Museum and must be considered as lost.

[2]*Gitona bivisualis* Patterson (1943, p. 35) from southern U.S.A. and Mexico probably belongs here.

[3]*Cacoxenus punctatus* Duda 1924 is a synonym; I determined this by examination of three syntypes from the Berlin Museum. A male labelled "Takao, Formosa, X.26.1907, Sauter; *Cacoxenus punctatus* n. sp., det. Dr. O. Duda", and with the genitalia exposed, is hereby designated as the lectotype.

[4]*Gitona vlasovi* Duda is similar to *Gitonides perspicax* Knab (Figs. 16, 26, 27) in general appearance, but it has no eye band, lacks a pleural stripe and is paler in colour throughout. It agrees with *G. perspicax* in lacking a strong set at the second costal break and in the absence of anterior gonapophyses in the male genitalia, but the surstyli are twisted mesad through 90° on their vertical axes and the ventral margins of same are armed with four or five fully exposed, stout, peg-like setae; in addition the anterior gonapophyses are broader and more blade-like, and the aedeagus is slenderer.

Lectotype designation: Through the courtesy of Prof. A. A. Stackelberg, Zoological Institute, USSR Academy of Sciences, Leningrad, I studied the four syntypes (1 ♂, 3 ♀) of *G. vlasovi* deposited there. The male syntype (District of Ashkhabad, Hilly Sands, Transcaspia, from burrows of *Spermophilopsis leptodactylus* Licht., Vlasov, 24.VI.1933) is hereby designated as the lectotype.

10, 11); male hind metatarsus swollen and bearing a brush of elongate hairs ventrally (Fig. 10) ..... *Cacoxenus* Loew[5] (1858)
[Type and only known species, *C. indagator* Loew (*loc. cit.*), by monotypy, from Europe. For detailed description see Hardy and Wheeler 1960.]

Acrostical setulae in 8–10 irregular rows (Fig. 2); bristles on anterodorsal surface of mid coxae weakly developed, scarcely distinguishable from other setulae; preapical dorsal tibial bristles present, at least on mid tibiae (Figs. 8, 9); male hind metatarsus normal (Fig. 11) ..... *Paracacoxenus* Hardy (*in* Hardy and Wheeler 1960)
[Type, *P. guttatus* Hardy and Wheeler (*loc. cit.*), by original designation, from western North America. For other species of this genus see key below.]

15. Size very small, that is, body length under 2 mm; prescutellar acrostical bristles weak; lower reclinate orbital weak, that is, not or scarcely half as long as upper reclinate orbital bristle; anal vein absent ..... some species of *Baeodrosophila* Wheeler and Takada (1964)
[Type, *B. pubescens* Wheeler and Takada (*loc. cit.*), by original designation, from Caroline Is. Three other species with plumose aristae are described in genus, for key see Wheeler and Takada (*idem*).]

Size large, that is, body length about 3 mm; prescutellar acrostical bristles strong (Fig. 2); lower reclinate orbital bristle about equal in size to upper reclinate orbital; anal vein present 16

16. Mesonotum uniformly yellowish brown; ocellar bristles weak, that is, less than half as long as lower reclinate orbital bristles; mid femur with a series of stout black bristles on basal anterior surface ..... *Hyalistata* Wheeler (1960*a*)
[Type, *H. pictiventris* Wheeler (*loc. cit.*), by original designation, from Mexico. One other species, *H. pallida* Wheeler (*idem*) is known from Trinidad.]

Mesonotum spotted or mottled (Fig. 2); ocellar bristles strong, that is, longer and stronger than lower orbital bristles (Figs. 1, 3), mid femur without outstanding bristles ..... Nearctic species assigned to *Gitona*
[Two species, *G. americana* Patterson (1943, p. 33) and *G. sonoites* Wheeler (1949, p. 158) fall here; it seems unlikely that they are true *Gitona sensu* Meigen (1830) (see couplet 13 above).]

Paracacoxenus Hardy

(Figs. 1, 2, 4, 8, 9, 11–14, 19–23)

Paracacoxenus Hardy, *in* Hardy and Wheeler 1960, p. 358.

DIAGNOSIS. Size small, length 3.0–3.5 mm. Colour dull brown, mesonotum, especially, often with a dark-brown spot at base of each seta (Fig. 2). Wings uniformly hyaline.

Head (Fig. 1) higher than long. Compound eye high-oval, ostensibly bare, uniformly coloured. Cheek fairly broad to nearly linear. Oral vibrissa moderately strong, remaining oral setulae relatively weak. Facial carina rather low and narrow, not nose-like as in many drosophilids. Prelabrum (tormae) moderately broad, distance between anterior and posterior margins fully as great as distance between bases of ocellar bristles. Parafacials linear. Frontal orbit with three orbital bristles on upper half of frons, that is, with two nearly equal-sized reclinate orbital bristles, and a similar-sized proclinate orbital bristle arising below the lower reclinate one; in addition orbits with a series of fine reclinate setulae extending from lower limits to about midway between bases of proclinate orbital bristle and lower reclinate orbital bristle. Ocellar bristles about equal in size to frontal and vertical bristles, directed anterolaterally. Ocellar plate with 8–10 anterolaterally directed ocellar setulae arranged in two irregular rows mesad of the ocelli. Inner and outer vertical bristles subequal to each other and to the ocellar bristles. Postvertical bristles weak, convergent. Postocellar bristles very weak, divergent. Frons broad, somewhat narrowed anteriorly. Frontal vitta

[5]*Paragitona* Kröber (1912) [Type, *P. obscura* Kröber (*loc. cit.*) (= *C. indagator* Loew), by monotypy] is a synonym (Duda 1934). According to D. G. Morge (*in lit.*) Kröber's types in the Hamburg Museum were probably destroyed in World War II.

sparsely setulose. Lunule small, apparently bare. Second antennal segment (as in all drosophilids) with a well-developed longitudinal seam along dorsolateral surface. Third antennal segment scarcely longer than broad. Arista finely and densely micropubescent; penultimate segment slightly longer than broad. Maxillary palpus moderately small. Proboscis short, labellae fleshy.

Mesonotum (Fig. 2) less humped than in most drosophilids, brown in ground colour with each setula and bristle arising from a dark spot, frequently heavily pollinose, the pollen denser and usually more or less silvery in males. Uniformly setulose, with 8–10 rather irregular rows of acrostical setulae between the dorsocentral series. Chaetotaxy as follows: one humeral, one posthumeral, two notopleurals, two supraalars, two dorsocentrals, one prescutellar acrostical, two scutellars, the lateral one arising about half way between apical one and base of scutellum. Proscutellum undeveloped. Propleural bristle very weak. Mesopleuron and pteropleuron bare. Sternopleuron with two strong bristles near dorsal margin and a single bristle at extreme posteroventral corner; above the latter with a row of setulae extending dorsad to point between the two dorsal bristles.

Bristles of all coxae relatively weak, laterodorsal bristles often undeveloped on mid coxae. Femora setulose but without outstanding bristles. Preapical dorsal tibial bristle present on mid tibia (Fig. 9); frequently weak or absent on remaining tibiae (Fig. 11). Tarsi unmodified (Figs. 8, 9, 11).

Wing (Fig. 4) uniformly hyaline. Costa extending to m_1 (4th vein), although much weaker beyond r_{4+5} (3rd vein); without an outstanding setulae at second costal break. Cross vein *r-m* (anterior crossvein) near middle of discal cell. First basal cell and discal cell separated by a crossvein. Last section of *cu* (5th vein) but little longer than posterior crossvein.

Abdomen (Figs. 12–15, 19–23) weakly patterned; terga 1–5 paler brownish anteriorly than posteriorly, but the different shades not strongly contrasting; with six functional spiracles in both sexes.

In male, syntergum preceding epandrium (terga 6–8 ?) frequently with a spinous process at posterior corners (Figs. 19–22). Surstylus free and moveable. Aedeagus elongate. Anterior gonopophyses elongate, with spatulate or club-shaped apices. Posterior gonopophyses bifurcate. Cerci simple.

Female with two spermathecae. Ovipositor blade triangular in side view with smooth ventral margin and rounded apex.

REMARKS. As indicated above, *Paracacoxenus* species are most likely to be confused with those of *Cacoxenus* and *Gitonides*. In addition to the differences mentioned in the key, all members of *Paracacoxenus* examined differ from *Cacoxenus indagator* and *Gitonides perspicax* in having a much broader prelabrum (Fig. 1) (sublinear in *C. indagator* and *G. perspicax*), simple hind metatarsi in both sexes (Fig. 11) [swollen with a ventral comb in male of *C. indagator* (Fig. 10); first three segments of hind tarsi with coarsely serrated ventral comb in male of *G. perspicax*], an enlargement or prolongation at posterior corner of the pregenital syntergum (Figs. 19–22) (absent in *C. indagator* and in *G. perspicax*), an elongate, tube-like aedeagus (Figs. 19–22) [short, rather boat-shaped in *C. indagator* (Figs. 24, 25) and *G. perspicax* (Figs. 26, 27)], an elongate rather club-shaped anterior gonapophysis (Figs. 19–23) [short and evenly tapered in *C. indagator* (Figs. 24, 25) and in *G. perspicax* (Figs. 26, 27)], and a forked posterior gonite (Figs. 19–23) [simple in *C. indagator* (Figs. 24, 25) and in *G. perspicax* (Figs. 26, 27)].

Four species, *P. guttatus* Hardy and Wheeler from North America, and *P. argyreator* Frey (new combination), *P. exiguus* Duda (new combination), and *P. inquilinus* Hendel (new combination) from Europe belong to this genus.

The only information known about the immature stages of *Paracacoxenus* species is that obtained by Powell (Powell, in preparation) for *P. guttatus*.

Key to *Paracacoxenus* Species

1. Mesonotum uniformly subshining dark brown; knob of halter brownish ..... *exiguus* Duda (Silesia)
   Mesonotum greyish pollinose with dark-brown spots at base of each hair (Fig. 2); halter white 2
2. Posterior reclinate orbital bristle arising much nearer to anterior reclinate orbital than to inner vertical bristle ..... *inquilinus* Hendel (Austria)
   Posterior reclinate orbital bristle arising slightly nearer to inner vertical bristle than to anterior reclinate orbital 3
3. Ocellar plate (mesad of ocelli) with two or three pairs of divergent setulae (Fig. 3); male with extremely long preapical dorsal tibial bristle on mid tibia (Fig. 8) ..... *argyreator* Frey (Scandinavia)
   Ocellar plate with four or five pairs of divergent setulae (Fig. 1); preapical dorsal tibial bristle of mid tibia very short in both sexes (Fig. 9) ..... *guttatus* Hardy and Wheeler (Western North America)

✓ *Paracacoxenus guttatus* Hardy and Wheeler

(Figs. 1, 2, 4, 9, 11, 12, 15, 19, 20)

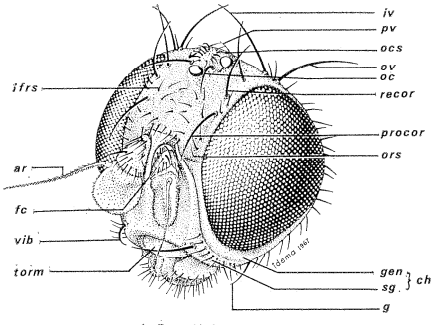
Paracacoxenus guttatus, Hardy and Wheeler, 1960, p. 358–359; Wheeler, 1965, p. 762; Hardy, 1965, p. 36.

Cacoxenus species, Wheeler, 1952*a*, p. 173.

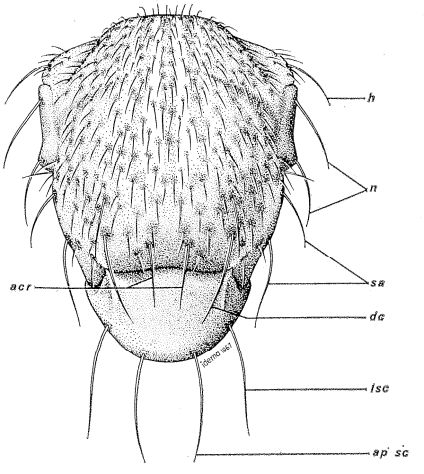
Diagnosis. Male: Mainly greyish brown with brown legs; mesonotum silvery or somewhat golden in some lights. Frons (Fig. 1) dull chocolate-brown, with slightly paler orbital plates; strongly narrowed anteriorly, about 1.3 times as wide at anterior ocellus as at lunule. Proclinate orbitals, ocellars, and vertical bristles subequal in size; reclinate orbitals weaker, the lower reclinate weakest; postverticals very weak, convergent postocellars extremely weak, divergent; upper reclinate orbital arising slightly nearer to inner vertical than to lower reclinate; with five or six reclinate intraorbital setulae, the uppermost one or two arising between the bases of the proclinate orbital and the lower reclinate orbital. Ocellar plate with two irregular rows of four or five tiny, divergent setulae.

Figs. 1, 3, 5, 7. Anterolateral views of heads of *Paracacoxenus guttatus* (♂), *Gitona sonoites* (♂), *Mayaguesa argentifera* (redrawn from Wheeler 1960), and *Acletotoxenus formosus* (♀).
Fig. 2. Dorsal view of thorax of *P. guttatus* (♂).
Figs. 4, 6. Dorsal views of right wing of *P. guttatus* and *Pseudiastata nebulosa*, respectively.
Figs. 8, 9. Anterior views of mid legs of *Paracacoxenus argyreator* (♂) and *P. guttatus* (♂), respectively.
Figs. 10, 11. Anterior views of hind legs of *Cacoxenus indagator* (♂) and *P. guttatus* (♂), respectively.

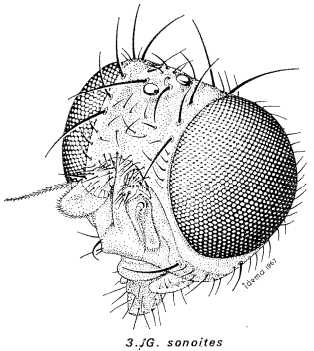
(Abbreviations: *acr*, prescutellar acrostical bristle; *an*, anal vein; *ap sc*, apical scutellar bristle; *ar*, arista; B_1, first basal cell (= 1st M_2); B_2, second basal cell; *ch*, cheek; *cu*, cubital vein; *dc*, dorsocentral bristles; *Disc*, discal cell (= 2nd M_2); *fc*, facial carina; *g*, genal bristle; *gen*, gena; *h*, humeral bristle; *ifrs*, interfrontal setulae; *iv*, inner vertical bristle; *lsc*, lateral scutellar bristle; m_1, first branch of median vein; *n*, notopleural bristles; *oc*, ocellar bristle; *ocs*, ocellar setulae; *ov*, outer vertical bristle; *ors*, orbital setulae; *pdt*, preapical dorsal tibial bristle; *pmet*, posterior metatarsus; *procor*, proclinate orbitals; *pv*, postvertical bristle; r_1, r_2, r_{4+5}, first, second, etc. branch of radial vein; *recor*, reclinate orbital bristle; *sa*, supraalar bristles; *sc*, subcostal vein; *sg*, subgena; *ta*, anterior crossvein; *torm*, tormae or prelabrum; *tp*, posterior crossvein; *vib*, oral vibrissa.)



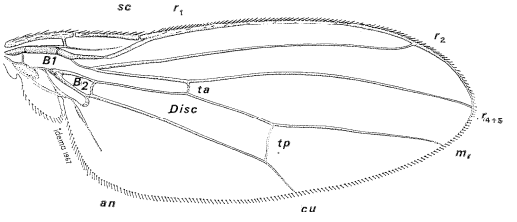
1. P. guttatus



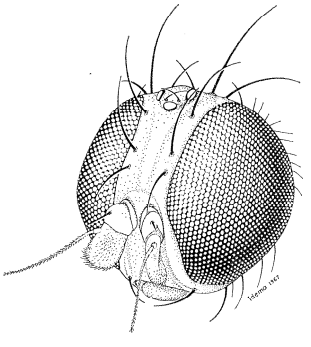
2. P. guttatus



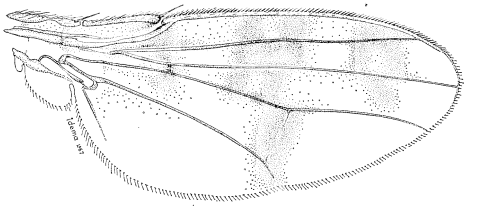
3. G. sonoites



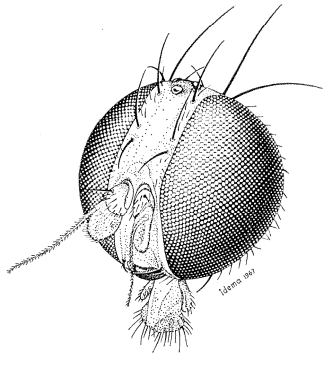
4. P. guttatus



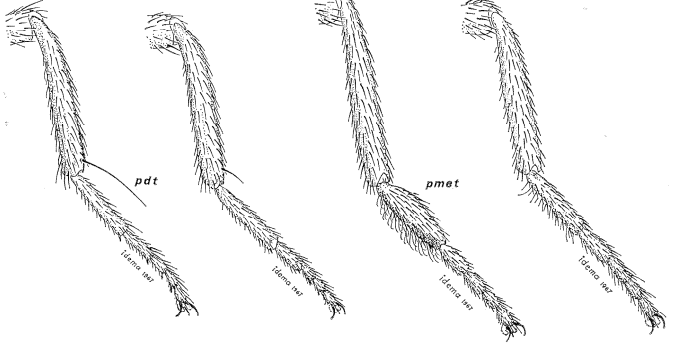
5. M. argentifera



6. Pseud. nebulosa



7. A. formosus



8. P. argyreator 9. P. guttatus 10. C. indagator 11. P. guttatus

Parafacials sublinear. Facial carina about as wide as narrowest part of parafacial, very low. Prelabrum moderately broad, about equal in width to distance between posterior ocelli. Cheeks slightly broader than prelabrum. Oral vibrissa about same size as proclinate orbital; preceded by eight or nine tiny orbital setulae, the largest being scarcely one-fourth as long as oral vibrissa. Third antennal segment slightly longer than broad; mostly brown, but paler yellowish-brown at inner base. First and second antennal segments yellowish brown. Dorsal bristle of second antennal segment about equal in size to postvertical bristle. Arista a little less than three times as long as third antennal segment; micropubescence very short; penultimate segment about 1.5 times as long as wide. Palpus yellowish brown; small, about as broad as prelabrum.

Mesonotum (Fig. 2) and scutellum brownish grey with a distinct silvery lustre in anterodorsal views. Uniformly setulose, but the setulae short, depressed, and rather sparse; with about eight rows of acrostical setulae between anterior dorsocentral bristles. Prealar bristle weak, that is, about half as large as prescutellar acrosticals. Each bristle and setula of mesonotum and scutellum arising from small dark-brown spot. Lateral scutellar bristles arising about same distance from apical scutellars as distance between bases of latter, and about the same distance from base of scutellum. Thorax in side view mostly brown with three poorly defined, dark-brown pleural stripes as follows: a median stripe running from propleuron through centre of mesopleuron and pteropleuron to base of halter, a dorsal stripe running through the notopleuron to base of wing, and a ventral one passing along dorsal margin of sternopleuron. Propleural bristle present, but extremely weak. Sternopleuron with two, equally strong dorsal bristles; usually with one setula in front of anterior sternopleural, and with two similar setulae between the two dorsal bristles; extreme posteroventral corner with a weak bristle, this bristle being the lowermost of a vertical row of setulae which extends dorsad to the dorsal sternopleural bristles.

Legs and tarsi (Figs. 9, 11) brown, without bands or other outstanding features. Preapical dorsal bristle of mid tibia about equal to postvertical bristles; these bristles not or scarcely distinguishable on front and hind tibiae. Hind metatarsus with numerous, rather stout, straw-coloured setulae on ventral surface.

Wings (Fig. 4) clear with brownish veins. Proportions of costal sections 1 to 5 as follows: 3.0:3.5:12.0:4.0:2.25. Last section of m_1 about twice as long as penultimate section (8.1:4.0). Apical section of *cu* about 1.25 times as long as hind crossvein (1.75:2.2). Halter entirely white.

Abdomen dull-brown; each tergum narrowly yellowish along posterior margins. Spine-like process at posterolateral margin of syntergum 6+7 short and rather triangular (Figs. 19, 20); tergum 5 with a blunt protrusion at same place.

Genitalia (Figs. 19, 20). Epandrium rather triangular in lateral view, the sides very narrow; with several setulae on middorsal surface. Surstylus short

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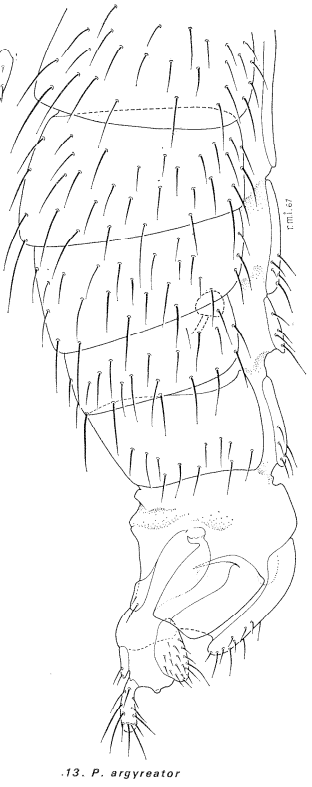
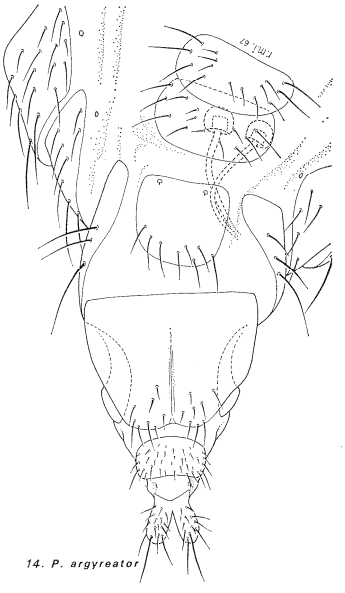
FIGS. 12, 15. Right lateral and ventral aspects, respectively, of female abdomen of *Paracacoxenus guttatus*.
FIGS. 13, 14. The same of *P. argyreator*.
FIG. 16. Ventral aspect of female abdomen of *Gitonides perspicax*.
FIGS. 17, 18. Right lateral and ventral aspects, respectively, of female abdomen of *Cacoxenus indagator*.

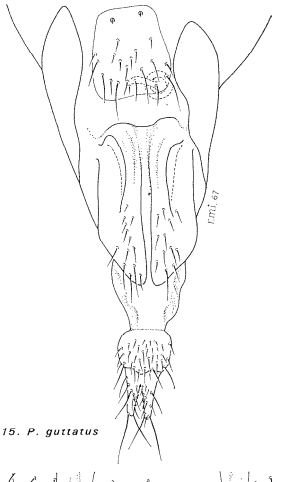
12. P_2 guttatus



13. P. argyreator



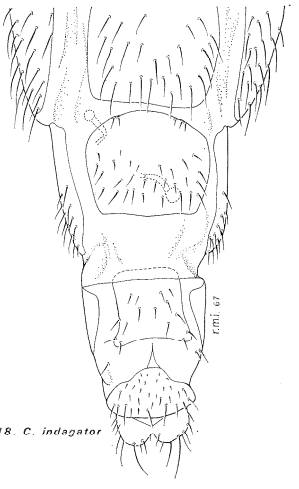
14. P. argyreator



15. P. guttatus

16. G. perspicax

17. C. indagator



18. C. indagator

and broad; not as long from base to apex as wide at base; with numerous fine setulae along apical margin. Hypandrium U-shaped; each side with a hinge-like articulation near base. Anterior gonopophysis long and slender; pale with capitate apex; arising from the hypandrium where latter is hinged. Anterior gonopophysis two-branched; anterior branch larger and shorter, curved downward, forward and outward; posterior branch longer and slenderer; directed first posteriorly and then outward; base of each anterior gonopophysis arising from a median plate that connects with bases of surstyli and cerci. Aedeagus elongate with a right angle bend near the middle; apex flared and somewhat asymmetrical.

Female: Agreeing with male except as follows: darker in colour throughout, the brown spots at the base of each bristle and hair larger. Mesonotum and scutellum without silvery lustre. Bristle at posteroventral corner of sternopleuron stronger. With two mushroom-shaped spermathecae (Figs. 12, 15). Genitalia as in Figs. 12, 15. Ovipositor blade triangular in lateral view, the ventral surface longer than either of the other two margins; with numerous fine setulae along apical margins. Cerci short and weakly sclerotized; with several outstanding hairs at apex.

REMARKS. This species is closely related to *P. argyreator* (Frey) from Europe but is larger in size and darker in colour. The male has a much shorter preapical tibial bristle on the mid tibiae, is less intensely silvery pollinose on the mesonotum, and has very different genitalia (see below).

Detailed information on the immature stages and biology of this species is being prepared for publication by J. M. Powell.

MATERIAL EXAMINED. 32 adults, 17 larvae, and 10 puparia as follows: 1 ♂, 1 ♀, (paratypes) Wenatchee, Wash., 5 Aug. 1951, M. R. Wheeler. 8 ♂, 4 ♀, Ribbon Creek, Kananaskas Forest Reserve, Alta., 8 Mar. 1965, reared ex log of *Pinus contorta* infested with *C. commandrae*, collection No. 64A1151, J. Powell. 2 ♀, 13 larvae, 1 puparium, Wedge, Bow River Forest Reserve, Alta., 28 July 1966, ex *Pinus contorta* infested with *C. commandrae*, collection No. 1427, J. Powell. 2 ♀, 5 larvae, 7 puparia, same data but collected 10 Aug. 1966, collection No. 1428. 1 larva and 1 puparium, same data but collected 17 Aug. 1966, collection No. 1436. 2 ♀, 1 larva, Marmot Creek, Alta., collected 10 Aug. 1966, on same host, collection No. 1438. 1 puparium, same data, but collected 30 Sept. 1966, collection No. 1435. 3 ♀, Kananaskas Forestry Experiment Station, Kananaskas Forest Reserve, Alta., 16 Aug. 1966, visiting pycnia of *C. commandrae* on *P. contorta*, collection No. 1423, J. Powell. 1 ♂, 1 ♀, 15 mi SSW. of Seebe, Alta., reared ex puparia from *P. contorta* infested with *C. commandrae*, collected 17 Oct. and 17 Aug. 1966 respectively, emerged 1 Feb. 1967, collection Nos. 1432 and 1436 respectively, J. Powell. 1 ♂, 1 ♀, Summit Lake, B.C., Mile 1392 Alaska Hwy., 21 July 1959, 4200 ft R. E. Leech.

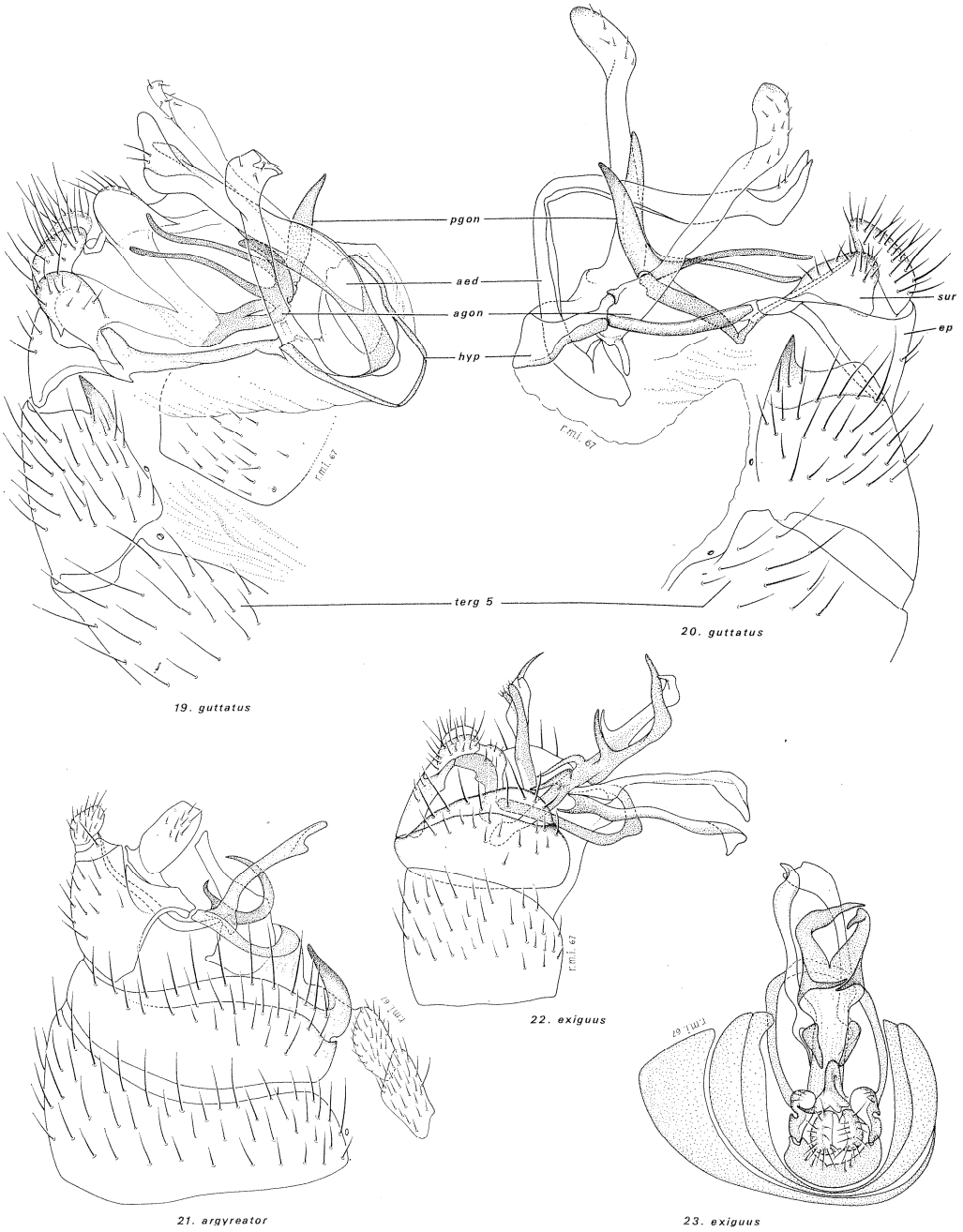
Holotype (♂, Olympic National Forest near Sequim, Wash., in U.S. National Museum). Not seen.

Paracacoxenus argyreator (Frey) new combination

(Figs. 8, 13, 14, 21)

Cacoxenus argyreator Frey 1932, p. 84; Duda 1934, p. 23; Basden 1956, pp. 9, 11; Basden and Harnden, 1956, 160; Hardy and Wheeler, 1960, p. 356.

DIAGNOSIS. Male: Similar to *P. guttatus*, but with following differences: Slightly smaller in size. Paler in colour; mostly greyish with pale brownish undertones. Frons yellowish brown with grey orbital plates and ocellar plate;



FIGS. 19, 20. Left and right lateral views, respectively, of male genitalia and terminal abdominal segments of *Paracacoxenus guttatus*.
FIG. 21. Left lateral view of male genitalia and terminal abdominal segments of *P. argyreator*.
FIGS. 22, 23. Left and caudal views, respectively, of male genitalia and terminal abdominal segments of *P. exiguus*.

(ABBREVIATIONS: *aed*, aedeagus; *agon*, anterior gonopophysis; *ep*, epandrium; *hyp*, hypandrium; *pgon*, posterior gonopophysis; *sur*, surstylus; *terg 5*, fifth abdominal tergum).

weakly narrowed anteriorly, about 1.2 times as wide as lunule as at anterior ocellus; orbital setulae and interfrontal setulae sparser but somewhat stronger. Mesonotum and scutellum much more intensely silvery grey; brown flecks at bases of setulae and bristles scarcely evident. Setulae somewhat stronger and more erect. Apical scutellar bristles slightly closer to each other than to basal scutellars. Thorax in side view paler greyish-brown, pleural stripes not evident.

Preapical dorsal bristle of mid tibia extremely long, that is, as long as mid metatarsus (Fig. 8).

Wing clear with paler yellowish-brown veins. Proportions of costal sections 1–5 as follows: 3.0:3.25:12.0:3.5:2.0. Last section of *m* well over twice as long as penultimate section (7.75:3.5). Apical section of *cu* about equal to hind crossvein. Halter entirely creamy-white.

Abdomen (Fig. 21) with spine-like process at posterolateral margin of syntergum 6+7, much longer and more sickle-shaped. Fifth tergum lacking a protuberance at this position, but sixth tergum with a short point protruding beyond base of the large sickle-shaped spine on the following tergum.

Genitalia (Fig. 21) with epandrium longer and with many more setulae dorsally; sides broader; with one suture running anterodorsally from base of surstylus and another near posterior margin separating a small bristle-bearing sclerite from the main body of the epandrium. Surstylus about twice as long as broad at base, rectangular in side view. Anterior gonopophysis shorter and stouter; apical portion somewhat less expanded but more emarginate. Posterior gonopophysis with anterior branch strongly sickle-shaped; posterior branch shorter than anterior branch and more sharply curved at apex than in *P. guttatus*. Aedeagus much shorter with much more swollen base; apex much simpler and more nearly symmetrical.

Female: Much less silvery tomentose than in the male, the mesonotum thus appearing very similar to that of *guttatus* female. In the genitalia (Figs. 13, 14) the 8th sternum is not so strongly modified as in female of *guttatus*; whereas it is clearly divided mesally to form two triangular ovipositor blades in *guttatus*, it is only slightly weakened along the midline in *argyreator*.

Preapical dorsal bristle of mid tibia much shorter than in the male, that is, very similar to condition in *guttatus* male and female (Fig. 9).

REMARKS: *P. argyreator* is more closely related to *guttatus* than to any other species, but is readily distinguished by the differences outlined. The species is known only from Finland and Norway.

Frey (1932) originally found it in considerable numbers on Lepidoptera bait at Tvarminne, southwest Finland, from 25 June to 7 July 1932; three other specimens were taken at Lojo on aspen catkins 22–30 June 1932. Basden and Harnden (1966) captured one female at Furflaten, Norway, 11–18 July 1953, in a trap baited with apple and set near the ground in an alder thicket in the gulley of a small stream (alt. 650 ft).

SPECIMENS EXAMINED AND DESIGNATION OF A LECTOTYPE: In the Frey Collection, University of Helsinki, are many specimens from Tvarminne, including the four type specimens Nos. 4831–4834 listed in Frey's (1932) description. Type No. 4831, a male, is hereby designated as the lectotype.

In addition I examined a single male from Karislojo, Finland (R. Frey, No. 1044) and another from Ruotsinkyla, Kunsen, Kavijista, 19–20 June 1942, Talivonen.

Paracacoxenus exiguus (Duda) new combination

(Figs. 22, 23)

Cacoxenus exiguus Duda, 1924, p. 225; 1934, pp. 24–25; Séguy, 1934, p. 372; Kloet and Hincks, 1945, p. 400; Hardy and Wheeler, 1960, p. 356.

DIAGNOSIS: Male: Head mainly black; thorax and abdomen uniformly dark brown; length 2.0–2.5 mm. Face about as long as distance between bases of vibrissae; in profile dropping in a straight line to oral margin; facial carina rather sharp but not nose-like. Frons velvety-black, longer than broad, narrowing toward lunule. Ocellar triangle and orbital plates sharply delimited; dull blackish-grey; ocellar triangle about one-third as long as frons; orbital plates adjoining compound eyes, narrow and about two-thirds as long as frons. Ocellar bristles slightly longer than orbital bristles, but slightly shorter than vertical bristles. Orbital bristles subequal; proclinate orbital arising just before middle of frons; anterior reclinate orbital closer to posterior reclinate orbital than to proclinate orbital; posterior reclinate orbital closer to inner vertical than to anterior proclinate orbital. Postverticals very fine and short. Compound eyes practically bare; under high magnification with some very fine, short, scattered pubescence. Cheek much narrower than width of third antennal segment. Vibrissa about three times as long as following oral setulae. Proboscis short; blackish with pale labellae. Palpus small, black. Antenna predominantly black; basal segments brownish; third segment nearly round, slightly shorter than broad, distinctly but shortly pubescent. Arista densely but shortly pubescent.

Mesonotum, scutellum, and pleura uniformly subshining blackish-brown, very lightly brownish pollinose. Mesonotum densely covered with short, black setulae. Anterior dorsocentral bristles about equal in size and strength to prescutellar acrosticals, arising slightly closer to posterior dorsocentrals than the latter are to the prescutellars. Humeral bristle strong, with several fine setulae preceding it. Anterior and posterior notopleural bristles considerably stronger than presutural or posthumeral and prealar bristles. Supraalar bristle weaker than anterior postalar, but slightly stronger than posterior postalar. Scutellum slightly more than half as long as broad, gently rounded posteriorly, lightly greyish pollinose, and lacking setulae. Scutellar bristles strong, arising at equal intervals.

Legs variably coloured, but predominantly brown. Femora, tibiae, and tarsi often darkened to entirely black. Anterior femur with numerous long setae on posterodorsal and posteroventral surfaces. Preapical dorsal bristle strong on mid tibia, weak on anterior tibia, and not or scarcely distinguishable on hind tibia. Each metatarsus about equal in length to combined length of the three following segments; hind metatarsus with extremely short setulae.

Wings hyaline with dark-brown veins, rather narrow. Costa barely reaching m_1. Proportions of costal sections 2–5 inclusive about 5.0:2.0:1.0:3.4. Vein r_2 gently convex in middle, apex slightly curved toward costa. Vein r_{4+5} very convex in middle, terminating closer to apex of wing than does m_1. Apical section of m_1 quite straight, fully twice as long as distance between anterior and posterior crossveins. Anterior crossvein near middle of discal cell. Distance between anterior and posterior crossveins about twice as long as posterior crossveins and slightly longer than apical section of *cu*. Anal vein fading about half way to wing margin. Halter distinctly brown in some specimens, yellowish brown in others.

Abdomen feebly shining dark-brown, terga without grey posterior margins. Terga 1–5 about equal in length. Terga 6 and 7 (Fig. 22) closely joined, the former three or four times as broad in side view as the latter; posteroventral angles enlarged but not forming elongate spinous processes on either side.

Genitalia (Figs. 22, 23). Epandrium very small, with greatly reduced surstyli. Anterior gonapophyses yellow with enlarged apices much as in *P. guttatus*. Posterior gonapophyses black, bases fused and continuous with aedeagal apodeme, apex of each with an elongate posteromesally directed spine, proximad of which is a smaller mesally directed spine. Aedeagus asymmetrical at apex, terminating with a long slender spine arising from left side.

Female: Agreeing with male except in usual sexual characters. Anal lamellae covered with long, wavy hairs, and seemingly very similar to those of *P. guttatus*.

REMARKS. This species is the smallest of the *Paracacoxenus* species studied and it is the darkest in colour. The absence of dense grey bloom with darker brown spots at the base of each hair on the mesonotum are useful diagnostic features. The male genitalia are extremely distinctive; the greatly reduced surstyli and the absence of spine-like prolongations at the posterolateral angles of the sixth and seventh abdominal terga are particularly noteworthy features.

SPECIMENS EXAMINED AND DESIGNATION OF A LECTOTYPE: This species was described from Silesia (Duda 1924) and it is recorded from the British Isles (Kloet and Hincks 1945). Through the courtesy of Dr. C. Morge, Deutsches Entomologische Institut, Berlin, I have examined six cotypes [5 ♂ and 1 ♀, Wustung b. Habelschwerdt, 8 May 1921 (1 ♂), 2 June 1922 (1 ♀), 6 May 1923 (2 ♂), 21 May 1923 (1 ♂), 31 May 1923 (1 ♂)], and one other male (27.5.29, locality unknown, wings and abdomen missing) from the Berlin Museum. All are determined as *Cacoxenus exiguus* Duda in Duda's handwriting. They all appear to belong to the same species, and I hereby designate the first specimen, the male collected 8 May 1921, as the lectotype.

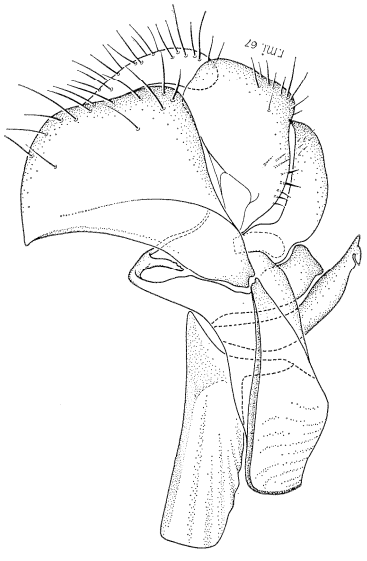
✔ *Paracacoxenus inquilinus* (Hendel) new combination

Cacoxenus inquilinus Hendel, 1933, p. 46; Hardy and Wheeler, 1960, p. 356.

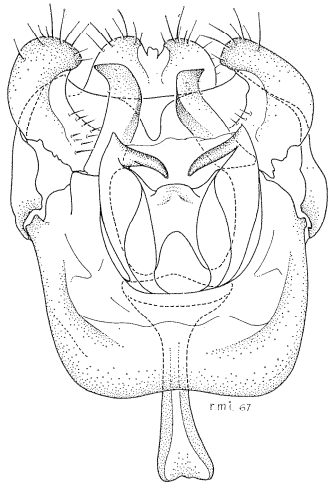
DIAGNOSIS. Male (adapted from Hendel (1933)): General colour peach-brown, with reddish-brown abdomen and legs. Brown spots at bases of setulae and bristles apparently indistinct or absent. Length, 2.0 mm.

Frons about as long as wide; reddish brown anteriorly. Frontal vitta dull; ocellar plate and orbital plates somewhat shiny. Posterior reclinate bristle arising much nearer to anterior reclinate bristle than to inner vertical. Facial carina rather weakly developed; not nose-like. Third antennal segment large and rounded; inner surface slightly longer than second antennal segment; brownish; covered with dense pubescence. Basal segments paler reddish-brown. Arista short, scarcely as long as antenna; little thickened at base and densely but very shortly pubescent. Proboscis short. Mesonotum and scutellum rather thinly greyish pollinose; without distinct brown spots at bases of setulae and bristles.

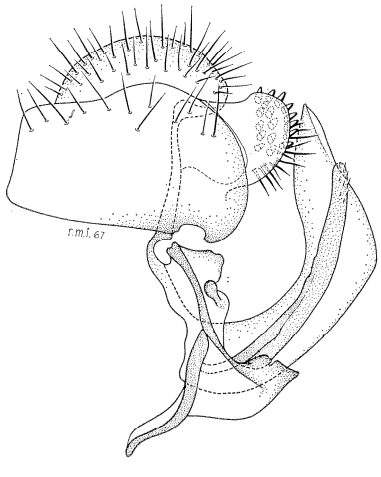
FIGS. 24, 25. Left lateral and ventral aspect, respectively, of male genitalia of *Cacoxenus indagator*.
FIGS. 26, 27. Same of *Gitonides perspicax*.
FIGS. 28, 30. Same of *Acletotoxenus formosus*.
FIG. 29. Details of processes at base of aedeagus of *A. formosus*, as seen from body cavity looking into base of aedeagus.



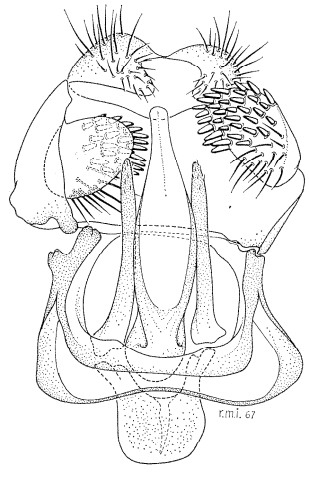
24. C. indagator



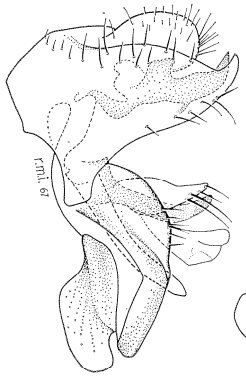
25. C. indagator



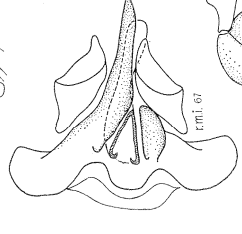
26. G. perspicax



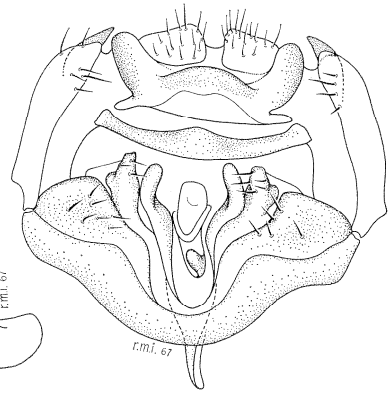
27. G. perspicax



28. A. formosus



29. A. formosus



30. A. formosus

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