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A revision of the former family Pseudopomyzidae (Diptera, Acalyptratae, Cypselosomatidae)

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Abstract

former family Pseudopomyzidae Morphological characters and multiple genes are used to assess relationships among the families of Nerioidea, concluding that the family Pseudopomyzidae as currently defined is paraphyletic with respect to Cypselosomatidae Hendel; the family Cypselosomatidae is therefore redefined to include the Pseudopomyzidae. The subgeneric classification of the large genus Pseudopomyza Strobl is updated by synonymizing the subgenera Macalpinella Papp and Rhinopomyzella Hennig with Pseudopomyza s.s., and reinstating the subgenus Heluscolia (Harrison), resulting in four valid subgenera: Apops McAlpine, Dete McAlpine, Heluscolia and Pseudopomyza s.s. The subgenus Apops is composed of two previously included species (P. flavitarsis (Harrison) (New Zealand) and P. arenae McAlpine (Australia, Tasmania)) and three new species (P. chilensis Yau and Marshall (Chile), P. medianentis Yau and Marshall (Australia, Western Australia) and P. nigritarsis Yau and Marshall (New Zealand)). The subgenus Dete includes P. collessi McAlpine (Australia). The subgenus Heluscolia includes P. antipoda (Harrison) and P. brevis (Harrison), both from the New Zealand Subantarctic Islands. The subgenus Pseudopomyza includes P. aristata (Harrison) (New Zealand), P. atrimana (Meigen) (Palaearctic), P. brevicaudata (Harrison) (New Zealand), P. brevifacies (Papp) (Oriental and Palaearctic) and the P. nigrimana species group (formerly treated as the subgenus Rhinopomyzella). The P. nigrimana species group, shown here to be the sister group to P. atrimana, includes P. albimana (Hennig), P. nigrimana (Hennig) and fifteen new species (P. adunca Yau and Marshall, P. ampliata Yau and Marshall, P. angustifrons Yau and Marshall, P. binaevia Yau and Marshall, P. brunneicacumen Yau and Marshall, P. cordata Yau and Marshall, P. cyathiformis Yau and Marshall, P. flavicacumen Yau and Marshall, P. gambiformis Yau and Marshall, P. inflexa Yau and Marshall, P. machaera Yau and Marshall, P. parabinaevia Yau and Marshall, P. proboscis Yau and Marshall, P. prolata Yau and Marshall, P. simulatrix Yau and Marshall).

Key words: Taxonomy, phylogeny, comparative morphology, molecular analysis, new species

Introduction

Pseudopomyzids are small to medium-sized acalyptrate flies, with body lengths between 1.5–5.5 mm and a general habitus ranging from stout to slender. The larger species of *Heloclusia* Malloch and *Latheticomyia* Wheeler superficially resemble heleomyzids and neriids respectively, while the smaller species of *Pseudopomyza* Strobl and *Pseudopomyzella* Hennig are more similar to clusiids, drosophilids and ephydrids. All of the genera traditionally treated as Pseudopomyzidae differ from the above families by the following combination of characters:

Two to four pairs of fronto-orbital setae, distinct vibrissae. Face ventromedially desclerotized to various

degrees (Figs. 9.3, 12.1, 27.3, 101.3). Thorax with at least four pairs of dorsocentral setae (Figs. 9.2, 12.3, 27.2, 101.2). Femora with ventrobasal seta. Wing cells bm and dm often confluent (Figs. 9.1, 12.3, 27.2, 101.2). Abdominal tergite 6 large in both sexes; male sternite 6 with strong arcuate sclerotization (Figs. 10.2, 13.2, 28.2, 31.2, 39.1, 102.2), phallic plate complete and close to phallus (Figs. 10.4, 13.4, 39.4, 102.5); female tergite and sternite 7 fused and forming a sclerotized oviscape; usually with 1+1 spermathecae, sometime 1+2 or 0+1.

The family Cypselosomatidae is often considered to be the sister group to Pseudopomyzidae. The genera of Cypselosomatidae s.s. (Clisa (Australia), Cypselosoma (Oriental and Palaearctic) and Formicosepsis (Oriental and Palaearctic)) differ from the genera traditionally treated as Pseudopomyzidae in having an interfrontal seta (exceptions in Formicosepsis), a ridge on the katepisternum forming a shelf on the dorsal surface, M₄ extending at most only slightly past dm-m, posterodistal corners of cell dm rounded, and a pair of outstanding setae on S7+8.

The family Pseudopomyzidae as traditionally defined, excluding the Cypselosomatidae s.s., is composed of six extant genera and one fossil genus, arranged into three probable monophyletic groups by McAlpine (1996): Group 1, *Latheticomyia* Wheeler (New World) and *Tenuia* Malloch (Palaearctic and Oriental); Group 2, *Heloclusia* Malloch (Chile), *Polypathomyia* Krivosheina (eastern Palaearctic) and *Pseudopomyza* Strobl (Palaearctic, Oriental, Australasian and Neotropical); Group 3, *Pseudopomyzella* Hennig (Neotropical) and *Eopseudopomyza* Hennig (Baltic amber).

Biology

Pseudopomyzidae are found worldwide except for the Afrotropical region and occur at a wide range of elevations. They are generally uncommon and little is known of their biology (McAlpine & Shatalkin, 1998) although we here record numbers of Pseudopomyza flavitarsis (Harrison) from recently cut hardwood stumps in New Zealand, and adults of Pseudopomyza Strobl have been reported from decomposing plant material (Harrison, 1976; Roháček, 1981; Papp, 1998; Belgers, 2010). Roháček (2012a, 2012b) noted a mass occurrence of P. atrimana Meigen adults, many of which were in copula, on a large pile of grass clippings. Schacht (1997) and Stuke (2009) report the same species from umbelliferous flowers and Frey (1952) documented P. atrimana adults gathering over fallen logs in Finland. Harrison (1976) found Pseudopomyza brevis (Harrison) and Pseudopomyza antipoda (Harrison) in seabird nests and carrion, and under plant litter; P. antipoda specimens were also found near seal or sea-lion wallows and kelp; Pseudopomyza brevicaudata (Harrison) was collected in a fowl yard. McAlpine (2019) collected Pseudopomyza arenae McAlpine in dunes densely penetrated by burrows of penguins (Eudyptula minor) and shearwaters (Puffinus sp.) on Bruny Island, southern Tasmania. Most specimens

of the *Pseudopomyza nigrimana* species group in the University of Guelph Insect Collection were collected in pan traps or swept near fallen trees.

Larvae of Polypathomyia stackelbergi Krivosheina have been found under bark or roots of rotten deciduous trees (Krivosheina, 1979, 1984) and large numbers were found swarming around small vertebrate carcasses (McAlpine and Shatalkin, 1998). Some specimens of Pseudopomyzella Hennig were collected near tree falls and kitchen compost. Tenuia smirnovi Shatalkin has been collected in a locality overgrown with willow and was also recorded on willow sap and rotten fig fruit (McApline and Shatalkin, 1998; Yatoo et al., 2022). Latheticomyia tricolor Wheeler and L. lineata Wheeler were collected from banana-baited trap cans set out for Drosophila (Wheeler, 1956). Several Latheticomyia Wheeler specimens at the University of Guelph Insect Collection were collected in dung-baited traps set out to collect Sphaeroceridae, often near waterways. A female Heloclusia specimen at the University of Guelph Insect Collection was photographed and collected by the second author on a carrion trap (chicken feet) in southern Chile (Fig. 9.5).

Classification of Pseudopomyza

Buck and McAlpine (2010) defined the genus Pseudopomyza to include 12 species organized into five subgenera, Pseudopomyza s.s. (Palaearctic, Oriental and Australasian), Rhinopomyzella Hennig (New World), McAlpine (Australasian), Dete McAlpine (Australasian) and Macalpinella Papp (Oriental). However, the phylogenetic analysis herein shows that the existing subgeneric classification does not accurately reflect the species relationships within *Pseudopomyza*. The subgeneric classification is therefore updated here to include only four subgenera, resulting from two new synonymies (Macalpinella and Rhinopomyzella synonyms of Pseudopomyza) and one resurrected taxon (Heluscolia).

Historical treatment of the families Pseudopomyzidae and Cypselosomatidae

Several authors, most recently Lonsdale (2020),have re-examined the relationships and relative status of the putative families Pseudopomyzidae and Cypselosomatidae. The name Pseudopomyzidae first appeared in a checklist by Frey in the 1941 catalogue of Finnish Diptera as a nomen nudum (Sabrosky, 1999) without characterization and description, but D.K. McAlpine (1966) considered Pseudopomyzidae to be a natural group and was the first to officially assign it family rank. McAlpine (1966) and Hennig (1971b) treated Pseudopomyzidae as the sister family to Cypselosomatidae but Griffiths (1972) considered Pseudopomyzidae to be paraphyletic because some synapomorphies (symmetry of S7+8 and the absence of the "8th tergum vestige")

are shared by some Pseudopomyzidae (Pseudopomyza Cypselosomatidae atrimana) and (Formicosepsis tinctipennis); he therefore combined the two groups into one family, Cypselosomatidae (= Cypselosomatidae + Pseudopomyzidae). This treatment was, and is, followed by multiple authors (Rohdendorf, 1977; Nartshuk, 1977; Prado, 1984; Harrison, 1976; Hackman, 1980; Hackman & Väisänen, 1985; McAlpine, 1987, 1989; Wiegmann et al., 2011; Pape et al., 2011; Carvalho-Filho & Esposito, 2011). Anderson (1976) did not agree with the unification of the two groups and argued that the characters considered to be synapomorphies by Griffiths (1972) were instead convergent. He provided a list of characters supporting the monophyly of Cypselosomatidae (without providing equivalent evidence for the monophyly of Pseudopomyzidae), concluding that the two groups are strongly differentiated. Krivosheina (1979) came to a similar conclusion, providing characters supporting the monophyly of each family. Shatalkin (1994) argued that there is no clear evidence supporting the monophyly of Cypselosomatidae s.l. (including Pseudopomyzidae), and therefore followed Andersson (1976) in abstaining from including Pseudopomyzidae in the Cypselosomatidae. J.F. McAlpine (1989) followed Griffiths' system, treating the two groups (Cypselosomatinae + Pseudopomyzinae) as a single family, Cypselosomatidae, and providing a list of supporting synapomorphies for the clade. D.K. McAlpine (1996) instead argued for Pseudopomyzidae as a family distinct from Cypselosomatidae, a system followed by many other recent authors including Papp (2005), Buck and McAlpine (2010), Marshall (2012), Roháček (2012), Marques and Rafael (2016), and D.K. McAlpine (2019). Lonsdale (2020) reconsidered the morphological evidence for the monophyly of Pseudopomyzidae and for its sister-group relationship with Cypselosomatidae.

We here consider new morphological and molecular data, including newly assessed genitalic characters, from a more complete set of pseudopomyzid taxa that has been previously considered, revising the former family Pseudopomyzidae and clarifying its relationship to Cypselosomatidae and other Nerioidea.

Placement of the Pseudopomyzidae and Cypselosomatidae in the superfamily Nerioidea

D.K. McAlpine (1966) was the first to add Pseudopomyzidae Cypselosomatidae and superfamily Nerioidea. Griffiths (1972) also treated Cypselosomatidae (including Pseudopomyzidae) part of the superfamily and Hennig (1971b, 1973) eventually settled on a superfamily concept consisting Cypselosomatidae, Pseudopomyzidae, and Micropezidae (= Micropezidae + Calobatidae + Taeniapteridae in Hennig's system). Wiegmann et al. (2011) showed some support for the monophyly of the superfamily when Micropezidae, Neriidae and Pseudopomyzidae (=Cypselosomatidae) were recovered as a clade in a phylogenomic study. Marshall (2012) listed

Cypselosomatidae, Pseudopomyzidae, Micropezidae and Neriidae as members of the superfamily. Other families such as Clusiidae, Megamerinidae, Nothybidae and Tanypezidae (P.J.M. Macquart, 1835, 1843; Blanchard, 1840; Osten-Sacken *et al.*, 1882; Cresson, 1912; Enderlein, 1922; Collin, 1945; Aczél, 1949, 1951, 1954, 1955, 1959, 1961; Hennig, 1952; Brues *et al.*, 1954; McAlpine, 1966, 1996, 1997a, 1997b, 1998; Colless & McAlpine, 1970, 1991) have been separately or collectively included in or excluded from the superfamily over the years. Lonsdale (2020) suggested that Fergusoninidae, Strongylophthalmyiidae and Tanypezidae should also be included in Nerioidea, in addition to Micropezidae, Neriidae, Pseudopomyzidae and Cypselosomatidae.

A wide variety of taxa have been suggested as provisional sister groups to the superfamily, including Agromyzidae, Aulacigastridae, Chloropidae, Conopidae, Heleomyzidae, Milichiidae, Psilidae, Tanypezidae, and families of Tephritoidea and Diopsoidea (Frey,1921; Hendel, 1922; Aczél,1951; Hennig, 1958; Rohdendorf, 1964, 1974, 1977; J.F. McAlpine, 1989; D.K. McAlpine, 1996; Han *et al.*, 2002; Gibson *et al.*, 2010; Wiegmann *et al.*, 2011; Bayless *et al.*, 2021).

D.K. McAlpine (1966) suggested that the families he included in the Nerioidea (Pseudopomyzidae + Cypselosomatidae + Neriidae + Micropezidae Megamerinidae) could be arranged phylogenetically along a single radiating branch (Pseudopomyzidae (Cypselosomatidae (Neriidae, Micropezidae))). was equivocal about the precise relationship between Megamerinidae and the other families but suggested that it "should probably also be placed near Micropezidae". This arrangement was adopted by Shatalkin (1994) and supported by his interpretation of the evolution of the male aedeagal dorsal sclerite in Nerioidea, but most other authors treat Pseudopomyzidae plus Cypselosomatidae as a monophyletic group. Hennig (1971a) and Griffiths (1972) considered the clade to be relatively plesiomorphic based on the fronto-orbital setae and 6th sternite respectively and treated it as the sister group to the Micropezidae plus Neriidae. Lonsdale's (2020) morphological analysis indicated similar relationships. J.F. McAlpine (1989) stated that no single Nerioidea family embodies all the ground-plan features of the group but found Micropezidae to retain the most plesiomorphic characters and suggested Neriidae as the sister group to the Pseudopomyzidae + Cypselosomatidae clade based on wing morphology, head chaetotaxy and thoracic chaetotaxy. A sister group relationship between Neriidae and Pseudopomyzidae or Cypselosomatidae was also identified by Wiegmann (2011) (only Pseudopomyzidae used) and Koch et al. (2015) (only Cypselosomatidae used).

Materials and Methods

Adult morphological characters and terminology

Morphological terminology follows Cumming and Wood (2017) and Buck and McAlpine (2010). The **sub-antennal**

depression is the triangular depression below the antennal socket (Fig. 49q). The inner face is the area delineated by the carina and medial to the outer face, often absent or highly reduced when the face is mostly desclerotized ventromedially; the outer face is the area delineated by the frontogenal suture and lateral to the inner face (Fig. 49q), often still present, reduced and narrowed, when the face is mostly desclerotized. The vibrissal angle is the anterior area of the gena where the ventral cranial margin is still at an oblique angle. The scapular setae (=suprahumeral setae) are located on the anterior surface of the notum, they are in-line with the dorsocentral setae and horizontally level with the postpronotal seta; their numbers range from 1-4 on each side of the thorax (Fig. 9.2). The anterior intra-alar seta is immediately postsutural and in-line with the intrapostalar seta (Figs. 30.3, 35.2, 59.2).

The male terminalia are deflexed 180° forward at resting position, however the positional descriptions used in this paper follow the groundplan structural orientations (i.e., the functional upper surface is referred to as "ventral"). The postspiracular sclerite(s) are found posterior to right spiracle 7, on the genital pouch and enclosed within segment 7+8 in Nerioidea families. Micropezidae often have 1-2 variously developed sclerites (absent in many derived genera) immediately posterior to the seventh right spiracle; Neriidae often have one elongate sclerite parallel to the left ventral edge of S8 and another sclerite articulating with the first in a y-formation; the former Pseudopomyzidae often have an elongated sclerite extending from S8; no similar sclerites are found in Cypselosomatidae s.s.. The inner lamella of the male surstylus is the thin plate on the inner margin of the surstylus (marked red in the Figures). The phallic guide in Cyclorrhapha is the connection between the hypandrium and the phallapodeme and often appears to be a ventral extension of the anterior part of the phallapodeme; in the Cypselosomatidae s.l. (former Pseudopomyzidae + Cypselosomatidae s.s.), it is often finlike and is usually shielded by the hypandrium (Fig. 53.2). The anterior bridge (Fig. 105) of the hypandrium is found in Micropezidae and other Schizhophora families such as the Diopsidae, Megamerinidae, Strongylophthalmyiidae, Tanypezidae etc. It often gives the hypandrium a round shield-like appearance. The anterior bridge is often modified in the taeniapterine micropezids, complete but sometimes loop-like or scoop-like; it is absent in the Neriidae and Cypselosomatidae s.l.. The ventral bridge of the hypandrium is the ventral bridging in the middle of the hypandrium. It is found in all Cypselosomatidae s.s. and most taxa of the former Pseudopomyzidae (Figs. 3.5, 6.5, 10.5, 36.5). The **dorsal bridge**, previously called the hypandrial dorsal bridge by J.F. McAlpine (1989) and Shatalkin (1994) (dorsal brucke in Hennig (1976)), is the dorsal fusing of the dorsal arms of the hypandrium. The ventral surface of the dorsal bridge serves as the point of origin for the phallic plate in Nerioidea. The dorsal surface of the dorsal bridge is sometimes extended posteriorly to create a second sheet (never as long as the phallic plate) that shields the terminalia dorsally (Figs.

10.4, 28.6, 36.4). When the dorsal surface of the dorsal bridge happens to be extended, the subepandrial sclerite is usually proportionally shorter than the epandrium (Figs. 10.4, 36.4). The posterior margin of the dorsal surface of the dorsal bridge is often loosely connected to the anterior margin of the subepandrial sclerite. The terms basal distiphallus and distal distiphallus (Fig. 53.2) are used for the sclerotized basal portion and the variably sclerotized distal portion of the distiphallus; these two portions are separated by a distinct phallic bulb in most Micropezidae. The basal distiphallus of members of the former Pseudopomyzidae is fused with the basiphallus (considering the articulation points with the phallapodeme and the phallic plate), no break is present but there is often a ventral notch suggesting the boundaries between the two sclerites. When the basiphallus and basal distiphallus is in a fused state, the structure is referred to as the basal distiphallus.

The texture of the body surfaces is described as glossy, pruinose or pollinose. Glossy surfaces are generally smooth, without microtrichia, and appear polished. Pruinose surfaces are covered with microtrichia, and individual microtrichia can be distinguished. Pollinose surfaces appear to be covered with fine powder, and individual microtrichia cannot be distinguished with a light microscope at 150×.

Seta(e) and setula(e) are large and small socketed macrotrichia respectively, always tapered and relatively rigid with a natural curvature. Hair(s) are uniformly thin, flexible macrotrichia.

Specimen preparation and dissection

Most specimens were initially preserved in alcohol and later prepared for point mounting using a critical point drier. Some specimens were pinned in the field and airdried. Male and female terminalia were prepared for examination by separating entire abdomens from mounted specimens. Some abdomens were cleared in hot 10% KOH for 10 to 15 min, neutralized in glacial acetic acid for at least 15 min, and finally rinsed in deionized water. Most of the abdomens were cleared using enzymatic contact lens cleaner solution (used according to package directions) and a few were cleared using trypsin (0.5%) EDTA solution and in small plastic vials ("cryovials") of 1.5 to 2 ml for 12 to 16 h at room temperature (usually 22-25°C), and finally rinsed in deionized water (Yau & Marshall, 2015). Fewer specimens were cleared in capsule form digestive enzyme (pancreatin) supplements (with inconsistent results) with similar parameters as above. Cleared abdomens were transferred to glycerin in depression slides for examination. All dissected parts were stored in microvials and pinned below the specimens. Specimen labels for type material of previously described species are cited verbatim when enclosed in quotation marks. Type material in the specimen lists were examined unless specified otherwise.

Photography

Digital photographs of whole specimens were taken using a Canon 70D camera mounted on a StackShot system (Cognisys Inc., Michigan USA). Photos of the terminalia were taken using a Nikon D300s camera mounted on a Nikon compound microscope. Photo series were stacked in HeliconFocus (Helicon Soft Ltd., Kharkiv Ukraine), and visually enhanced in Adobe Photoshop CC (Adobe, California USA). Live images were taken with Nikon digital cameras with off-camera flash, 105 macro lens and extension tubes.

Measurements and ratios

Measurements are based on a sample of approximately 10 specimens for each sex (or the entire series in the case of rarer species), selected from a variety of localities. Measurements are taken from their maximum distance unless specified. Measurements and ratios should be treated as an approximation since dried specimens vary in size and position. Measurements and ratios used are as follows:

Body length—distance from anterior-most part of head not including antennae to tip of abdomen

Eye height—distance from most ventral point to most dorsal point of eye; measured in lateral view and parallel to occipital margin of head

Genal height—distance from most ventral point of gena to most ventral point of eye; measured in lateral view and parallel to occipital margin of head

Epandrium width—the greatest distance from side to side of the epandrium

Epandrium length—the greatest distance from anterodorsal edge of the epandrium to the most basal point of the anal opening

Basal distiphallus width—the greatest distance from side to side of the basal distiphallus

Basal distiphallus length—the greatest distance from base to apex of the basal distiphallus

Distal distiphallus length—the greatest distance from base to apex of the distal distiphallus

Length of phallapodeme beyond phallic plate—linear distance from level of anterior edge of phallic plate (Fig. 53.2) to apex of phallapodeme

Length of phallapodeme shielded by phallic plate linear distance from base of phallapodeme to level of anterior edge of phallic plate

Abbreviations for characters

c—costal sector

T—Tergite(s)

S—Sternite(s)/ Syntergosternite

Abbreviations for frequent collectors

SAM—S.A. Marshall; LM—L. Masner

Abbreviations for common collecting methods

MT—Malaise trap; FIT—Flight intercept trap

Acronyms of depositories

AMNH (American Museum of Natural History, New York, New York, United States of America)

AMSA (Australian Museum, New South Wales, Sydney, Australia)

ANIC (Australian National Insect Collection, Canberra, Australian Capital Territory, Australia)

CBFC (Colección Boliviana de Fauna, La Paz, Bolivia) CMNZ (Canterbury Museum, Christchurch, New Zealand)

CNC (Canadian National Collection of Insects, Arachnids & Nematodes, Ottawa, Ontario, Canada)

CSCA (California State Collection of Arthropods, California Department of Food and Agriculture, Sacramento, California, United States of America)

DEBU (School of Environmental Sciences, University of Guelph, Guelph, Ontario, Canada)

ISEA (Institute of Ecology and Evolution, Russian Academy of Sciences, Novosibirsk, Russia)

MEUC (Universidad de Chile, Santiago, Chile)

MIZA (Museo del Instituto de Zoología Agrícola, Maracay, Venezuela)

MNCR (Museo Nacional de Costa Rica, San Jose, Costa Rica)

MNNC (Museo Nacional de Historia Natural, Santiago, Chile)

MONZ (Museum of New Zealand, Wellington, New Zealand)

MUSM (Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru)

MZUSP (Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil)

NHMUK (The Natural History Museum, London, United Kingdom)

NMBA (Naturhistorisches Museum der Benediktiner-Abtei, Admont, Austria)

NZAC (New Zealand Arthropod Collection, Landcare Research, Auckland, New Zealand)

QCAZ (Museo de Zoología, Pontificia Universidad Católica del Ecuador, Quito, Ecuador)

SDEI (Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany)

SMNS (Staatliches Museum für Naturkunde, Stuttgart, Germany)

TFRI (Forestry Research Institute, Taipei, Taiwan)

UNAM (Universidad Nacional Autónoma de México, Mexico City, Mexico)

USNM (National Museum of Natural History, Smithsonian Institution, Washington DC, USA)

UVGC (Collección de Artrópodos, Universidad de Valle de Guatemala, Guatemala City, Guatemala)

WAM (Western Australian Museum, Perth, Western Australia, Australia)

ZISP (Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia)

ZMUM (Moscow State University, Moscow, Russia)

Taxonomy

The following treatment of the former family Pseudopomyzidae as part of the family Cypselosomatidae is predicated on a phylogenetic analysis (see below) that demonstrates the paraphyly of the former family Pseudopomyzidae with respect to Cypselosomatidae s.s. The genera of the former family Pseudopomyzidae are fully revised; the genera of Cypselosomatidae s.s. Clisa, Cypselosoma and Formicosepsis, Eopseudopomyza†, Latheticomyia and Tenuia are reviewed with keys to the described species.

Cypselosomatidae sensu lato (Cypselosomatidae s.s. + former Pseudopomyzidae)

Type genus: *Cypselosoma* Hendel 1913: 105, by Hendel (1931: 5). Type species of genus: *Cypselosoma gephyrae* Hendel, 1913: 105 (original designation).

Diagnosis

Fronto-orbital setae in 2–4 pairs; vibrissae distinct. Face ventromedially desclerotized to various degree. Scutum with at least 1 scapular seta; intra-alar setae often absent, if present, only anterior intra-alar present. Prosternum narrow and not forming precoxal bridge. Ventrobasal setae on femur usually present. Subcostal break present, subcosta incomplete. Cells bm and dm usually confluent, crossvein bm-m weakened, incomplete or absent. Male S6 more or less symmetrical, with an arcuate (sometimes angulate) sclerotization running though middle of sclerite. Epandrium with at least 1 pair of outstanding setae. Subepandrial sclerite undivided with 1-5 setae. Hypandrium usually with ventral bridge; phallic plate complete and well sclerotized; phallic guide usually reduced to a triangular remnant or absent. Pregonites usually with 2 sensory setulae. Postgonite with 1 outstanding seta/setulae. Spermathecae (1+1 or 1+2, sometimes 0+1) on independent ducts.

Description

Length 1.5–5.5 mm. Compact to slender flies. Colour mostly brown to black but often with colour patterns of white to yellow on head, legs and thorax.

Head: Usually 3 fronto-orbital setae (some with 2 or 4), proclinate, reclinate or lateroclinate; frontal vitta usually with numerous uniformly scattered minute setulae; 0–1 interfrontal seta; 1 inner vertical; 1 outer vertical; 1 ocellar

(long); 1 postocellar, convergent, parallel or divergent; paravertical usually present. Occiput flat or convex, bare or with scattered setae; supracervical chaetotaxy variable. Antenna porrect, shape of first flagellomere variable but usually discoid; arista bare or pubescent. Vibrissa present and well developed, subvibrissa present or absent. Gena either with a row of setulae dorsal to groove on gena or with small, scattered setulae; gena-postgena junction or postgena with at least 1 well developed seta. Face ventromedially membranous to various degree but subantennal depression and outer face usually somewhat sclerotized.

Thorax: usually pruinose, sometimes glossy. Usually with at least 4 dorsocentral setae, but sometimes with only 1; acrostichal setae/ setulae between dorsocentrals often in irregular lines, medial acrostichal setae often present, prescutellar acrostichal setae usually present. Intra-alar setae often absent, if present, only anterior intra-alar present; usually with 1 presutural supra-alar and postsutral supra-alar setae; postalar seta present; intrapostalar present or absent. Scutum with at least 1 scapular seta. Usually with 1, sometimes 2, postpronotal seta and small setulae on postpronotum; 2 notopleural setae; 1 proepimeral seta. Scutellum with 1-5 marginal setae (usually 2–3) increasing in size posteriorly, and often with discal setulae. Prosternum narrow and not forming precoxal bridge. Katepisternal setae, when present, strong and well-developed or very fine.

Legs: Ventrobasal setae on femur usually present. Fore femur usually with posteroventral row of strong setae.

Wing: Clear or pigmented with clear bands. Usually well-developed but sometimes reduced. Subcostal break present, humeral break or weakening present or absent. Subcosta incomplete. Cells bm and dm usually confluent, crossvein bm-m weakened, incomplete or absent. M₄ and CuA+CuP not reaching wing margin.

Abdomen: T1–6 at least setose laterally, well-developed and sclerotized. S1–5 small but well sclerotized and setose.

Male terminalia (Figs. 3, 6, 10, 13, 16, 31, 36, 39, 102): Deflexed forward. S6 more or less symmetrical, with an arcuate (sometimes angulate) sclerotized band running though middle of sclerite, area posterior to band desclerotized to membranous, with or without setae, anterior area reduced or extended ventrally but always with sensory setulae; posterior corners articulating with S7. S7+8 sometimes asymmetrical and weak on ventral right but sometimes symmetrical and form a closed ring; cleft on left ventral margin delineating S7 and S8 usually present; postspiracular sclerite present or absent; S7+8 with or without outstanding pair of setae. Epandrium with at least 1 pair of outstanding setae, sometime 2. Surstylus shape variable but mostly simple and elongate. Cerci converging distally, enclosing anal opening, apices fused or closely approximated, setose along entire length. Subepandrial sclerite undivided, lying between epandrium and phallic plate, shape variable but more or less flat; with 1-5 setae. Dorsal bridge of hypandrium complete; hypandrium usually with, but rarely without,

ventral bridge; phallic plate usually flat, straight and well sclerotized; phallic guide reduced to a triangular remnant or absent. Pregonite usually narrow and elongated, usually with but rarely with more than 2 sensory setulae, usually arising from mid-width but rarely from side of hypandrium. Postgonite shape variable but often forked or trilobate; arising at apex of pregonite; with 1 outstanding seta/setulae and some "sensory setulae" or remaining pits. Phallapodeme usually relatively straight, rarely arched. Basiphallus independent of or fused to base of distiphallus (basal distiphallus). Distiphallus divided into basal distiphallus and distal distiphallus, distiphallus usually elongate, asymmetric and skewed to the right. Apex of basal distiphallus often very well sclerotized. Shape of ejaculatory apodeme and bulb variable.

Female terminalia: Tergite and sternite 7 fused to form a sclerotized oviscape. Spermathecae (usually 1+1, sometimes 1+2 (*Pseudopomyzella* and *Latheticomyia*) or 0+1 (*Formicosepsis*)) on independent ducts arising close together from dorsal surface of bursa copulatrix. Shape of ventral receptacle variable.

Key to genera of Cypselosomatidae s.l.

- 2) Body slender, ant-like. Gena short; occiput convex (Figs. 4.1, 5.1, 8.1). Pronotal collar well developed; wing narrow, with anal lobe and alula strongly reduced (Figs. 4.2, 5.2, 8.2)
- Six acrostichal setae. Posterodistal corner of cell dm angulate (Fig. 2.2).....

4) Anepisternum with a few setulae and one posterior seta, katepisternal seta strongly curved forward, postsutural dorsocentral setae in four pairs. Male with laterally flattened apical scutellar setae (Figs. 101.1-2, 4) and 2 pairs of long dorsal setae on S7+8 (Fig. 102.1)..... Anepisternum bare, katepisternal seta (posterior seta if 2 are present) curved posteriorly, postsutural dorsocentral setae in 3 pairs, apical setae of scutellum not laterally flattened (Figs. 9.1-2, 12.2-5, 27.2). Male S7+8 dorsally bare or setulose but without long outstanding setae (Figs. 5) Subvibrissa absent, genal setulae arranged more or less in a Subvibrissa usually present, genal setulae scattered or Four pairs (1+3) of dorsocentral setae.... 6) 7) Head, thorax and legs often with highly contrasting black and white patterns appearing as stripes running through entire body (Figs. 12.1-5). Costa with small setulae but without spines..... Latheticomyia Wheeler (Southern North America, Central and South America) Head, thorax or legs may have black and yellow to tan patterning, but patterns never highly contrasting or appear as described above. Costa with single row of spines...... 8 Three fronto-orbital setae. Cell bm and dm separated by 8) crossvein bm-m Tenuia Malloch (Oriental and Palaearctic) Four fronto-orbital setae. Cell bm and dm confluent, crossvein bm-m reduced to a stub..... .. Eopseudopomyza† Hennig (Baltic and Bitterfeld amber) Subvibrissa greatly enlarged, subequal to vibrissa. Costa with spines in c2; katepisternum with 2 dorsal setae; tibiae with 2-5 dorsal setae distinctly longer than background chaetotaxy (Figs. 9.1, 9.3) Heloclusia Malloch (Chile) Subvibrissa at most 0.5× vibrissa. Costa without spines in c2; katepisternum with 1 dorsal seta; tibiae only with uniformly short dorsal background chaetotaxy.....Pseudopomyza Strobl (including "Macalpinella") (Worldwide except North America and Africa)

Cypselosomatidae sensu stricto Hendel, 1931 (Figs. 1.1–3, 2.1–3, 3.1–5, 4.1–3, 5.1–5, 6.1–5, 7.1–4, 8.1–3)

Diagnosis

Three fronto-orbital setae; 1 interfrontal (minute in most *Formicosepsis*); postocellar setae parallel to divergent. Arista usually bare, rarely short pubescent; basal aristomere often round and swollen. Subvibrissa absent or not distinguishable from background setulae. Gena with a row of setulae dorsal to groove on gena; lower margin of genapostgena junction with 1 well developed seta. Intra-alar setae absent; intrapostalar seta absent. Proepimeron broad;

posterior margin of anepisternum grooved; katepisternum and meron fused; dorsal 1/3 of katepisternum with ridge forming a shelf on dorsal surface. Fore femur with anteroventral distal spines. M₄ past crossvein dm-m short (*Cypselosoma*) or absent, posterodistal corner of cell dm rounded (angulate in *Cypselosoma*, but M₄ subapically bowed). Male S7+8 symmetrical and form a closed ring; S7 and S8 not divided by cleft on left ventral margin; postspiracular sclerite absent; S7+8 with an outstanding pair of setae. Subepandrial sclerite with 1–2 setae. Phallic plate lying further from phallapodeme than pregonites from phallapodeme; hypandrium with ventral bridge; pregonites arising from mid-width of hypandrium.

Description

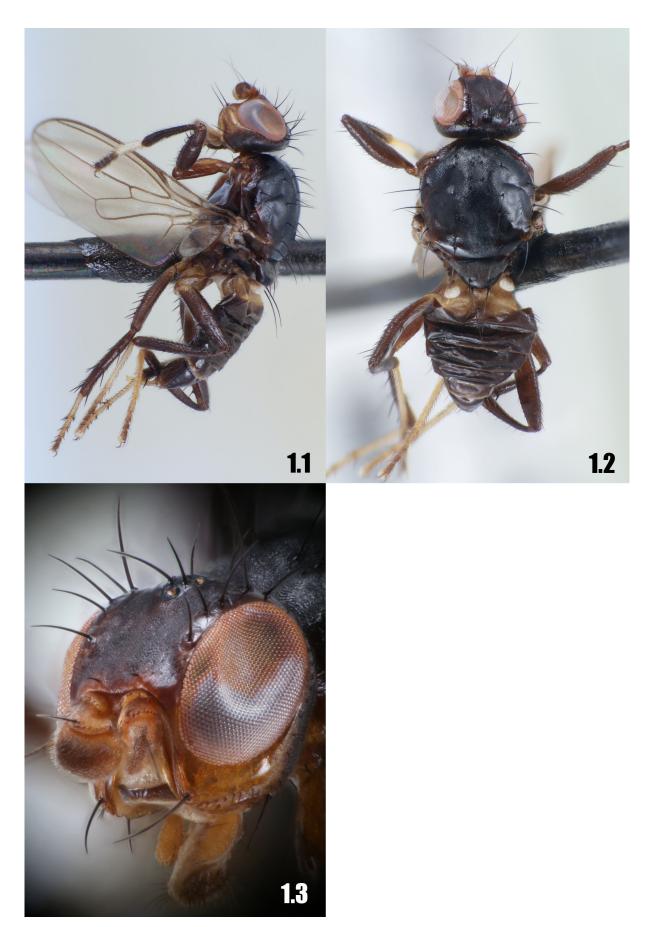
This description is based on the examination of *Clisa*, *Cypselosoma* and *Formicosepsis* species from Australia and the Oriental region.

Length 2.5–5.0 mm. *Cypselosoma* and *Clisa* compact; *Formicosepsis* very slender and ant-like. Colour mostly brown to black but often with colour patterns of white to yellow on head, legs and thorax.

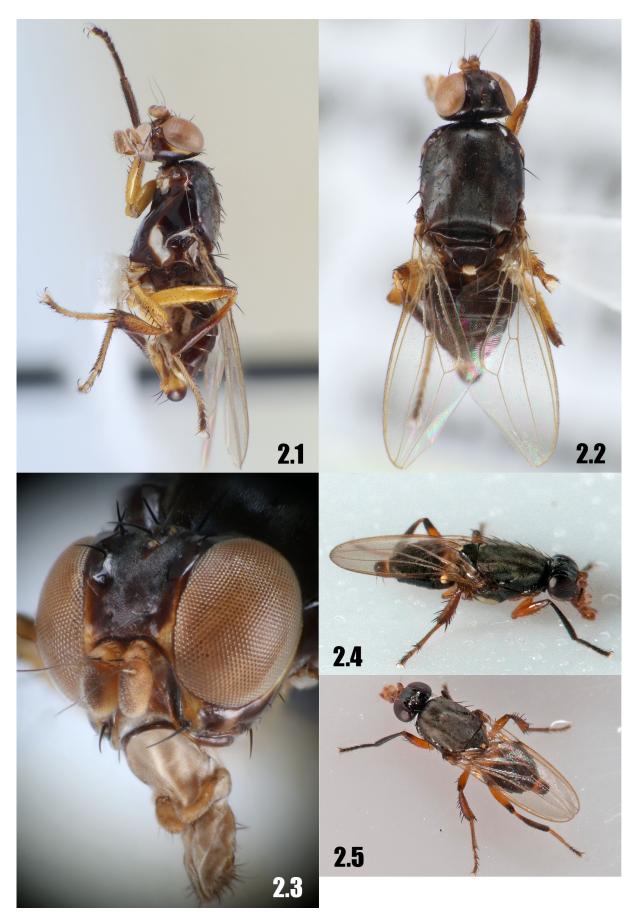
Head: Three fronto-orbital setae, anterior 2 setae proclinate to lateroclinate, posterior seta reclinate to lateroclinate; fronto-orbital plate glossy; frontal vitta pruinose; 1 interfrontal, usually small, hair-like, indistinguishable from surrounding setulae in most Formicosepsis; postocellar setae parallel to divergent. Occiput often bare with some scattered setae at postgena; supracervical area with few setae or bare. First flagellomere discoid; arista at most half head width, rarely short pubescent but mostly bare, arising from first flagellomere submedially; basal aristomere often round and swollen. Subvibrissa absent or not distinguishable from background setulae. Gena 0.3-0.25× eve height but reduced in Formicosepsis; with a row of setulae dorsal to groove on gena; lower margin of gena-postgena junction with 1 well developed seta. Carina often short to obsolete, inner face reduced or absent.

Thorax: Usually pruinose, often glossy in Formicosepsis. Usually with 4-6 dorsocentral setae, but some Formicosepsis with only 1; medial acrostichal setae often present, prescutellar acrostichal setae sometimes present. Intra-alar setae absent; postalar seta large; intrapostalar seta absent. Scutum with 1 scapular seta. 1–2 postpronotal seta(e). Scutellum flat to convex, upturned in some Formicosepsis; usually with 2 pairs of marginal setae (sometimes 1 in Formicosepsis) (sometimes on apices of tubercles in Formicosepsis). Proepimeron broad. Anepisternum bare, posterior margin grooved. Katepisternum and meron fused; dorsal 1/3 of katepisternum with ridge forming a shelf on dorsal surface; katepisternum with 0–2 very fine setae. Formicosepsis with developed pronotal collar and fused katepisternum, proepimeron, proepisternum and postpronotum.

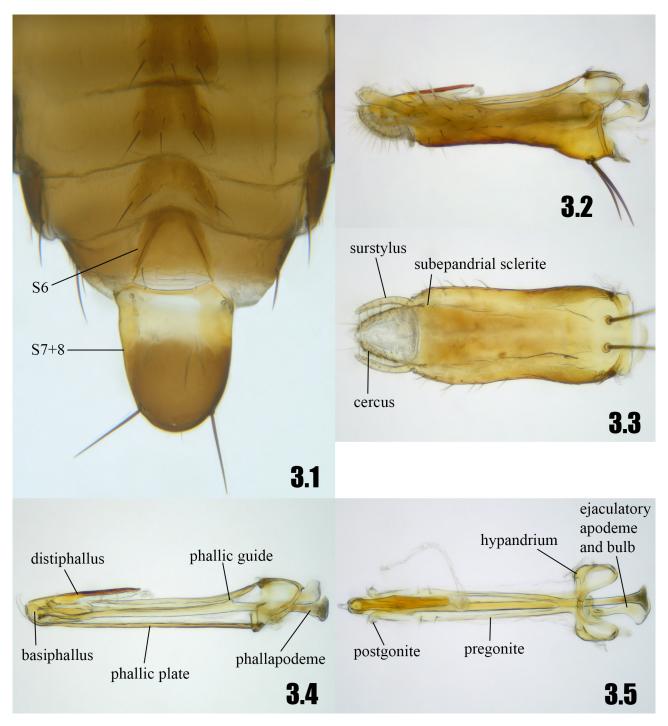
Legs: Ventrobasal setae on femur present in *Cypselosoma*. Fore femur with anteroventral distal spines and posteroventral row of strong seta(e) (absent in some *Formicosepsis*).



FIGURES 1.1–3: Clisa australis female habitus (Australia). 1.1, left lateral; 1.2, dorsal; 1.3, head.



FIGURES 2.1–3: *Cypselosoma gephyrae* male habitus (Thailand). 2.1, left lateral; 2.2, dorsal; 2.3, head; 2.4, 2.5, photographed in Daming Mountain near Nanning, China by SAM.



FIGURES 3.1–5: *Cypselosoma* sp. male abdomen (Nepal). 3.1, terminalia ventral; 3.2, epandrium left lateral; 3.3, epandrium ventral; 3.4, phallus and associated structures left lateral; 3.5, phallus and associated structures ventral.

Wing: Clear or pigmented with clear bands. *Clisa* and *Cypselosoma* with well-developed anal lobe and alula, *Formicosepsis* wings narrow, anal lobe and alula strongly reduced. Humeral break or weakening absent but costa bare at humeral crossvein. Subcosta distally separate from R₁. Crossvein bm-m absent. Part of M₄ past crossvein dm-m short (*Cypselosoma*) or absent, posterodistal corner of cell dm rounded (angulate in *Cypselosoma*, but M₄ subapically bowed).

Abdomen: T1–6 glossy to pollinose, setose laterally. Male terminalia (Figs. 3.1–3, 6.1–5): S7+8 symmetrical and forming a closed ring without a cleft on left ventral margin delineating S7 and S8; postspiracular sclerite absent; S7+8 with outstanding pair of setae. Epandrium with 1 outstanding pair of setae. Cerci with apices closely approximated. Subepandrial sclerite with 1–2 setae. Phallic plate lying further from phallapodeme than distance between pregonite and phallapodeme;

hypandrium with ventral bridge; pregonite arising from mid-width of hypandrium. Phallic guide reduced to a triangular remnant. Pregonite with 2 sensory setulae on distal sixth to eighth. Postgonite shape variable but generally forked and trilobate. Phallapodeme straight. Basiphallus independent of distiphallus. Apex of basal distiphallus often long. Ejaculatory apodeme elongate, apically fan shaped.

Female terminalia: Spermathecae (usually 1+1, sometimes 0+1 (Formicosepsis)) shape variable but usually sac- or rod-like, sclerotization variable, one sometimes atrophied. Ventral receptacle linear, narrow to relatively broad.

Clisa McAlpine

Clisa McAlpine, 1993: 2. Type species: Cypselosoma australis McAlpine, 1966 (original designation).

McAlpine, 1993: 2 (key to species), 3 (comparison with *Cypselosoma*).

The genus includes two species found in Australia, *C. australis* (McAlpine) and *C. disneyi* (McAlpine).

Diagnosis

With 1 well-developed interfrontal. Scutellum flat. Pronotum relatively flat. Ventrobasal setae on femur absent. Wing with well-developed anal lobe and alula. M₄ past crossvein dm-m absent, posterodistal corner of cell dm rounded. Subepandrial sclerite with 1 seta.

Key to described species of Clisa McAlpine

- - C. disneyi (McAlpine) (Lord Howe Island, Australia)

Cypselosoma Hendel

Cypselosoma Hendel, 1913:105. Type species: Cypselosoma gephyrae Hendel, 1913 (by monotypy).

Hendel, 1923: 260 (keyed and diagnosis as part of Cypselidae);
Hennig, 1941:131 (systematic position, relationships);
McAlpine, 1966: 675 (diagnosis); Andersson, 1976:176 (keyed);
Steyskal, 1977: 5 (Oriental catalogue);
McAlpine, 1978:64 (keyed);
Mathis, 1989: 463 (Australasian catalogue);
Shatalkin, 2014: 152 (diagnosis).

Lipotherina de Meijere, 1914: 271. Type species: Lipotherina flavinatata de Meijere, 1914 (by monotypy). Hennig, 1958: 554 (synonymized with *Cypselosoma*).

The genus includes two described species, both found in the Oriental region, but undescribed species are known from China (SAM, Figs. 2.4, 2.5; Zhou Jiale, pers. Comm.¹) and Nepal (CNC 700638, debu00153246).

Diagnosis

With 1 pair of well-developed interfrontal setae. Scutellum flat. Pronotum relatively flat. Ventrobasal setae on femur present. Wing with well-developed anal lobe and alula. M_4 past crossvein dm-m short, subapically bowed, posterodistal corner of cell dm angulate. Subepandrial sclerite with 2 setae.

Key to described species of Cypselosoma Hendel

- Tarsomeres 3–5 of mid leg brown, mid tibia yellow, hind tibia brownish on apical fifth; fore femur with thick setae but no spines. Length of posterior seta of postpronotum 2.6–3.1× length of anterior seta.....

Formicosepsis de Meijere

Formicosepsis de Meijere, 1916: 199. Type species: Formicosepsis tinctipennis de Meijere, 1916 (by monotypy).

Duda, 1925:24 (keyed, diagnosis, synonymy); Hennig, 1941: 129
(systematic position, relationships); McAlpine, 1966: 675
(keyed to separate from *Cypselosoma*); Andersson, 1976: 176 (keyed), 178 (diagnosis), 179 (key to species); Steyskal, 1977: 5 (Oriental catalogue); McAlpine, 1978:64 (keyed); Mathis, 1989: 463 (Australasian catalogue).

Lycosepsis Enderlein, 1920:60. Type species: *Lycosepsis hamata* Enderlein, 1920 (by monotypy). Duda, 1925: 24 (synonymized with *Formicosepsis* (as *Lyxosepsis err*.)).

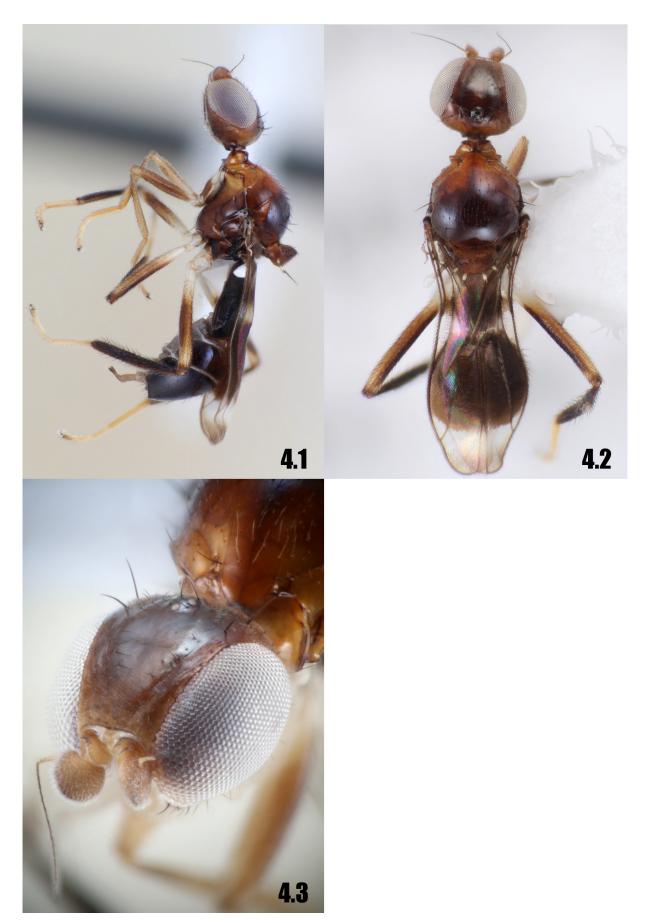
Enderlein, 1920: 60 (diagnosis); Andersson, 1976:182 (as subgenus of *Formicosepsis*, diagnosis); Steyskal, 1977: 6 (Oriental catalogue).

The genus is found in the Oriental region and includes two subgenera, *Formicosepsis* de Meijere and *Lycosepsis* Enderlein. Subgenus *Formicosepsis* includes four species, *F. barbipes* Andersson, *F. defecta* Andersson, *F. paratinctipennis* Papp and *F. tinctipennis* de Meijere. Subgenus *Lycosepsis* includes five species, *F. biseta* (Papp), *F. brincki* Andersson, *F. hamata* (Enderlein), *F. metatarsata* (de Meijere) and *F. oedipus* (Papp).

Diagnosis

Interfrontal seta usually minute. Scutellum convex and sometimes upturned. With developed pronotal

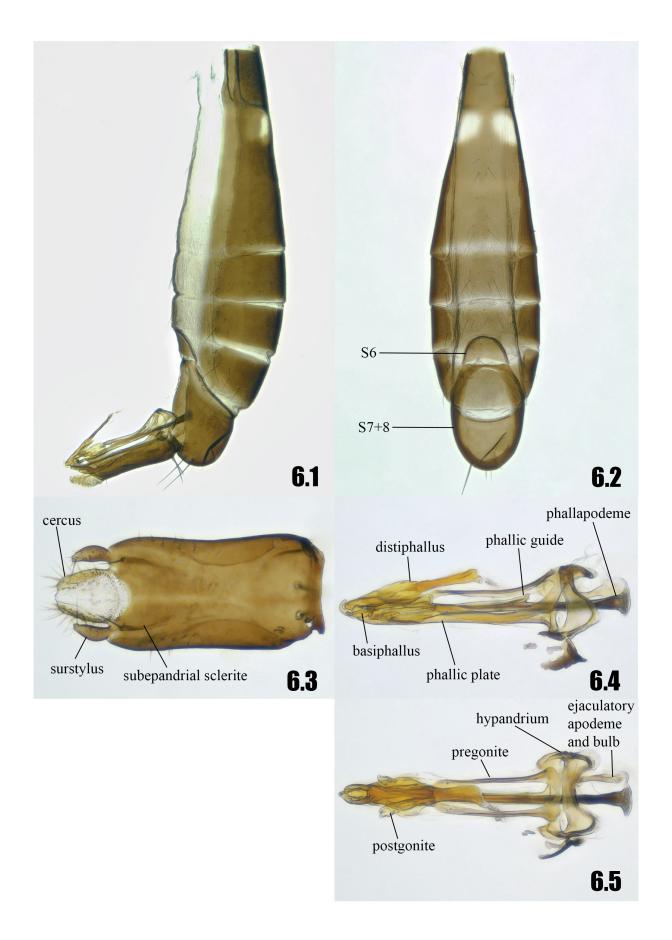
PhD, Institute of Zoology, Chinese Academy of Sciences, Beijing, China. zhou_jl1994@163.com



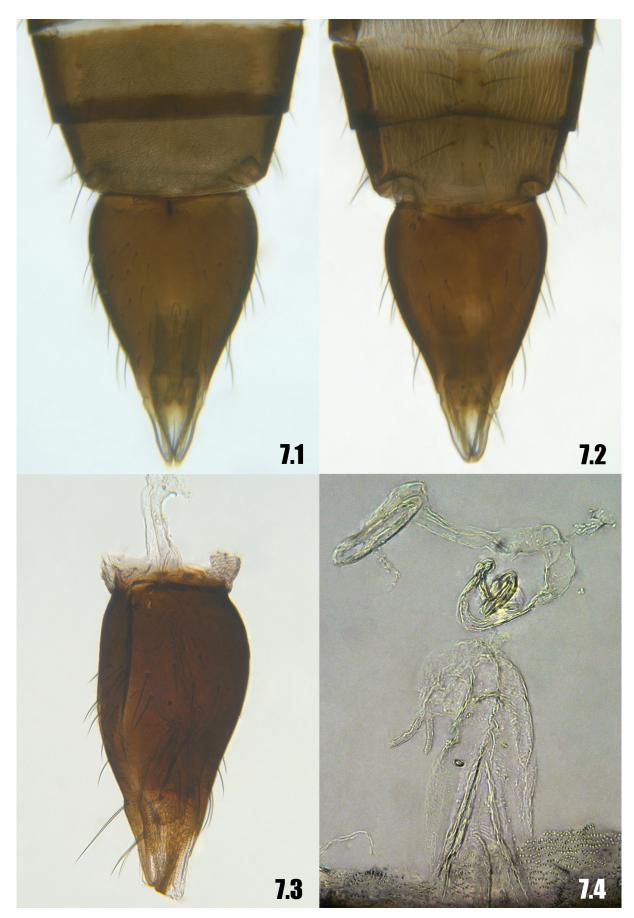
FIGURES 4.1–3: Formicosepsis (Formicosepsis) sp.1 female habitus (Philippines). 4.1, left lateral; 4.2, dorsal; 4.3 head.



FIGURES 5.1–5: *Formicosepsis* (*Formicosepsis*) sp.2 (Philippines). 5.1, male habitus left lateral; 5.2, dorsal; 5.3, head; 5.4, photographed in Los Banõs by SAM; 5.5, pair *in copula* photographed in Los Banõs by SAM.



FIGURES 6.1–5: *Formicosepsis* (*Formicosepsis*) sp.2 male abdomen (Philippines). 6.1, terminalia left lateral; 6.2, terminalia ventral; 6.3, epandrium ventral; 6.4, phallus and associated structures left lateral; 6.5, phallus and associated structures ventral.



FIGURES 7.1–4: *Formicosepsis* (*Formicosepsis*) sp.2 female abdomen (Philippines). 7.1, terminalia dorsal; 7.2, terminalia ventral; 7.3, terminalia left lateral; 7.4, spermatheca and associated structures.



FIGURES 8.1–3: Formicosepsis (Lycosepsis) sp.3 male habitus (China). 3.8.1, lateral; 8.2, dorsal; 8.3, head.

collar. Katepisternum, proepimeron, proepisternum and postpronotum fused. Ventrobasal setae on femur absent. Wing narrow, anal lobe and alula strongly reduced. M_4 past crossvein dm-m absent, posterodistal corner of cell dm rounded. Subepandrial sclerite with 1 seta.

Key to described species of *Formicosepsis* de Meijere

1) Scutellum with large apical conical tooth. Fore femur with 6-8 short anteroventral spines in apical half. Mid femur with at most one anterior seta.....2 (subgenus *Lycosepsis* Enderlein) Scutellum without tooth but sometimes distinctly pointed at apex. Fore femur without anteroventral spines. Mid femur with 2 anterior setae on distal half..... 2) With 5 dorsocentral setae. Distal third of hind femur (distal to anteroventral seta) without anteroventral and posteroventral spinesF. (L.) metatarsata de Meijere (Indonesia) With 4 dorsocentral setae. Distal third of hind femur with 3) Mesonotum with distinct microsculpture and medial dusted stripe. First tarsomere of fore leg yellow, tarsomere 2-5 Mesonotum without distinct microscupture nor medial dusted stripe. Fore tarsi yellow to tan, tarsomere 3-5 may be somewhat darkened in colour......5 Mid femur with 1 indistinct anterior seta. Wing brownish 4) with pale transverse band posterior to crossvein dm-mF. (L.) hamata Enderlein (Taiwan) Mid femur with 1 distinct anterior seta. Wing uniformly brownish without transverse band but apex of cell r, slightly darker.....F. (L.) oedipus Papp (Thailand) With 3 dorsocentral setae. Mid femur with 2 anterior setae. 5) F. (L.) biseta Papp (Thailand) With 4 dorsocentral setae. Mid femur without anterior seta.F. (L.) brincki Andersson (Sri Lanka) Mesonotum pollinose; with 5 dorsocentral setae. Scutellum 6) completely rounded-off at apex.....F. (F.) defecta Andersson (Indonesia) Mesonotum not pollinose but sometimes less shining due to coarse microsculpture; with 4 dorsocentral setae. Scutellum Male fore tibia and tarsi with long black, more or less 7) irregularly curved hairs that are at least as long as width of tibia and metatarsus.....F. (F.) barbipes Andersson (Indonesia) 8) Length of mid femoral setae subequal.....F. (F.) paratinctipennis Papp (Thailand) Mid femoral distal seta much longer than proximal setaF. (F.) tinctipennis de Meijere (Indonesia)

Former Pseudopomyzidae, now Cypselosomatidae in part

Type genus: *Pseudopomyza* Strobl 1893: 284; McAlpine, 1966: 683 (as family). Type species of genus: *Pseudopomyza nitidissima* Strobl, 1893: 284 [=*Opomyza atrimana* Meigen, 1830: 106].

Diagnosis

Length 1.5–5.5 mm. Compact to slender flies. Colour mostly variegated brown to black, usually with white to yellow on head, legs and sometimes thorax and terminalia. Mesonotum and frons (excluding orbital plate) usually pruinose to matte, but sometimes glossy; pleuron pruinose to glossy.

Head: Usually 3 fronto-orbital setae (2 in some Pseudopomyza, 4 in Pseudopomyzella), anterior seta sometime reduced, reclinate to latero-reclinate; 1 pair of convergent postocellar setae; dorsomedial seta(e) behind ocellar tubercle and lateral to postocellar setae usually enlarged as paraverticals. Occiput often with scattered setae; supracervical setae dense and pronounced or sparse and inconspicuous. First flagellomere discoid or slightly truncated to shallowly pointed; arista short pubescent, sometimes elongate, arising from first flagellomere apically to subapically. Subvibrissa usually present. Gena usually with scattered small setulae on ventral 2/3; lower margin of postgena with 2-4 well developed setae. Carina rarely well developed, often short to obsolete, usually with 2 columns of minute setulae along length; inner face rarely well developed, often reduced or absent.

Thorax: With at least 4 dorsocentral setae; medial acrostichal and prescutellar acrostichal setae often present and strong. Anterior intra-alar seta present or absent, postalar and intrapostalar setae always present. Scutum with 1–3 (rarely 4) scapular setae. Usually with 1 postpronotal seta and small setulae at base of seta. Scutellum flat to convex, with 2–5 (usually 3) pairs of marginal setae. Katepisternum with 1–2 outstanding katepisternal setae.

Legs: Femora with ventrobasal seta. Fore femur with posteroventral row of strong setae.

Wing: Clear, without markings. Costa with humeral break or weakening; sometimes with spines. Subcosta sometimes distally merged with R₁. R₄₊₅ and M₁ parallel to slightly convergent before reaching wing margin. Crossvein bm-m weakened, incomplete or absent.

Abdomen: T1–6 usually pollinose, setose.

Male terminalia (Figs. 10.1–5, 13.1–5, 16.1–6, 31.1–6, 36.1–5, 53.1–3, 102.1–6): S7+8 usually asymmetrical and weak on ventral right but sometimes symmetrical and form a closed ring; cleft on left ventral margin delineating S7 and S8 usually present; postspiracular sclerite usually present; S7+8 rarely with outstanding pair of setae. Epandrium with 1–2 outstanding pairs of setae. Cerci apically fused. Subepandrial sclerite with 2–5 setae. Phallic plate lying close to phallus; hypandrium with or without ventral bridge; pregonites arising from side or mid-width of hypandrium. Phallic guide reduced to a triangular remnant or absent. Pregonite usually narrow and elongated, rarely shortened; rarely with more than 2 sensory setulae along body, sensory setulae sometimes longer than normal. Postgonite shape variable.

Phallapodeme usually relatively straight, rarely arched. Basiphallus fused to base of distiphallus. Ejaculatory apodeme fan-shaped or reduced, ejaculatory bulb often bent.

Female terminalia: Spermathecae (1+1 or 1+2) usually uniform, but sometimes asymmetrical, shape variable but usually bulbous or mushroom-shaped, texture and sclerotization variable. Ventral receptacle mushroom-shaped, with distinct head and stem.

Genus Eopseudopomyza† Hennig

Eopseudopomyza Hennig, 1971: 7 (Figs. 1–11). Type species: Eopseudopomyza kuehnei Hennig, 1971 (by monotypy).

Hennig, 1971: 7 (diagnosis, relationships, illustr.); Spahr, 1985: 96 (catalog of fossil species); Evenhuis, 1994: 400 (catalog of fossil species); Hoffeins & Woźnica, 2013: 318 (diagnosis, relationships).

The genus includes two species, *E. kuehnei*† Hennig from Baltic amber (female type in SMNS) and *E. szadziewskii*† Hoffeins & Woźnica from Baltic and Bitterfeld amber (male type in SDEI). *Eopseudopomyza* is thought to be closely related to *Tenuia* and *Pseudopomyzella* (Hennig, 1971; Hoffeins & Woźnica, 2013).

Diagnosis

With 4 fronto-orbital setae. Subvibrissa absent. With 1+4 dorsocentral setae, anterior intra-alar and supra-alar (1+1) and 3 scapular setae. Scutellum with discal setulae and 3 marginal setae. Katepisternum with 2 setae. Cells bm and dm confluent. Epandrium with 2 pairs of outstanding setae.

Description

The description below is a compilation of Hennig (1971) and Hoffeins & Woźnica (2013).

Length 1.44–2.66 mm (males), 1.67–2.12 mm (females). Small, compact flies. Coloration not vividly shown through amber.

Head: Ocellar triangle dark brownish. Frontal vitta with few scattered minute setulae, some on the fronto-orbital plate. With 4 fronto-orbital setae, anterior seta about half length of posterior seta. Ocellar, inner vertical and outer vertical setae well developed, inner vertical of greatest length. Postocellar setae strong and cruciate; paravertical seta small and thin; seriate postocular setulae present. Vibrissa strong, subvibrissa absent, gena with a row of 7 setulae, slightly longer near vibrissa. Postgena with 2 long setae at lower margin. Antennae porrect, pedicel with entire circlet of setulae apically including some longer setae; first flagellomere discoid; arista arising from first flagellomere mid-dorsally, longer than height of head, short pubescent.

Thorax: Dorsocentral setae (1+4) subequal except posterior most setae long and strong. Three rows of somewhat irregular setae between dorsocentrals, middle

row slightly longer, prescutellar pair present. Anterior intra-alar, supra-alar (1+1) setae subequal, postalar seta large, intrapostalar seta small; 3 scapular setae; 1 strong postpronotal and multiple small, scattered setae; 2 strong notopleural setae; 1 proepisternal seta. Scutellum with several scattered discal setulae and 3 pairs of strong marginal setae. Katepisternum with 2 subequal setae.

Legs: Fore femur with 1–2 rows of strong dorsal setae; mid femur chaetotaxy variable; hind femur with 1–2 subapical dorsal setae. Fore tibia with short background setulae only; mid and hind tibiae chaetotaxy variable but always with strong apical seta(e).

Wing: Second costal sector with spines. Cells bm and dm confluent.

Male terminalia: Epandrium elongate, with 2 pairs of outstanding setae, pair near anterior margin longer than posterior pair. Cercus setose, shape variable. Surstylus shape variable but elongate and larger than cercus.

Key to fossil species of Eopseudopomyza Hennig

Genus Heloclusia Malloch

(Figs. 9.1–5, 10.1–5, 11.1–3)

Heloclusia Malloch, 1933: 184–187 (Figs. 36, 37). Type species Heloclusia imperfecta Malloch, 1933 (Monotypy).

Harrison, 1959: 119 (diagnosis, relationships, systematic position);
Gill, 1968: 4 (catalog of Neotropical species); Hennig, 1969:
591 (keyed); Krivosheina, 1979: 188 (keyed, phylogenetic notes); Prado, 1984: 1 (Neotropical catalog); McAlpine, 1989: 1432; Buck & McAlpine, 2010: 824 (keyed).

Diagnosis

With 3 fronto-orbital setae. Carina bare, without rows of minute setulae. Subvibrissa well developed. Arista short pubescent. Postcranium somewhat convex. With 1+3 dorsocentral setae, anterior intra-alar, supra-alar (1+1), 3-4 scapular setae. Scutellum with discal setulae and 3 marginal setae. Katepisternum with 2 setae. Second costal sector of wing with spines. Subcosta distally merged with R₁. Crossvein bm-m absent, cells bm and dm confluent. Male S6 with π-shaped sclerotization. S7+8 asymmetrical, S7 ventral arm ending shortly after right nub. Epandrium with 2 large pairs of setae. Subepandrial sclerite with anterior pair of setae at approximately mid-length and 1 large seta at subepandrial-surstylus articulation. Ventral bridge of hypandrium present, dorsal surface of dorsal bridge extended posteriorly. Pregonites arising from midwidth of hypandrium.

Monotypic

Heloclusia imperfecta Malloch

Description

Length 4.6–4.7 mm (males), 5.1–5.6 mm (females). Slender flies with elongated body, relatively long legs and conspicuously long setae. General colour tan-yellow with inconspicuous darker brown markings.

Head: Fronto-orbital plate glossy, tan-yellow (white around eye when live (Figs. 9.4-5)); frontal vitta brown, darkest medially; ocellar triangle dark brown to black, shading extend posteriorly to middle of median occipital sclerite. Three reclinate fronto-orbital setae increasing in size posteriorly. Frontal vitta with numerous uniformly scattered minute setulae, some on the fronto-orbital plate. Ocellar, inner vertical and outer vertical setae well developed, inner vertical of greatest length and subequal to upper orbital seta. Postocellar setae cruciate; paravertical seta small, length similar to most ventral postocular setae. Postcranium somewhat convex, with uniformly scattered small setae, ones close to occipital foramen longest; supracervical setae dense. Vibrissa and subvibrissa very well developed, gena with scattered small setulae clustering around vibrissa, subvibrissa and along ventral margin through to postgena, lower margin of postgena with a row of 4 well developed setae. Face mostly membranous, but margins of sub-antennal depression and outer face sclerotized; carina obsolete or indistinct; face bare (without minute setulae). Antennae porrect; arista short pubescent, inserted dorsally and subapically, almost 2× total length of 3 basal antennomeres.

Thorax: Tan-yellow, mesonotum with 3 brown stripes running in between well-developed supra-alar, intra-alar and dorsocentral setae; an episternum with indistinct stripe along dorsal and ventral margins, ventral stripe reaching dorsal posterior corner of katepisternum. Dorsocentral setae (1+3) long; prescutellar acrostichal setae short; anterior intra-alar, supra-alar (1+1) and postalar setae large, intrapostalar seta small; postpronotal seta large; anterior notopleural seta large, posterior notopleural seta small; scutum with 3-4 scapular setae; notum with uniformly scattered minute black setulae. Scutellum with 3 pairs of marginal setae progressively longer basal to distally, disc with uniformly scattered minute black setulae. Proepimeral seta large, with several small setulae at base. Katepisternum with a pair of equal length dorsal setae; posterior half with scattered minute black setulae; ventral half with numerous setae.

Legs: Tan-yellow except dorsal portion of fore femur, apical quarter to third of fore tibia, apex of first and remaining tarsomere brown. Fore femur with 2 rows of strong setae on posterodorsal surface; ventral surface of male fore femur with dense fine setae of decreasing length towards apex, female with only a long fine seta at base of femur; apical third with a row of strong posteroventral setae of decreasing length towards apex. Fore tibia with 1 small dorsal and a pair of long distal dorsal (dorsal and posterodorsal) setae. Base of

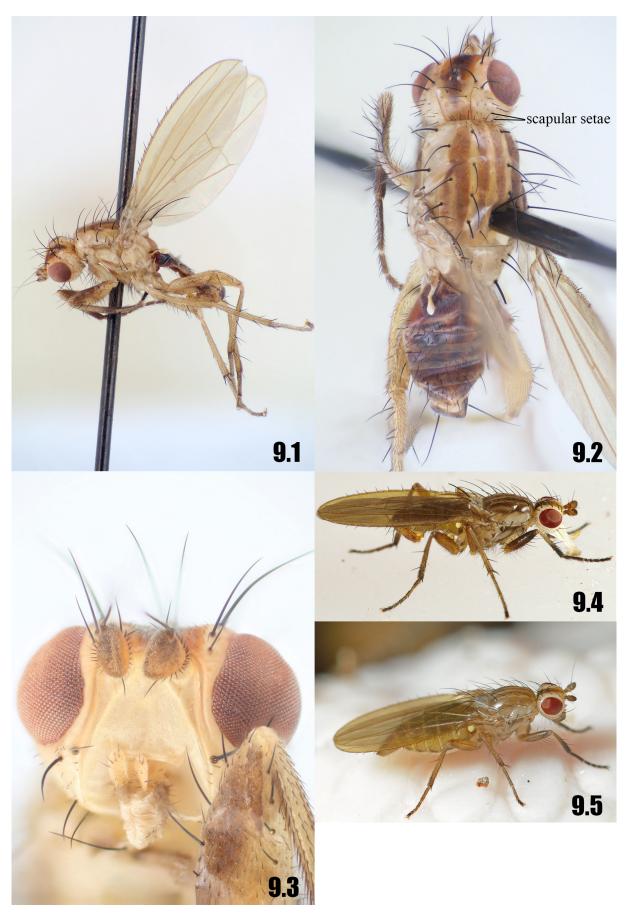
first tarsomere with 2 laterally flattened strong setae on posterior edge of dense ventral comb of setae. Mid and hind femur with a row of anterior setae slightly longer than background setae, and a long anterior seta at distal two third of femur and slightly below the row of setae. Mid tibia with posterodorsal seta at mid-length, 2 pairs of distal dorsal (anterodorsal and posterodorsal) setae at distal end and two thirds of tibia length; ventroapical edge with 2 small median and 2 large lateral setae. Hind tibia with 2 anterodorsal and 4 posterodorsal setae on distal two thirds; anteroventral-apical edge with 1 large and 2 smaller stronger setae, posteroventral-apical edge with a small comb of setae.

Wing: Second costal sector with spines, densest on ventral edge. Costa surpassing R_{4+5} and reaching M_1 . Subcosta incomplete, distally merged with R_1 . Crossvein bm-m absent, cells bm and dm confluent. Cell cua open.

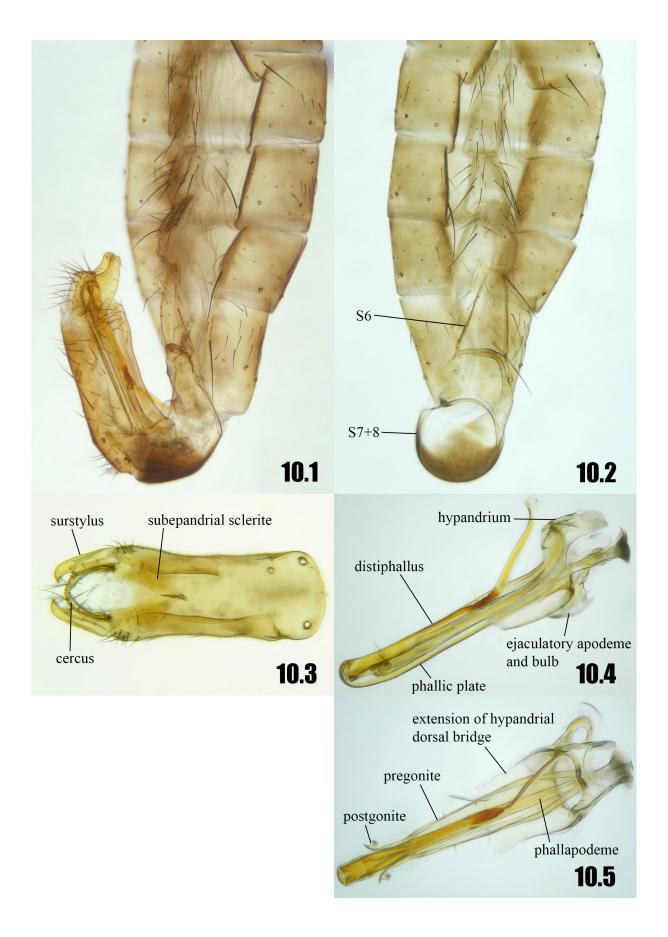
Abdominal T1–6 brown to dark brown, large, well sclerotized, with numerous black setae, longer setae on posterior margin of tergite. S1–5 small but well sclerotized, with numerous black setae.

Male terminalia (Figs. 10.1–5): Anterior half of S6 subquadrate; sensory setulae at upturned anterolateral corners; with scattered black setae and a π-shaped sclerotization starting from anterior margin of sternite with arms extending to posterolateral corners of S6 and articulating with nubs of S7 ventral arm. S7+8 dorsally dark brown, without any setae, asymmetrical, weak on right; left side of S7+8 with cleft indicating boundaries of S7 and S8 S7 ventral arm ending shortly after right nub; S8 ventral arm present; space between two arms large and connected by weakly sclerotized plates. Epandrium long, uniform in width except for slight distal widening, with 2 large pairs of setae of which anterior pair longest; dorsal and distal surface with numerous black setae. Surstylus shoe-shaped, with few small setae on medial surface and apex. Cerci converging distally, setose along entire length, apices narrowly contiguous. Subepandrial sclerite sheetlike, V-shaped, with anterior pair of setae (large anterior and small posterior) at approximately mid-length and 1 large seta at subepandrial-surstylus articulation. Ventral bridge of hypandrium present, anterolateral corners of hypandrium flat and broad, posterolateral corners weakly developed; dorsal surface of dorsal bridge extended posteriorly, almost 1/3 of phallus length, distance between extension and phallic plate differentiable, phallic plate well sclerotized, straight, and relatively flat. Pregonites arising from mid-width of hypandrium, anteriorly arched and laterally bowed to flank phallapodeme, mid-section somewhat flattened with 2 (sensory) setulae. Postgonite flat at base, especially desclerotized on dorsal edge, apex sickle-shaped with a subquadrate lobe extending perpendicular from surface, lobe with 1 long (sensory) setulae. Phallapodeme straight, length anterior to dorsal bridge only slightly surpassing hypandrium. Distiphallus elongated, medially twisted, apex of basal distiphallus very well sclerotized. Ejaculatory apodeme fan-shaped, ejaculatory bulb long and strongly bent at base.

Female terminalia: Sternites progressively smaller posteriorly, S6 relatively weakly sclerotized and setose



FIGURES 9.1–5: *Heloclusia imperfecta* (Chile). 9.1, male habitus left lateral; 9.2, dorsal; 9.3, head; 9.4, living male photographed in Liquine, Chile by SAM; 9.5, living female on carrion bait (chicken feet) photographed in Puyehue, Chile by SAM.



FIGURES 10.1–5: *Heloclusia imperfecta* male abdomen (Chile). 10.1, terminalia left ventrolateral; 10.2, terminalia ventral; 10.3, epandrium ventral; 10.4, phallus and associated structures left lateral; 10.5, phallus and associated structures ventral.



FIGURES 11.1–3: *Heloclusia imperfecta* female abdomen (Chile). 11.1, terminalia dorsal; 11.2, terminalia ventral; 11.3, spermathecae and associated structures.

with a pair of long setae at posterolateral corners. T7 medially brown, S7 uniformly yellow except posterior tip; S7 with anteromedial key-hole-shaped sclerotization. Spermathecae (1+1) mushroom-shaped, basal opening as wide as its circumference, with apical depression.

Type specimens (not examined): Holotype: ♂:

CHILE: Concepción: Concepción, R.C. Shannon (NHMUK).

Paratype: **ARGENTINA: Río Negro:** Nahuel Huapi, Puerto Blest, R.C. Shannon (1° , NHMUK).

Other material examined: CHILE: Araucanía: Pucón, pond near mouth of Río Quelhue, 29.ix.2013,

SAM (1 \updownarrow , DEBU); **Los Ríos:** Hwy 201, between Liquine & Conaripe, bamboo seeps, 1–4.xii.2013, SAM (2 \circlearrowleft , 1 \updownarrow , DEBU); **Los Lagos:** Río San Pedro, 24 km NE of Los Lagos, riverbank slope forest, YPT, 13–18.xi.2000, L. Packer (1 \updownarrow , DEBU).

Comments: A photo of a living female was taken in Puyehue, Chile by SAM. The female was attracted to, and photographed on, carrion (chicken feet) (Fig. 9.5).

Genus Latheticomyia Wheeler

(Figs. 12.1–5, 13.1–5, 14.1–3)

Latheticomyia Wheeler, 1956: 306. Type species *Latheticomyia tricolor* Wheeler, 1956 (original designation).

Wheeler, 1956: 305 (descriptions, relationships, illustr.); Hennig, 1969: 591 (keyed, relationships); Krivosheina, 1979: 187 (diagnosis, keyed, phylogenetic notes); Prado, 1984: 1 (Neotropical catalog); McAlpine 1987: 760; Krivosheina, 1999: 502 (keyed); Buck & McAlpine, 2010: 824 (keyed); Marques & Rafael, 2016: 425 (diagnosis), 433 (key to species).

The genus includes seven described species, L. infumata Wheeler from Nicaragua (female type in USNM), L. lineata Wheeler from the United States of America (female type in USNM), L. longiterebra Hennig from Peru (female type in CNC), L. peruana Marques and Rafael from Peru (male type in MUSM), L. rotundicornis Hennig from Mexico (female type in CNC), L. tricolor Wheeler from North America (male type in USNM) and L. xantha Marques and Rafael from Peru (male type in MUSM). Many species remain to be described and we recognize 16 unnamed species currently in the University of Guelph Insect Collection. Little is known about the biology of *Latheticomyia* species, but we have seen adults attracted to small dung deposits and bird droppings in Bolivia and Costa Rica and some species (L. tricolor and L. lineata) have been collected in banana-baited trap cans set out for Drosophila (Wheeler, 1956). Some of the specimens at the University of Guelph Insect Collection were collected in dung-baited traps set out to collect Sphaeroceridae but most of the specimens we have seen were collected by sweeping or taken in Malaise traps, often at higher elevations (above 1000 m). The genus is closely related to the Oriental genus Tenuia.

Diagnosis

With 3 fronto-orbital setae. Carina with 2 rows of minute setulae. Subvibrissa absent. Arista with weak, short pubescent. With 5 dorsocentral setae, 1+1 supra-alar setae, usually 2 scapular setae, but no anterior intra-alar setae. Scutellum with discal setulae and 2–4 marginal setae. Katepisternum with 2 setae. Subcosta distally merged with R₁. Crossvein bm-m absent or faint. S7+8 asymmetrical, S7 arm ends shortly after right articulation with S6. Base of cercus articulating only with surstylus. Subepandrial sclerite with 2–3 setae on protuberance. Hypandrium with weak or no ventral bridge. Pregonites arising from sides of hypandrium, short and dorsally bent.

Postgonite usually short. Pregonite ending position and postgonite starting position within hypandrium hugging boundaries. Female with 1+2 spermathecae.

Description

This description is based on the examination of *L. infumata*, *L. longiterebra*, *L. peruana*, *L. tricolor* and undescribed species from the New World, with reference to Hennig (1969), Marques and Rafael (2016) and Wheeler (1956).

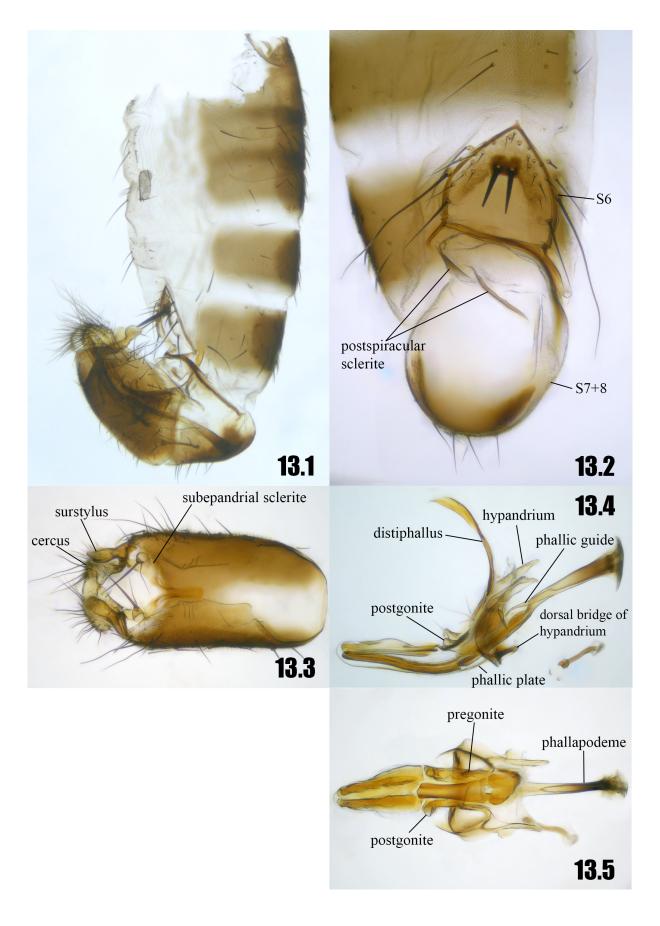
Length 2.5–3.5 mm (males), 3–3.8 mm (females). Slender flies with elongate body and relatively long legs. General colour dark brown to black, with variegated ivory white to orange and dark brown patterns on head, mesonotum, scutellum, pleuron, and legs.

Head: Fronto-orbital plate mostly ivory white through to occiput with dark brown portion near base of antennae; frontal vitta (including ocellar triangle) mostly dark brown to black through to postcranium with ivory white to orange median strip of various size starting at anterior margin; face ivory white; antennae dorsally dark brown to black, ventrally ivory white to orange; gena anteriorly usually ivory white, posteriorly with variegated white brown patterning, pattern often continue through to postgena. Length of 3 reclinate (posterior seta slightly more lateroreclinate) fronto-orbital setae increasing consecutively; anterior margin of fronto-orbital plate and anterolateral corners of frontal vitta densely setulose, other setulae scattered mainly on anterior half of frontal vitta with a few occurring on fronto-orbital plate between setae. Frontal vitta longitudinally depressed, more so anteriorly. Ocellar, inner vertical and outer vertical setae well developed, inner vertical of greatest length. Postocellar setae well developed and cruciate; paravertical seta small, length similar to most ventral postocular setae. Postocular plate flat to slightly convex, median occipital sclerite flat to slightly concave, occiput without macrotrichia, supracervical setae dense. Vibrissa well developed, no distinguishable subvibrissa from a row of setulae along length of gena. Gena 0.2× eye height. Postgena with 2 strong setae, and uniformly scattered setulae. Face membranous ventromedially and often sunken, sub-antennal plate and outer face plate intact but weak; carina weak, at most extending to ventral points of sub-antennal depression, with 2 rows of minute setulae. Antennae somewhat porrect; arista weak to short pubescent, inserted dorsally and subapically, only slightly longer than total length of the 3 basal antennomeres.

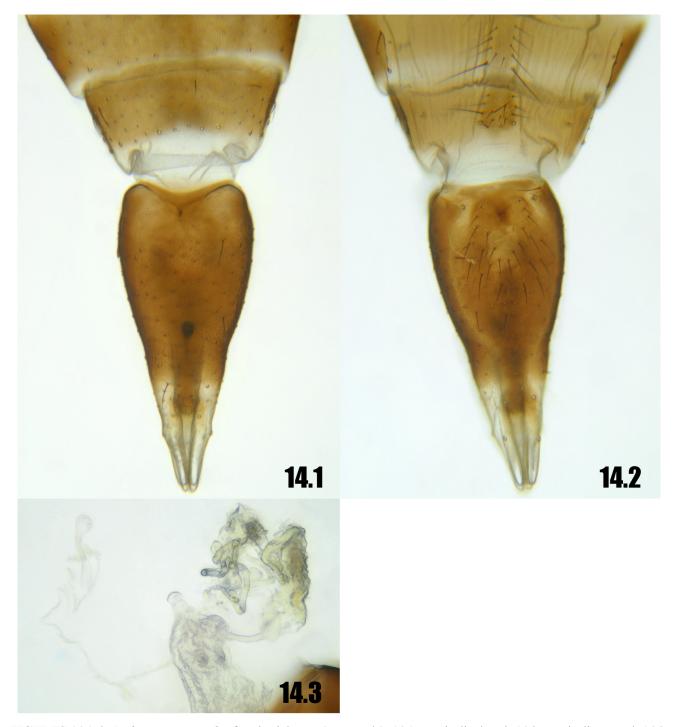
Thorax: Mesonotum with or without longitudinal patterns; scutellum often ivory white medially and brown laterally; pleuron often with transverse bandings. Five pairs of well-developed dorsocentral setae (1 presutural, 1 near transverse suture, 3 postsutural); anterior 4 similar in length, posterior pair longest. Prescutellar acrostichal seta only slightly longer than background setulae. Intrapostalar seta small. Supra-alar (1+1) and postalar setae as strong as posterior-most dorsocentral seta. Usually 2 scapular setae; 1 large postpronotal seta; 1 large anterior and 1 smaller posterior notopleural setae; minute black setulae uniformly scattered on notum; 1 proepisternal seta. Scutellum often with scattered setulae and 2–4 pairs of marginal setae



FIGURES 12.1–5: *Latheticomyia* male habitus. 12.1, *Latheticomyia infumata* head (Costa Rica); 12.2, *Latheticomyia tricolor* left lateral (U.S.A.); 12.3, *Latheticomyia tricolor* dorsal (U.S.A.); 12.4, *Latheticomyia infumata* species group sp. left lateral (Bolivia); 12.5, *Latheticomyia infumata* species group sp. dorsal (Bolivia).



FIGURES 13.1–5: *Latheticomyia infumata* species group sp. male abdomen (Bolivia). 13.1, terminalia left ventrolateral; 13.2, terminalia ventral; 13.3, epandrium ventral; 13.4, phallus and associated structures left lateral; 13.5, phallus and associated structures ventral.



FIGURES 14.1–3: *Latheticomyia tricolor* female abdomen (Guatemala). 14.1, terminalia dorsal; 14.2, terminalia ventral; 14.3, spermathecae and associated structures.

progressively longer basal to distally. Katepisternum with a pair of equal length setae and setulae scattered at base, ventral corner with several setae.

Legs: With various banding patterns of ivory white and brown. Fore femur with a row of strong setae on posterodorsal surface; posteroventrally with a row of strong setae of increasing length until ³/₄, setae on apical quarter gradually decreasing in length. Base of first tarsomere with 2 stronger setae on posterior edge of ventral comb of setae. Mid tibia with a pair of ventroapical seta. Hind tibia with a stronger anteroapical seta.

Wings: Costa surpassing $R_{_{4+5}}$ and weakening before reaching $M_{_{1}}$. Subcosta incomplete, distally merged with $R_{_{1}}$. Crossvein bm-m absent or faint. Crossvein CuA present and cell cua closed.

Abdominal tergites well developed and sclerotized; with numerous black setae; dorsally brown, except sides of tergites, anterior half of T1, dorsal triangle of T2 ivory white. Sclerites 1–5 small and subquadrate, with black setae.

Male terminalia (Figs. 13.1–5): Colour pattern on S7+8 and epandrium variable. S6 shape variable but usually with

sclerotization close to outer margin. S7+8 anterodorsally convex; asymmetrical because sclerotization of S7 arm ends shortly after right articulation with S6; left side of S7+8 with cleft indicating boundaries of S7 and S8; S8 arm partial or absent. Surstylus variable but usually elongate and dilated apically. Cerci variable but fused or contiguous below anal opening and covered with long dense setae, base articulating only with surstyli. Subepandrial sclerite variable, setae (2-3) close to base of articulation with surstylus and on protuberance. Hypandrium with weak or no ventral bridge, dorsal surface of dorsal bridge not extended posteriorly but dorsal bridge long and very well sclerotized. Phallic plate well sclerotized, flat, straight to slightly bent medially. Pregonites arising from sides of hypandrium, short and dorsally bent, not flanking phallapodeme. Postgonite variable but usually short. Phallapodeme usually relatively straight, sometimes with some curvature, often flattened posteriorly with an apparent kink at base of flattened portion. Phallic guide arising before the phallapodeme kink, often small and narrow. Distiphallus often with some curvature, distal segment often twisted to the right. Ejaculatory apodeme variable but usually long and at least somewhat fanshaped apically, ejaculatory bulb simple.

Female terminalia: S6 slightly shorter and wider than preceding sternites but similarly well sclerotized, setose with a pair of long setae anterior to posterolateral corners. S7 usually well sclerotized throughout, with or without variegated cream and brown patterns. Spermathecae (1+2) usually small, bulbous and weakly sclerotized; variable in shape.

Key to described species of *Latheticomyia* Wheeler (A key to the 23 species of *Latheticomyia*, including 16 new species, is currently in manuscript and will appear elsewhere)

- 1) Scutum dark without medial white or yellow patterns 2
 Scutum with medial white or yellow patterns 3

- 4) Medial white marking extending entire length of scutum; meron white with some yellow. Mid femur yellow; hind femur dark brown
- L. infumata Wheeler (Nicaragua, Costa Rica and Panama)Scutum with V-shaped white marking posterior to transverse

Genus Polypathomyia Krivosheina

Polypathomyia Krivosheina 1979: 180. Type species Polypathomyia stackelbergi Krivosheina, 1979 (Monotypy).

.....L. lineata Wheeler (United States of America)

Krivosheina, 1979: 185 (description, position in Pseudopomyzidae, illustr.); Shatalkin, 1994: 142 (diagnosis, relationships, key to *Tenuia*, *Polypathomyia* and *Pseudopomyza atrimana*); Krivosheina, 1999: 502 (keyed).

Diagnosis

With 3 fronto-orbital setae. Carina with 2 rows of minute setulae. Subvibrissa absent. Arista weakly pubescent. With 1+3 dorsocentral setae, anterior intra-alar and 1+1 supra-alar setae. Scutellum with 3 marginal setae. Katepisternum with 2 setae. Second costal sector of wing with spines. Subcosta incomplete but not merging with R₁. Crossvein bm-m present. Ventral bridge of hypandrium present. Pregonites arising from mid-width of hypandrium.

Monotypic

Polypathomyia stackelbergi Krivosheina

Description

This description is compiled from Krivosheina (1979) and Shatalkin (1994). No specimens of the genus were examined.

Slender flies with elongate body and relatively long legs. General colour dark brown with variegated yellow to ivory white and dark brown patterns on head and legs.

Head: Fronto-orbital plate glossy, tan-yellow to ivory white through to postocular plate; frontal vitta dark brown to black except anterior margin, pruinose; face ivory white with dark brown patterning; antennae colouration variable; gena with variegated white and brown patterning; coloration of postcranium variable. Three reclinate fronto-orbital setae increasing in size posteriorly. Frontal vitta with numerous uniformly scattered minute setulae. Frontal vitta longitudinally depressed, more so anteriorly. Ocellar, inner vertical, outer vertical and postocular setae well developed; paravertical seta small. Postocular plate flat to

slightly convex, median occipital sclerite flat to slightly concave, occiput with uniformly scattered small setae, ones close to occipital foramen longest; supracervical setae dense. Vibrissa well developed, no distinguishable subvibrissa from a row of setulae along length of gena. Gena $0.2\times$ eye height. Postgena with 2 strong setae, and uniformly scattered setulae. Face membranous ventromedially and often sunken, sub-antennal plate and outer face plate intact and somewhat sclerotized; carina weak, at most extending to ventral point of sub-antennal depression, with 2 rows of minute setulae. Antennae somewhat porrect; pedicel with large dorsal and ventral seta; first flagellomere round; arista weakly pubescent, inserted dorsally and subapically, $2\times$ total length of the 3 basal antennomeres.

Thorax: Dark brown to black. Mesonotum with 3 hardly discernible stripes along acrostichal and dorsocentral lengths. Dorsocentral setae (1+3) long; acrostichal in 2 rows of setulae; anterior intra-alar and supra-alar (1+1) setae present; 1 postalar, 1 postpronotal, 2 notopleural setae; notum with scattered minute black setulae. Scutellum with 3 pairs of marginal setae. One proepimeral seta. Katepisternum with a pair of equal length setae and a few small setulae.

Legs: Coxa and base of fore femur and entire middle and hind legs yellow, last two segments of fore tarsus white, remaining dark brown to black, hind tibia slightly darkened basally and apically. Coxa with groups of strong black setae on anterior surface. Fore tibia and tarsi, especially first tarsal segment, with massive dense setae erect along lateral sides, giving a slightly flattened appearance. Middle and hind tibia and tarsi with sparser and finer setae. Middle tibia with several terminal setae varying in length. Hind tibia with 1 small preapical seta.

Wing: Costa surpassing R_{4+5} and reaching M_1 ; second costal sector with spines. Subcosta incomplete but not merging with R_1 . Crossvein bm-m present. Crossvein CuA present and cell cua closed.

Abdominal T1–6 brown to dark brown, large, well sclerotized, with numerous black setae, posterior margin of tergites with longer setae. S1–5 small but well sclerotized, with numerous black setae.

Male terminalia: S6 triangular with strong setae. S7+8 convex anterodorsally. Epandrium with a pair of long anterior setae. Surstylus elongate, posteriorly directed, with apical small black spines ventrally. Cerci posteriorly directed, fused below anal opening. Ventral bridge of hypandrium present, anterolateral corners pointed. Pregonites arising from mid-width of hypandrium, straight, not flanking phallapodeme, with 2 "sensory" setulae on distal 1/4. Apex of postgonite sickle-shaped, with 1 long setulae. Phallapodeme straight, length anterior to hypandrial bridge 1/3 of remaining length. Distiphallus elongate and apically curly. Ejaculatory apodeme thin and elongate, ejaculatory bulb short and wide.

Female abdomen and terminalia descriptions unavailable.

Type specimens: Holotype: ♀: **RUSSIA: Kuril Islands:** Kunashir Island, Mandeleyevo, reared from larva developed underneath bark of *Aralia* sp., emergence

date 20.vi.1977, collection date 11.v.1977, A.I. Zaytsev (ZISP).

Paratypes: Same collection data as holotype $(1 \circlearrowleft, 2 \circlearrowleft, 1SEA)$.

Comments: Other specimens examined by Krivosheina were also collected as larvae and reared from under *Amur maackia* bark and roots or oak timber. The species is found in the Khabarovsk Territory and Kunashir Island of Russia.

Genus Pseudopomyza Strobl

Pseudopomyza Strobl, 1893: 284. Type species P. nitidissima Strobl (= Opomyza atrimana Meigen 1830) (by monotypy).

Hendel, 1902: 261 (diagnosis, systematic position); Becker, 1905: 251 (catalogue of Palaearctic species); Melander, 1913: 228 (diagnosis, relationships); Frey, 1952: 7 (diagnosis, systematic position); Hennig, 1969: 591 (keyed); Stackelberg, 1969: 325 (key to species of the European part of the USSR); Chandler, 1983: 89 (diagnosis); Mathis, 1989: 470 (catalogue of Australasian species); McAlpine, 1994: 181 (diagnosis), 182 (key to subgenera); Shatalkin, 1994: 143 (diagnosis); Merz, 1998: 132 (list of species in Switzerland); Krivosheina, 1999: 503 (keyed); Papp, 2001: 268 (checklist of species of Hungary); Shtakelberg & Chudzicka, 2007: 198 (list of Polish species); Roháček, 2009: 1 (list of species of the Czech Republic and Slovakia); Beuk, 2013: 1 (checklist of species of the Netherlands); Kahanpää & Stuke, 2014: 254 (checklist of species of Finland); McAlpine, 2019: 88 (key to Australian species); Chandler, 2021: 271 (list of species of the British Isles).

Diagnosis

With 2–3 fronto-orbital setae. Carina pollinose without minute setulae. Subvibrissa present. Arista pubescent. With 1+3 dorsocentral setae, anterior intra-alar present or absent, 1+1 supra-alar setae, usually with 1 scapular seta, but sometimes with 2 or more. Scutellum usually with 2 marginal setae, without discal setulae but sometimes with a cluster of 3 minute setulae at base of basal seta. Katepisternum with 1 seta. Subcosta distally merged with R₁. Crossvein bm-m absent, cells bm and dm confluent. Male S6 U-shaped or H-shaped. S7+8 either symmetrical and close-ringed or asymmetrical and open-ringed; left side of S7+8 with or without cleft indicating boundaries of S7 and S8; postspiracular sclerite present or absent. Subepandrial sclerite with 2 setae. Ventral hypandrial bridge present. Pregonites arising from mid-width of hypandrium.

Description

This description is based on the examination of *P. antipoda*, *P. aristata*, *P. brevicaudata*, *P. brevis*, *P. flavitarsis* and *P. nigritarsis* **sp. nov.** from New Zealand; *P. atrimana* from Japan and Russia; *P. brevifacies* from Japan, Malaysia and Taiwan; *P. collessi* and *P. medianentis* **sp. nov.** from Australia; *P. adunca* **sp. nov.**, *P. albimana*, *P. ampliata*

sp. nov., *P. angustifrons* **sp. nov.**, *P. binaevia* **sp. nov.**, *P. brunneicacumen* **sp. nov.**, *P. chilensis* **sp. nov.**, *P. cordata* **sp. nov.**, *P. cyathiformis* **sp. nov.**, *P. flavicacumen* **sp. nov.**, *P. gambiformis* **sp. nov.**, *P. inflexa* **sp. nov.**, *P. machaera* **sp. nov.**, *P. nigrimana*, *P. parabinaevia* **sp. nov.**, *P. proboscis* **sp. nov.**, *P. prolata* **sp. nov.**, *P. simulatrix* **sp. nov.** from the Neotropical region.

Body compact, length 1.5–3.0 mm. General colour dark brown with variegated yellow to ivory white and dark brown patterns on head and legs.

Head: With 2–3 reclinate (posterior seta often slightly latero-reclinate) fronto-orbital setae; ocellar, inner vertical and outer vertical setae large and subequal; postocellar setae cruciate; paravertical seta small but differentiated from other setulae; lower frons with scattered small setulae. Antenna bicolored or uniformly brown; arista arising dorsoapically to dorso-preapically, pubescent, as long as or slightly shorter than head width; pedicel with long mediodorsal and medioventral setae, medial surface with 2 rows of smaller setae at margin and lateral surface with 1 row of smaller setae at margin, setae progressively larger when closer to medioventral long seta. Vibrissa distinct; subvibrissa usually present, at least slightly differentiated from the surrounding setulae; gena with setulae scattered along ventral 2/3; postgena with 2-4 setae at lower margin. Colour patterns and pruinosity on gena variable. Genal height 0.2-0.6× eye height. Desclerotization of face variable thus length of facial carina variable; carina pollinose. Facial colour patterns highly variable, sometimes with sexual dimorphism.

Thorax: One strong postpronotal seta and 2 notopleural setae present. Usually with 1 scapular seta, but sometimes with 2 or more. With 1+3 dorsocentral setae, anterior 3 of various lengths, but 2nd no longer than 1st and 3rd; last seta always longest. Medial acrostichal setae usually present, prescutellar acrostichal setae sometimes present and paired. Supra-alar (1+1) setae present (except *P. angustifrons*) and of various lengths, anterior intra-alar seta present or absent, postalar seta present and always longest of the two. Intrapostalar seta small. Scutellum heavily pruinose, usually with 2 pairs of marginal setae, apical pair convergent or cruciate and longer than basal pair, without discal setulae but sometimes with a cluster of 3 minute setulae at base of basal seta. Katepisternum with 1 seta.

Legs: Fore femur with posterodorsal and ventral row of setae along length of femur; posterodorsal setae generally shorter. Fore tibia distally with relatively large ventral comb of setae compared to mid and hind leg. Mid tibia with strong ventral apical seta. Hind femur with 1 strong distal anterodorsal seta. Leg colour patterns variable, sometimes with sexually dimorphic differences on fore tarsus.

Wing: Costa surpassing R_{4+5} and weakening until M_1 , a pair of setae present before humeral and subcostal breaks. Subcosta incomplete, distally merged with R_1 . Crossvein bm-m absent. R_{2+3} with minimal to no upturn, almost parallel to or slightly converging with R_{4+5} . Crossvein CuA absent and cell cua open.

Abdominal T1–6 dark brown, large, unmodified, usually dorsally pruinose laterally glossy.

Male terminalia (Figs. 16.1-6, 31.1-6, 34.1-5, 36.1-5, 53.1-3): S6 U-shaped or H-shaped; posterior lobes of S6 apically articulating with S7+8. S7+8 either symmetrical and close-ringed or asymmetrical and openringed; left side of S7+8 with or without cleft indicating boundaries of S7 and S8; postspiracular sclerite present or absent. Epandrium with a pair of outstanding setae, a pair of posterior setae slightly larger than the numerous shorter setae rarely present, posteroventral corners sometimes extended posteriorly. Surstylus variable. Cerci converging distally and apically fused, setose along entire length. Subepandrial sclerite sheet-like, sometimes raised at spots but never forming a lobe, narrow or broad, with two posterolateral setae on each side, anterior seta generally longer than posterior seta. Hypandrium shape variable; ventral hypandrial bridge present, length variable, medially connected to pregonite; dorsal hypandrial bridge short; phallic plate well sclerotized, usually relatively straight and flat (except subgenus Apops). Phallapodeme straight or strongly arched; phallic guide usually present but reduced to a triangular extension from phallapodeme. Pregonites straight and independent of each other or arched and fused, with 2 sensory setulae. Postgonite articulating with bifurcate phallapodeme base; shape variable. Basal distiphallus variable but usually tubular; distal distiphallus variable but usually end with membranous mass.

Female terminalia: S6 weakly sclerotized or membranous, usually with 1–2 pairs of setae, rarely bare or with additional macrotrichia. Sclerotization pattern of S7 variable; no colour patterns. Spermathecae (1+1) shape and texture variable, but usually more sclerotized than spermathecal duct, sometimes asymmetrical. Ventral receptacle mushroom-shaped, with distinct head and stem.

Key to species of Pseudopomyza Strobl

1) Pedicel with 1 long ventral seta (Fig. 27.3). Mesonotum and mesopleuron largely devoid of pruinescence, glossy.......P. collessi (Dete) McAlpine (Australia) Pedicel with several long ventral setae (Fig. 44.3). Mesonotum and mesopleuron usually with pruinescence, 2) Subvibrissa positioned posterior to vibrissal angle (Figs. 15.1, 18.1, 21.1). Anterior intra-alar seta absent. Female oviscape with spectacle or bow-tie-shaped desclerotization (Figs. 17.2, 20.1, 25.1) (P. medianentis only know from one male)...... 3 (subgenus *Apops*, 6 species) Subvibrissa positioned on vibrissal angle (Figs. 30.1, 35.1, 41.1, 48.1), rarely absent. Anterior intra-alar seta present, rarely small or absent. Female oviscape variously desclerotized but not spectacle or bow-tie-shaped 9 3) Presutural acrostichal setae reduced or absent 4 Presutural acrostichal setae well developed, at least 2× With 2 fronto-orbital setae..... medianentis Yau and Marshall (Western Australia) With 3 fronto-orbital setae.....

	Subgenus <i>Apops</i> sp. nov. 2 CNC729327 (Figs. 26.1–3), an undescribed species known from a single female from the North Island of New Zealand	_	and katepisternum pruinose. Legs all brown
5)	With 3 fronto-orbital setae (anterior seta sometimes very		Subvibrissa absent. Face and carina protruding, facial
	small)		desclerotization not passing ventral point of sub-antennal
-	With 2 fronto-orbital setae		depression (Fig. 44.3). An episternum and katepisternum
6)	Fore femur dark brown except basal quarter yellow. Male		mostly glossy. Legs with variegated yellow and brown
	S6 with both large and small setae. Desclerotized area of		colour patterns
	female oviscape uniform, without small, sclerotized spots	1.4)	
	P. (Apops) nigritarsis Yau and Marshall (New Zealand)	14)	Pedicel brown, first flagellomere uniformly brown. Pleuron
-	Fore femur dark brown except basal sixth. Male S6 with		pruinose or pollinose; katepisternum with a row of 5 setulae
	uniformly large setae. Female oviscape with a pair of small		ventral to katepisternal seta; scutellum with no setulae.
	well sclerotized spots in middle of desclerotization (Fig.		Male S7+8 asymmetrical, right lateral less sclerotized than
7)	17.2)		left lateral; surstylus without lamella
7)	Male S6 with 3 strong setae	-	Pedicel yellow, first flagellomere bicoloured. Pleuron
			mostly glossy, rarely pruinose or pollinose; katepisternum
-	Male S6 with 4–5 strong setae		without a row of 5 setulae ventral to ketepisteral seta, if
0)			rare setulae present, never as described above; scutellum
8)	First flagellomere entirely tan or brown. Fore tarsus		with a cluster of 3 setulae at base of basal seta. Male
	uniformly brown. Distiphallus tubular with rounded edges.		S7+8 symmetrical, right lateral as well sclerotized as left;
	Desclerotized area of female oviscape uniform, without	1.5)	surstylus with lamella (Figs. 39.1, 39.3)
	small, sclerotized spots	15)	Medial acrostichal setae reduced
	P. (Apops) nigritarsis Yau and Marshall (New Zealand)		P. (Pseudopomyza) aristata (Harrison) (New Zealand) Medial acrostichal setae well developed, at least 2× as long
-	First flagellomere yellow basally, distodorsally tan or	-	
	brown. Fore tarsomere 1 brown, 2–5 creamy white. Distiphallus with sharp dorsal angle and extended left base.		as background setulae
	Female oviscape with small well sclerotized spot in middle	16)	Prescutellar acrostichal setae absent, prescutellar area with
	of desclerotization (Fig. 20.1)	10)	only scattered setulae. Pregonites mostly separated and
			not strongly arched dorsally; postgonite apically shallowly
9)	Subvibrissa strong, at least 0.5× length of vibrissa, and		forked and weakly trilobate; distiphallus asymmetrical
))	differentiated from background setulae (Figs. 30.1–2, 33.3).		
	Anterior half of phallic plate with prominent dorsomedial	_	Paired prescutellar acrostichal setae present. Pregonites
	ridge (Fig. 31.5, 34.4)	_	fused over more than two thirds of length and strongly
			arched dorsally; postgonite shape variable but not apically
_	Subvibrissa weak, at most 0.3× length of vibrissa or only		forked; distiphallus symmetrical
	2× length of background setulae (Figs. 35.1, 38.3, 41.1,		
	48.1). Phallic plate straight or slightly arched ventrally	17)	Fore tarsus uniformly brown (Figs. 51a, b, c, d, u, v, 63.1,
	(Figs. 36.4, 39.4)	11)	68.1, 85.1, 90.1, 93.1, 96.1)
		_	Fore tarsus with tarsomere 1 and sometimes part of tarsomere
10)	Brachypterous, wing width only half body width. M ₁ and		2 brown, remaining tarsal segments white, creamy white, or
/	M ₄ shortened past r-m, CuA+CuP highly reduced or absent,		yellow (Figs. 51e, f, g, h, i, j, k, l, m, n, o, p, q, r, s, t, 52.1,
	dm-m absent (Fig 33.2)		54.1, 57.1, 59.1, 65.1, 71.1, 74.1, 77.1, 80.1, 83.1) 23
		18)	Basal third to half of fore femur yellow; mid femur yellow
_	Wings normal, at least as wide as body	,	(Figs. 51c, u, v, 63.1, 90.1, 96.1)
	P. (Heluscolia) antipoda (Harrison) (New Zealand)	-	Fore femur dark brown except basal quarter or less; mid
11)	Eye small, 2× genal height; facial desclerotization past		femur tan except base and apex (Figs. 51a, b, d, 68.1, 85.1,
,	ventral point of sub-antennal depression (Figs. 41.3, 48.3).		93.5)21
	Legs brown, without colour patterns (Figs. 41.1, 48.1)	19)	Frons without median yellow stripe; face yellow except
	12		for dark brown marking restricted to inner face (Figs. 49e,
-	Eye large, at least 2.5× genal height; facial desclerotization		96.3). Fused apices of male cerci extending into a long shaft
	not passing ventral point of sub-antennal depression. Legs		(Fig. 97.1)
	with variegated yellow and brown colour patterns 14		P. (Pseudopomyza) prolata Yau and Marshall (Ecuador)
12)	With 2 pairs of marginal scutellar setae	-	Frons with median longitudinal yellow stripe down entire
-	With 3 pairs of marginal scutellar setaeSubgenus		length of frontal vitta. Dark brown marking mainly on outer
	Pseudopomyza sp. nov. 1 CNC729345 (Figs. 48.1-3) an		face but bleeding into inner face; dorsal half of sub-antennal
	undescribed species known from a single female from the		depression also with dark brown marking, remainder of
	North Island of New Zealand		face yellow (Figs. 49p, 63.3, 90.3). Fused apices of male
13)	Antenna entirely brown to black. Subvibrissa present. Face		cerci not extending into a long shaft (male of P. binaevia
	and carina flat to concave, facial desclerotization past ventral		unknown) (Fig. 91.1)
	point of sub-antennal depression (Fig. 41.3). Apenisternum	20)	Scutum with glossy hand posterior to prescutellar acrostical

	setae; anepisternum and katepisternum glossy (Fig. 63.1)	27)	Male face with brown colour bleeding partially into inner face from outer face (Fig. 491); female inner and outer face
	binaevia Yau and Marshall (Costa Rica)		brown (Fig. 49m). Mid femur tan except base and apex; hind
_	Scutum uniformly pruinose; anepisternum pruinose and		femur brown to dark brown, except base (Figs. 51r, s, 80.1).
	katepisternum posteroventrally pruinose (Fig. 90.1)		Surstylus with inner margin slightly concave between inner
			lamella and slightly dilated apex; inner lamella narrow,
	parabinaevia Yau and Marshall (Peru and Venezuela)		outwardly bent from surface of surstylus (Figs. 80.4, 81.1)
21)			
21)	Anterior margin of frons yellow, sometimes only marginally		D (D 1): A V 1M 1 H (C + D')
	at midpoint. Dark brown marking restricted to inner face		P. (Pseudopomyza) inflexa Yau and Marshall (Costa Rica)
	(absent on specimens from Puerto Rico). Gena with dark	-	Male outer face brown (Fig. 49n); female inner and outer
	brown spot under eye (mostly yellow on specimens from		face brown with some bleeding to medial edge of facial
	Puerto Rico)		ridge, facial carina tan (Fig. 49o). Mid femur yellow; hind
	P. (Pseudopomyza) nigrimana (Hennig) (Neotropical)		femur apically and distodorsally dark brown, otherwise
-	Anterior margin of frons dark brown. Face mostly brown to		yellow (Fig. 51t). Surstylus with inner margin angulate near
	dark brown, dark area not restricted to inner face (Figs. 49d,		middle, with apex drawn out and pointed; inner lamella
	f, 68.3, 93.3). Gena entirely brown to dark brown (Figs.		large, extremely convex to form posterior-facing cup (Figs.
	50c, e, 68.3, 93.3)		71.4, 72.1)P. (Pseudopomyza) cyathiformis Yau and
22)	Fronto-orbital setae subequal in length. Inner face of darkest		Marshall (Costa Rica)
	brown, sub-antennal depression, facial ridge and parafacial	28)	Gena glossy anterodorsally, otherwise pruinose (Figs. 50f,
	tan to yellowish (Figs. 49d, 93.3). Male S6 trilobate, with		g, 57.3, 83.3). Mid femur mostly tan or dark brown (Figs.
	single ventromedial lobe; surstylus hatchet-shaped, inner		51e, f, 57.1, 83.1)
	lamella crescent-shaped with concave inner margin (Fig.	_	Gena entirely glossy. Mid femur yellow (Figs. 51k, m, 65.1,
	94.1). Female S7 medially flattened, without protuberance		74.1)
	(Fig. 95.2)	29)	Frons uniformly brown; male outer face brown (Figs.
	P. (Pseudopomyza) proboscis Yau and Marshall (Costa	27)	49g, 57.3); female unknown. Mid femur tan except basal
	Rica and Guatemala)		and distal quarter; hind femur distodorsally dark brown,
-	First fronto-orbital seta 0.4× as long as second, third 0.8×		remainder yellow (Figs. 51e, 57.1). Anterolateral arms
	as long as second. Outer face darker brown than remaining		of male S6 long and of uniform width, twisted medially,
	brown face (Figs. 49f, 68.3). Male S6 H-shaped, with a		apical margin of arms parallel to posterior margin of S5.
	pair of anterolateral arms; surstylus paddle-shaped, inner		Surstylus paddle-shaped, at most 2× length of cercus,
	lamella broad spindle-shaped with convex inner margin		gently tapering at 3/5 to rounded apex (Fig. 58.1)
	(Fig. 69.1). Female S7 with basomedial protuberance (Fig.		P. (Pseudopomyza)
	70.2)		ampliata Yau and Marshall (Guatemala)
	(Pseudopomyza) P. cordata Yau and Marshall (Costa Rica	-	Anterior margin of frons yellow, remainder dark brown.
	and Peru)		Male outer face dark brown, partially bleeding into inner
23)	Face partially yellow, always including at least sub-antennal		face and facial ridge; female unknown (Figs. 49h, 83.3).
	depression and most of facial ridge (Figs. 49g, h, i, m, o,		Mid femur brown to dark brown, except base; hind femur
	52.3, 57.3, 83.3)		mostly brown with distodorsally indistinctly of darker
-	Face all or mostly brown (Figs. 49f, j, 54.3, 59.3, 65.3,		brown, only yellow at base (Figs. 51f, 83.1). Anterolateral
	74.3)31		arms of male S6 not particularly long or twisted, but distally
24)	Gena with a dark brown band no more than half genal		dilated and rounded with anterior point. Surstylus almost
	height below lower eye margin, continuous with dark brown		3× length of cercus, widest at mid-length, distal third drawn
	posterior half of gena, remainder yellow or tan (Figs. 50 j,		out to point (Fig. 84.1)
	k, l, m, 52.3, 71.3, 77.3, 80.3)		P. (Pseudopomyza)
_	Only anterior margin of gena yellow or tan, remainder dark		machaera Yau and Marshall (Guatemala)
	brown (Figs. 50f, g, i, 57.3, 65.3, 74.3, 83.3)	30)	Scutum pruinose posterolaterally (Fig. 65.2). Hind femur
25)	Frons almost entirely dark brown, with at most very narrow	30)	yellow with apical quarter dark brown (Figs. 51k, 65.1)
23)	yellow anterior margin (Figs. 49g, k, 52.3, 77.3)		P. (Pseudopomyza) brunneicacumen Yau and Marshall
	Anterior margin of frons yellow, connecting with median		(males, in part) (Costa Rica, Guatemala and Venezuela)
_	longitudinal yellow stripe extending to mid-point of frontal		Scutum glossy posterolaterally (Fig. 74.2). Hind femur
		-	
26)	vitta (Figs. 49l, m, n, o, 71.3, 80.3)		completely yellow (Figs. 51m, 74.1)
26)	Anterolateral arms of male S6 apically tapered; apex of		P. (Pseudopomyza) flavicacumen Yau and Marshall (males,
	surstylus tapered and curved medially, slightly hooked	21)	in part) (Costa Rica, Ecuador and Venezuela)
	(Figs. 52.4, 53.1)	31)	Face and from narrow, width subequal to eye width; second
			fronto-orbital seta longer than third (Fig. 59.3). One or no
	and Marshall (Bolivia, Ecuador and Venezuela)		supra-alar seta present. Fore femur brown distodorsally
-	Anterolateral arms of male S6 apically rounded; apex of		(Figs. 51i, j, 59.1)
	surstylus obliquely truncated, not curved medially or		angustifrons Yau and Marshall (Guatemala and Mexico)
	hooked apically (Figs. 77.4, 78.1)P. (Pseudopomyza)	-	Face and frons wider, width 1.3× eye width; second fronto-
	gambiformis Yau and Marshall (males) (Ecuador)		orbital seta subequal to third (Figs. 49f, j, 54.3, 65.3, 74.3,

- Hind femur completely yellow. Scutum glossy posterolaterally (Fig. 74.2). Female spermathecae mushroom-shaped (Fig. 76.4).....
 - P. (Pseudopomyza) flavicacumen Yau and Marshall (males, in part, and females) (Costa Rica, Ecuador and Venezuela) Hind femur yellow with light tan apical third (Fig. 99.1). Scutum pruinose posterolaterally (Fig. 99.2). Female

Subgenus Apops McAlpine

Apops McAlpine, 1994: 183 (as subgenus). Type species Pseudopomyza flavitarsis (= Heloclusia (Heluscolia) flavitarsis Harrison, 1959) (original designation). McAlpine, 1994: 182 (keyed).

The subgenus *Apops* was described for *P. flavitarsis* (Harrison), *P. arenae* McAlpine and "species C" of McAlpine (which is suspected to be *P. medianentis*, described here). The subgenus now also includes three new, widely disjunct, south temperate species, *Pseudopomyza chilensis* (Chile), *Pseudopomyza medianentis* (Western Australia) and *Pseudopomyza nigritarsis* (New Zealand). One further new species from New Zealand known only from a female (CNC729327) is illustrated but not formally described.

Diagnosis

The subgenus *Apops* previously included two species from New Zealand and Tasmania, and was characterized as follows: Head with 2 fronto-orbital setae; subvibrissa distinct; facial plate moderately developed but face extensively desclerotized ventromedially (often up to ventral corners of sub-antennal depression). Pedicel with several moderately long ventral setae, but no one very

long seta. Anterior intra-alar setae absent, mesonotum almost uniformly pruinose.

The subgenus is here characterized more broadly to include some species with 3 fronto-orbital setae (although the anterior seta may be small) and is further defined by synapomorphies including the absence of the anterior intra-alar seta and the presence of spectacle or bow-tie-shaped desclerotization on the ventral surface of the oviscape. Other diagnostic characters of the redefined subgenus include a strong subvibrissa greater or equal to $0.5 \times$ the length of the vibrissa and distinguished from background setulae, subvibrissa positioned posterior to vibrissal angle, desclerotization of the face dorsal to the ventral point of sub-antennal depression, two pairs of marginal scutellar setae, basal scutellar seta not accompanied by a cluster of three setulae, and male S6 arcuate with rounded anterior corners.

Description

Body length 1.6–3.0 mm (males), 2.1–3.0 mm (females).

Head: With 2–3 reclinate fronto-orbital setae. Antenna mostly yellow; first flagellomere partially or entirely tan; arista arising dorso-preapically, pubescent, slightly shorter than head width; pedicel with at least one large seta medial to medioventral long seta. Vibrissa distinct, subvibrissa at least 0.5× vibrissa length, gena with setulae scattered along ventral 2/3 and positioned posterior to vibrissal angle, postgena with 4 consecutively smaller setae at lower margin, medial seta often unproportionally smaller. Colour patterns and pruinosity on gena variable. Genal height 0.2–0.4× eye height. Facial carina pollinose. Ventromedial desclerotization of face surpassing ventral point of sub-antennal depression; sub-antennal depression reduced, inner face highly reduced or absent, outer face well sclerotized.

Thorax: Presutural and postsutural acrostichal setae usually present and aligned in a single median row, prescutellar acrostichal setae absent. Anterior intra-alar seta absent; presutural and postsutural supra-alar setae, postalar setae present and of various lengths. Intrapostalar seta small. Scutellum with 2 pairs of marginal setae. Katepisternal seta well developed.

Legs: Colour patterns variable. Fore coxae pruinosity variable.

Male terminalia (Figs. 16.1–6, 19.1–5, 22.1–5, 24.1–5): S6 horseshoe-shaped (or U-shaped), length subequal or longer than width; width from arcuate sclerotization to sclerite margin uniform or widest posteriorly; posterior apices articulating with S7+8. S7+8 dorsally pruinose, usually asymmetrical, left side of S7+8 with cleft indicating boundaries of S7 and S8; postspiracular sclerite present. Epandrium with pair of outstanding setae in addition to numerous shorter setae. Surstylus usually simple rod-like. Cerci fused at posterior margin of anal-opening; shape variable; inner surface only with few setulae, outer surface setose. Subepandrial sclerite sheet-like, thin, V-shaped, setae not contiguous but crowded at posterolateral corner of sclerite, anterior seta usually 1.5× posterior seta. Dorsal bridge of hypandrium short; phallic plate relatively

flat and straight; ventral bridge short, well sclerotized, medially connected to independent, elongated, relatively straight but outwardly bowed pregonites that are sitting ventral to phallapodeme. Postgonite with 2 points and a rounded lobe. Phallapodeme straight, spatulate on distal third. Distiphallus asymmetrical, skewed to the right; basal distiphallus tubular, strongly sclerotized apically; distal distiphallus sclerotized basally and membranous distally.

Female terminalia: S6 with weak H-shaped sclerotization and usually 1 row of 4–5 pairs of setae.

Pseudopomyza (Apops) arenae McAlpine

Pseudopomyza (Apops) arenae McAlpine, 2019: 88.

Based on photographs of the type material and the original description by McAlpine (2019), *P. arenae* appears to be externally identical to *P. chilensis* except for the 3 strong setae on the posterior half of male S6.

Type specimens (not examined): Holotype: ♂: **AUSTRALIA: Tasmania:** The Neck, Bruny Island ["Penguin Rookery" on some maps, c. 43°17'S 147°21'E], 16–18.iii.2005, B.J. Day & D.K. McAlpine (AM).

Paratypes: Same collection data as holotype (1 \lozenge , 6 \lozenge , AM, CNC).

Pseudopomyza (Apops) chilensis Yau and Marshall sp. nov.

(Figs. 15.1-4, 16.1-6, 17.1-4)

Diagnosis

Frons brown. With 3 fronto-orbital setae. First flagellomere entirely tan to brown. Face mostly yellow except ventral half of outer face brown. Medial acrostichal setae well-developed. Fore femur brown except base; fore tarsus brown; mid femur brown except base. Male S6 ventral extension from arcuate sclerotization widest posteriorly, posterior half with 4 to 5 strong setae. S7+8 asymmetrical, weakly sclerotized on right lateral. Female S7 with spectacle-shaped desclerotization and a pair of small well sclerotized spots anterior to the desclerotization. Spermathecae with globules on dorsal surface, and one distal depression.

Description

Body length 2.9 mm (male) (head to wing tip = 3.1 mm), 3.1 mm (females) (head to wing tip measurement impossible due to folded wing).

Head: Frons brown, fronto-orbital plates sometimes paler than frons. With 3 reclinate fronto-orbital setae, length of first fronto-orbital seta of male specimen 0.28×2^{nd} , female specimen 0.48×2^{nd} , 2^{nd} subequal to 3^{rd} , decrease spacing between left 2^{nd} and 3^{rd} setae of male specimen. Ocellar, inner vertical and outer vertical setae large and subequal; postocellar setae cruciate; paravertical

seta 0.75× postocellar seta; lower frons with scattered small setulae. Antenna yellow; first flagellomere entirely tan to brown. Gena mostly yellow with light tan splotches especially at posteroventral corner, postgena brown; pruinose through to postgena and lower occiput; genal height 0.4× eye height. Face mostly yellow except ventral half of outer face brown.

Thorax: Mostly brown, scutum uniformly pruinose. Presutural acrostichal setae small, two postsutural acrostichal setae as strong as 2nd dorsocentral seta. Presutural supra-alar seta and postalar seta large and subequal, postsutural supra-alar seta small and subequal to intrapostalar. Notopleuron ventrally yellowish brown. Anepisternum and katepisternum glossy but lightly pruinose, except margins of katepisternum more densely pruinose.

Leg: All coxae and trochanters yellow. Foreleg brown except basal sixth of femur and tibia. Mid femur brown except yellow basal quarter and tan distal quarter, hind femur brown except basal quarter, mid and hind tibia yellow except tan super-basal band and brown distal quarter, mid and hind tarsi tan. Fore coxae medial, anterolateral surfaces and posterolateral surface ventrally sparsely pruinose. Male left hind femur with 2 strong distal anterodorsal seta instead of 1.

Abdomen: uniformly pruinose (female specimen suspected of left-right misalignment thus causing the appearance of two "additional" tergites).

Male terminalia (Figs. 16.1–6): S6 ventral extension from arcuate sclerotization widest posteriorly, posterior half with 4 to 5 strong setae. S7 tapering off past right articulation with S6, apex of S7 connected to right side of S7+8 by weak sclerotization or membrane; postspiracular sclerite uniformly thin, connected to right side of S7+8 by weak sclerotization or membrane. Epandrium entirely pruinose; widest at posterior end, width 0.7× length. Surstylus simple thin rod-like. Fused cerci forming an M-shape. Subepandrial sclerite V-shaped, with one (left) or two (right) posterolateral setae on each side; setae not contiguous but crowded at posterior end. Pregonites with sensory setulae at mid-length. Phallic guide present on mid-length of phallapodeme. Distal distiphallus with twisted sclerotized basal piece and distal membranous volume. Ejaculatory apodeme simple, apex acutely bent, ejaculatory bulb with acute basal dilation.

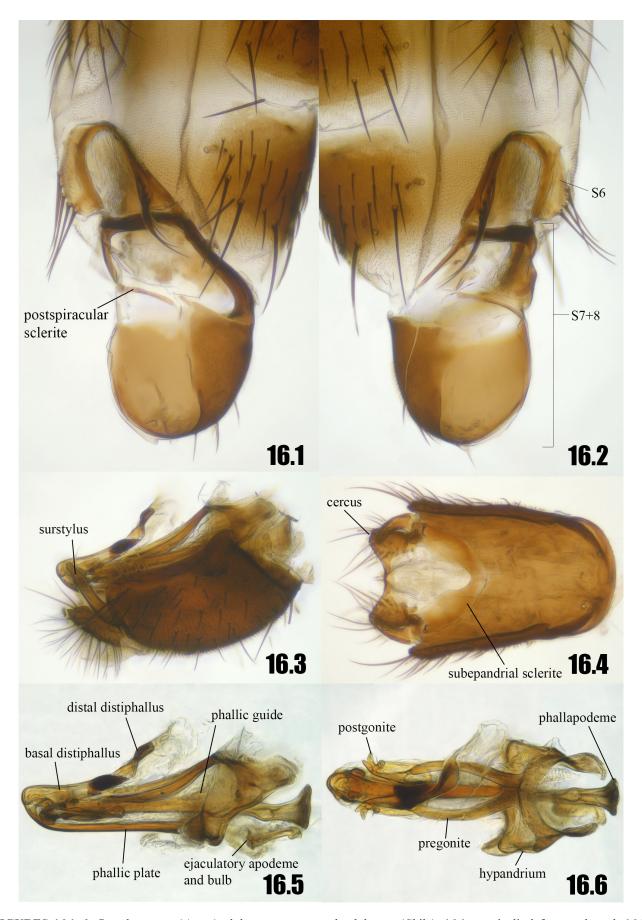
Female terminalia: S7 with spectacle-shaped desclerotization at anterior one third and a pair of small well sclerotized spots anterior to the desclerotization; setae mainly restricted to mid-section of sclerite; posterior-most seta with very well sclerotized protruding sockets. T7 posterior two thirds setose. Spermathecae with globules on distal surface, and one distal depression.

Etymology: The name refers the Chilean type locality.

Type specimens: Holotype: \lozenge : **CHILE**: **Araucanía:** Pucón, lakeshore, carrion trap, 15 Nov–2 Dec 1989, SAM, debu00309949 (MEUC).



FIGURES 15.1–4: *Pseudopomyza* (*Apops*) *chilensis* **sp. nov.** male habitus (Chile). 15.1, left lateral; 15.2, dorsal; 15.3, head; 15.4, abdomen ventral.



FIGURES 16.1–6: *Pseudopomyza (Apops) chilensis* **sp. nov.** male abdomen (Chile). 16.1, terminalia left ventrolateral; 16.2, terminalia right ventrolateral; 16.3, epandrium left lateral; 16.4, epandrium ventral; 16.5, phallus and associated structures left lateral; 16.6, phallus and associated structures ventral.



FIGURES 17.1–4: *Pseudopomyza (Apops) chilensis* **sp. nov.** female abdomen (Chile). 17.1, terminalia dorsal; 17.2, terminalia ventral; 17.3, terminalia left lateral; 17.4, spermathecae.

Paratype: Same collection data as holotype, debu00310028 (1 \bigcirc , DEBU).

Comments: Although *P. chilensis* is widely disjunct from the rest of the subgenus, it shows all the characters of the otherwise Australian-New Zealand subgenus *Apops* and lacks the distinct synapomorphies of the Neotropical *P. nigrimana* species group (fused and strongly arched pregonites, the equally arched phallapodeme and symmetrical distiphallus).

Pseudopomyza (Apops) flavitarsis (Harrison) (Figs. 18.1–5, 19.1–5, 20.1–3)

Heloclusia (Heluscolia) flavitarsis Harrison, 1959: 121. Pseudopomyza flavitarsis (Harrison)—Mathis, 1989b: 470. Pseudopomyza (Apops) flavitarsis (Harrison)—McAlpine, 1994: 183.

Diagnosis

Frons brown, gradually paler towards yellow anterior margin. With 2 fronto-orbital setae. First flagellomere distodorsally tan to brown. Face mostly yellow except outer face brown. Medial acrostichal setae welldeveloped. Fore femur dark brown except base; fore tarsus bicoloured; mid femur basal half or less vellow, remaining brown. Male S6 ventral extension of uniform width along entire sternite, posterior half with 1 small and 3 large setae on lateral margins. S7+8 asymmetrical, weakly sclerotized on right lateral. Basal distiphallus with sharp dorsal angle and expanded left base. Female S7 with short thin somewhat spectacle-shaped desclerotization at anterior quarter and a small well sclerotized spot in middle of desclerotization. Spermathecae smooth with one distal depression, depression of left spermatheca larger than that of the right.

Description

Body length 2.5-3.0 mm (male) (head to wing tip = 3.0-3.1 mm), 2.9-3.0 mm (female) (head to wing tip = 3.1-3.9 mm).

Head: Frons brown, gradually paler towards yellow anterior margin, fronto-orbital plates sometimes paler than frons. With 2 reclinate fronto-orbital setae, length of first fronto-orbital seta 0.84× 2nd. Ocellar, inner vertical and outer vertical setae large and subequal; postocellar setae cruciate; paravertical seta 0.58× postocellar seta; lower frons with scattered small setulae. Antenna yellow; first flagellomere distodorsally tan to brown. Gena dorsal half yellow, ventral half brown, postgena brown; pruinose through to postgena and lower occiput; genal height 0.2× eye height. Face mostly yellow except outer face brown.

Thorax: Mostly brown, scutum uniformly pruinose. Presutural acrostichal setae small, two postsutural acrostichal setae as strong as 2nd dorsocentral seta. Presutural supra-alar seta large and subequal to postalar seta, postsutural supra-alar seta 0.56× presutural supra-alar and slightly longer than intrapostalar. Notopleuron ventrally yellowish brown. Anepisternum and

katepisternum glossy, except surface posterior to and ventral to katepisternal seta pruinose.

Leg: Coxa and trochanters yellow except inner surface of fore coxa brown. Foreleg dark brown except basal quarter of femur yellow and terminal 4 tarsomeres creamy white. Mid and hind femur basal half or less yellow, remaining brown, mid and hind tibia yellow except tan to brown super-basal and preapical band, mid and hind tarsi tannish-yellow, tarsomere 5 often darker. Fore coxae medial, anterolateral surfaces and posterolateral surface ventrally sparsely pruinose.

Male terminalia (Figs. 19.1–5): S6 ventral extension wide and uniform along entire sternite, posterior half with 1 small and 3 large setae on lateral margins. S7 weakening past right articulation with S6, apex of S7 connected to right side of S7+8 by weak sclerotization or membrane; postspiracular sclerite uniformly thin, connected to right side of S7+8 by weak sclerotization. Epandrium entirely pruinose except anterior margin and sides glossy; widest at posterior end, width subequal length. Surstylus simple rod-like, slightly wider than thick, apex directing inwards and slightly flattened. Fused cerci forming a Ushape. Subepandrial sclerite U or V-shaped, posterior seta smaller than anterior seta; setae not contiguous but crowded at posterior end. Pregonites basal one third fused, relatively straight, distal portion sitting ventral to phallapodeme slightly outwardly bowed, with sensory setulae on apical half. Phallic guide on mid-length of phallapodeme, triangular. Basal distiphallus tubular with sharp dorsal angle, expanded left base and sclerotized apex; distal distiphallus bent right, distally membranous. Ejaculatory apodeme flat and dilated, ejaculatory bulb short and wide.

Female terminalia: S7 with short thin somewhat spectacle-shaped desclerotization at anterior quarter and a small well sclerotized spot in middle of desclerotization; setae mainly restricted to mid-section of sclerite and lateral surfaces. T7 posterior two thirds setose. Spermathecae smooth with one dorsal depression, depression of left spermatheca larger than that of the right.

Type specimens: Holotype: ♂: **NEW ZEALAND: Auckland:** Owairaka, on rotting fruit, 24.vii.1950, R. Harrison (NZAC).

Paratype: **NEW ZEALAND: Auckland:** Avondale, 6.i.1959, R.A. Harrison (1♂, NZAC) (not examined); Browns Bay, 15.ix.1951, R.A. Harrison (2♀, NZAC); ditto, in rotting-fruit trap, 15.x.1950 (1♂, NZAC) (not examined); ditto, 20.xi.1949 (1♀, NZAC); Henderson, Sunnyvale, 2.x.1954, K.A.J. Wise (1♂, 1♀, in copulation, NZAC) (not examined); Oratia, 27.viii.1949, R. Harrison (1♂, NZAC); ditto, 8.vii.1950 (3♂, NZAC) (2 not examined); Little Barrier Island, Kauri Gully and tracks, 24.xi.1954, R.A. Harrison (1♂, NZAC) (not examined); ditto, swept, 24.xi.1954 (1♀, NZAC) (not examined); Waipawa Stream, ex banana trap, 29.xi.1954, R.A. Harrison (1♂, NZAC) (not examined).

Other material examined: NEW ZEALAND: Auckland: Auckland, Symonds Str. Cemetery, 36.858°S 174.765°E, 24–25.iii.2010, YPT, LM (2\$\delta\$, CNC); Auckland City Albert Park, litter under Ficus



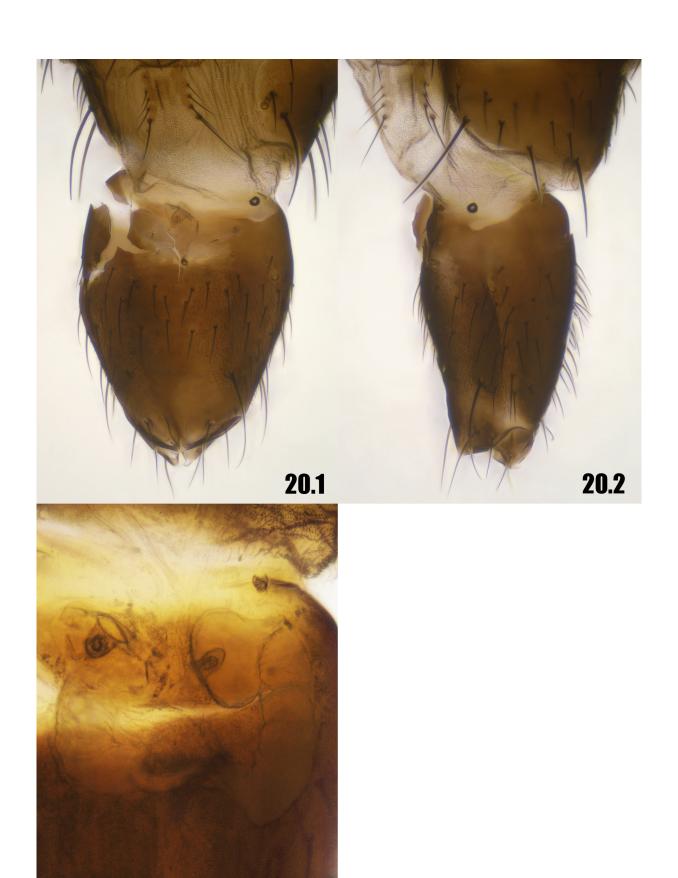
FIGURES 18.1–6: *Pseudopomyza (Apops) flavitarsis* (Harrison) male habitus (New Zealand). 18.1, left lateral; 18.2, dorsal; 18.3, head; 18.4, living female photographed in Masteron, New Zealand (S.A. Marshall); 18.5, living male on recently cut stump at Hollard Gardens, New Zealand (S.A.Marshall); 18.6, recently cut wood from which specimens were collected on cut surfaces.



FIGURES 19.1–5: *Pseudopomyza* (*Apops*) *flavitarsis* (Harrison) male abdomen (New Zealand). 19.1, terminalia left ventrolateral; 19.2, epandrium left lateral; 19.3, epandrium ventral; 19.4, phallus and associated structures left lateral; 19.5, phallus and associated structures ventral.

macrophylla, 13.viii.2006, S.E. Thorpe (1♂, NZAC); Auckland University City Campus, Clock Tower East Wing windows, 24.i.2007, S.E. Thorpe (1♂, NZAC); ditto, 30.i.2007 (1♀, NZAC); Moehau Community Co., 21–25.iv.1984, H. Oliver (2♀, NZAC); Waitakere Ranges, Titirangi Zig Zag Trail, 36.944°S 174.658°E, 28.iii.2010, LM (1♂, CNC); Canterbury: Banks Peninsula, Port Levy, 43.39S 172.49E, pans near sea streambed, 22–26.ii.1999, SAM (2♀, DEBU); Northland: Huia, in house, 5.viii.1967, B.M. May (5♀, NZAC); Taranaki:

Kaponga, Hollard Gardens, 39°24'0.66"S39°24'0.66"S, on recently cut stumps, 25.ii.2024, SAM (7♂, DEBU, NZAC); **Waikato:** Mercury Islands, Green Island, beating and to light at night, 11–23.xii.1987, G. Hall; Ruapuke, sweeping in bush relict, 27.ii.1971, H.A. Oliver (1♀, NZAC); **West Coast:** 13 Mile Creek, 21km N of Greymouth, 5–10 m, coastal veg, YP, 15–18.i.2000, D. Bickel (1♂, 1♀, AM); Franz Josef (Westland) forest, 43.24S 170.11E, 100–250m, pans, 14–19.ii.1999, SAM (1♂, 1♀, DEBU); Ōkārito, Trig Trail, 43.13S 170.10E,



FIGURES 20.1–3: *Pseudopomyza (Apops) flavitarsis* (Harrison) female abdomen (New Zealand). 20.1, terminalia dorsal; 20.2, terminalia left lateral; 20.3, spermathecae.

20.ii.1999, SAM (1♀, DEBU); Wanganui River river mouth, NW of Harihari, 7.ii.2000, R. Meier & D.K. McAlpine (1♂, AM); Westland NP, Alex Knob trial, 43.18S 170.11E, 15–19.ii.1999, SAM (1♀, DEBU).

Comments: Pseudopomyza flavitarsis seems to be widespread in New Zealand and is known from widely separated localities on both North Island and South Island. Individuals of this species recently collected in the Taranaki region of North Island were among many observed on a recently cut stump. They appeared to be ovipositing between the bark and stump and in cracks and crevices (Figs. 18.5–6). No further specimens were found upon visiting the same cut stump 2 weeks from the initial date of collection.

Pseudopomyza (Apops) medianentis Yau and Marshall sp. nov.

(Figs. 21.1–3, 22.1–5)

Diagnosis

Frons brown and gradually lighter towards anterior margin. With 2 fronto-orbital setae. First flagellomere distodorsally tan to brown. Face mostly yellow except ventral half of outer face brown. Medial acrostichal setae reduced. Fore femur basal two thirds yellow, remaining brown; fore tarsus bicoloured; mid femur yellow. Male S6 ventral extension on posterior two-thirds, posterior half with 2 small and 2 large setae on lateral margin, and 3 small setae on posteromedial margin. S7+8 symmetrical, close-ringed.

Description

Body length 2.5 mm (male) (head to wing tip = 2.8 mm, due to angle of wing, measurement was made by the sum of measurements from head to wing base and wing base to wing tip).

Head: Frons brown and gradually lighter towards anterior margin. With 2 reclinate fronto-orbital setae, length of first fronto-orbital seta 0.67×2^{nd} . Ocellar, inner vertical and outer vertical setae large and subequal; postocellar setae cruciate; paravertical seta 0.34×2^{nd} postocellar seta; lower frons with scattered small setulae. Antenna yellow; first flagellomere distodorsally tan to brown. Gena mostly yellow, postgena brown; anteriorly glossy, posteriorly pruinose through to postgena and lower occiput; genal height 0.24×20^{nd} eye height. Face mostly yellow except ventral half of outer face brown.

Thorax: Mostly brown, scutum uniformly pruinose. Median presutural acrostichal setae absent. Presutural supra-alar seta and postalar seta large and subequal, postsutural supra-alar seta $0.56\times$ presutural. Intrapostalar small. Notopleuron ventrally yellowish brown. Anepisternum and katepisternum glossy, except posterodorsal surface of katepisternum pruinose.

Leg: Coxae and trochanters yellow except mid coxa, ventral half of hind coxa and hind trochanter yellowish-brown. Foreleg brown except basal two thirds of femur

yellow and terminal 3 tarsomeres creamy white. Mid and hind legs yellow except distal half of hind femur brown. Fore coxae mostly glossy, anterolateral surface very sparsely pollinose, posterolateral surface ventrally with lines indicating spots of microtrichia.

Male terminalia (Figs. 22.1–5): S6 ventral extension on posterior two-thirds, posterior half with 2 small and 2 large setae on lateral margin, and 3 small setae on posteromedial margin. S7+8 forming a closed solid symmetrical ring. Epandrium entirely pruinose except sides glossy; uniform width, width 0.6× length. Surstylus simple, thin, rod-like. Cerci apices covered with thickened setae. Subepandrial sclerite Y-shaped, posterior seta very small; setae not contiguous but crowded at posterior end. Phallic plate narrow, well sclerotized, base strongly curved. Pregonites with basal one third fused, relatively straight, distal portion sitting ventral to phallapodeme slightly outwardly bowed, with sensory setulae on apical portion. Phallic guide present on basal one third of phallapodeme, very reduced, almost spike-like. Distal distiphallus with twisted sclerotized basal piece and distal membranous volume. Ejaculatory apodeme fan-like, ejaculatory bulb tapering.

Etymology: The name refers to the absent median presutural acrostichal setae.

Type specimen: Holotype: ♂: **AUSTRALIA**: **Western Australia:** Mt Frankland, ~30 km N Walpole, pans, 26 Nov 2003, SAM, debu00244490 (WAM).

Paratype: **AUSTRALIA**: **Western Australia**: Augusta, 1 mi E of Jewel Cave, 3.x.1970, D.H. Colless (1♀, AM); Stirling Range National Park, top of Bluff Knoll, 1100 m, 3.xii.2003, SAM (1♂, DEBU).

Comments: This is probably the species referred to by McAlpine (2019) as undescribed sp. C on the basis of one female (current paratype) from southern Western Australia deposited in ANIC.

Pseudopomyza (Apops) nigritarsis Yau and Marshall sp. nov.

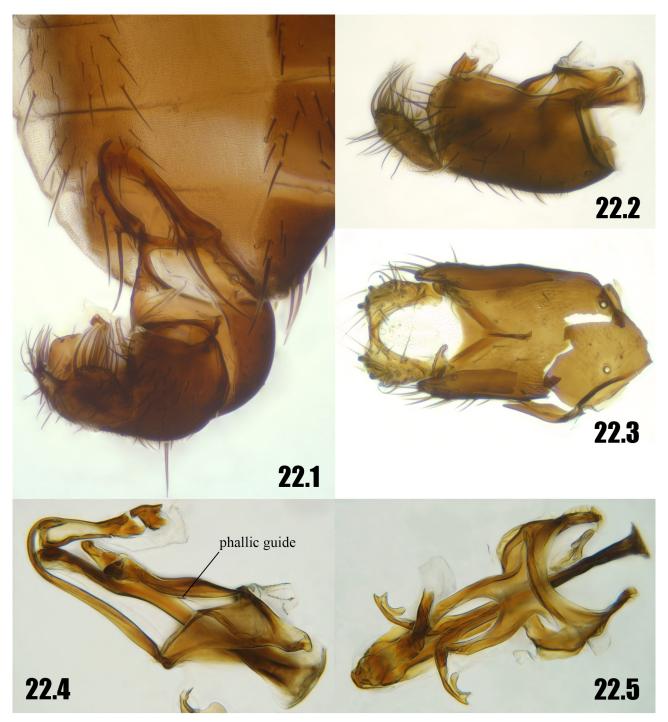
(Figs. 23.1–3, 24.1–5, 25.1–3)

Diagnosis

Frons brown, gradually paler towards yellow anterior margin. Sometimes with small anterior fronto-orbital seta in addition to 2 large fronto-orbital setae. First flagellomere entirely tan or brown. Face mostly yellow except outer face brown. Medial acrostichal setae well-developed. Fore femur dark brown except base; fore tarsus dark brown; mid femur apices and basal half or less yellow, remaining brown. Male S6 ventral extension uniform in width along entire sternite, posterior half with 1 small and 3 large setae on lateral margins. S7+8 asymmetrical, weakly sclerotized on right lateral. Female S7 with round spectacle-shaped desclerotization at anterior quarter. Spermathecae smooth with one distal depression, depression of left spermatheca larger than that of the right.



FIGURES 21.1–3: Pseudopomyza (Apops) medianentis sp. nov. male habitus (Australia). 21.1, left lateral; 21.2, dorsal; 21.3, head.



FIGURES 22.1–5: *Pseudopomyza (Apops) medianentis* **sp. nov.** male abdomen (Australia). 22.1, terminalia left ventrolateral; 22.2, epandrium left lateral; 22.3, epandrium ventral; 22.4, phallus and associated structures left lateral; 22.5, phallus and associated structures ventral.

Description

Body length 1.6-2.1 mm (male) (head to wing tip = 2.6-2.9 mm), 2.1-2.6 mm (female) (head to wing tip = 2.8-3.5 mm).

Externally similar to *P. flavitarsis* except sometimes with small anterior fronto-orbital seta in addition to 2 large subequal reclinate fronto-orbital setae. First flagellomere entirely tan or brown. Gena tan to brown with blotchy

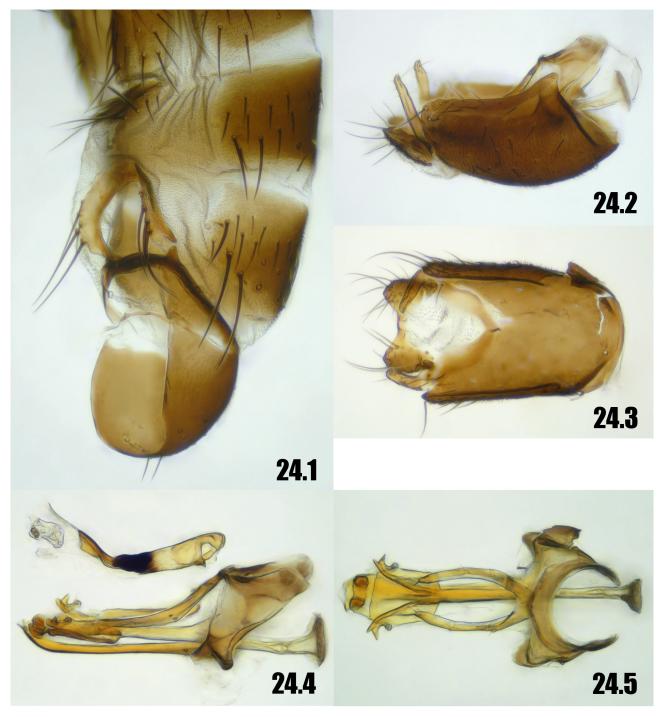
mix of yellow and brown but generally more yellow on dorsal half and brown on ventral half; genal height $0.35 \times$ eye height.

Foreleg dark brown except basal quarter yellow. Mid and hind femur apices and basal half or less yellow, remaining brown.

Male S6 ventral extension uniform in width along entire sternite, posterior half with 1 small and 3 large setae on lateral margins. Surstylus simple, thin, rod-like. Fused



FIGURES 23.1–3: *Pseudopomyza (Apops) nigritarsis* **sp. nov.** male habitus (New Zealand). 23.1, left lateral; 23.2, dorsal; 23.3, head.



FIGURES 24.1–5: *Pseudopomyza (Apops) nigritarsis* **sp. nov.** male abdomen (New Zealand). 24.1, terminalia left ventrolateral; 24.2, epandrium left lateral; 24.3, epandrium ventral; 24.4, phallus and associated structures left lateral; 24.5, phallus and associated structures ventral.

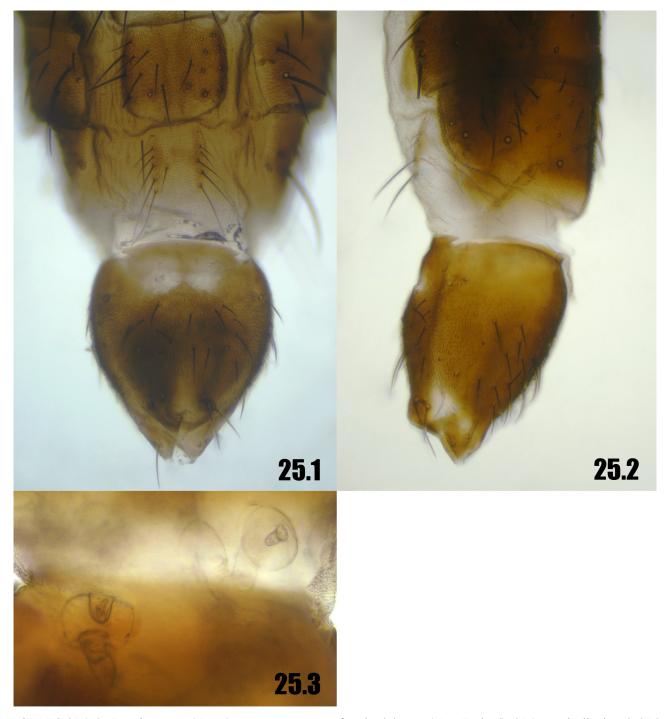
cerci forming an M-shape. Pregonites widely separated and outwardly bowed. Basal distiphallus without sharp dorsal angle or extended left base (Figs. 24.1–5).

Female S7 with round spectacle-shaped desclerotization at anterior quarter.

Etymology: This name parallels *P. flavitarsis* since the two species are very similar externally except for the dark brown fore tarsus of *P. nigritarsis* (Latin '*nigri*': black).

Type specimens: Holotype: ♂: NEW ZEALAND:

Waikato: Mercury Islands, Korapuki Island, MT, 11–13.xii.1987, G. Hall (NZAC).



FIGURES 25.1–3: *Pseudopomyza (Apops) nigritarsis* **sp. nov.** female abdomen (New Zealand). 25.1, terminalia dorsal; 25.2, terminalia left lateral; 25.3, spermathecae.

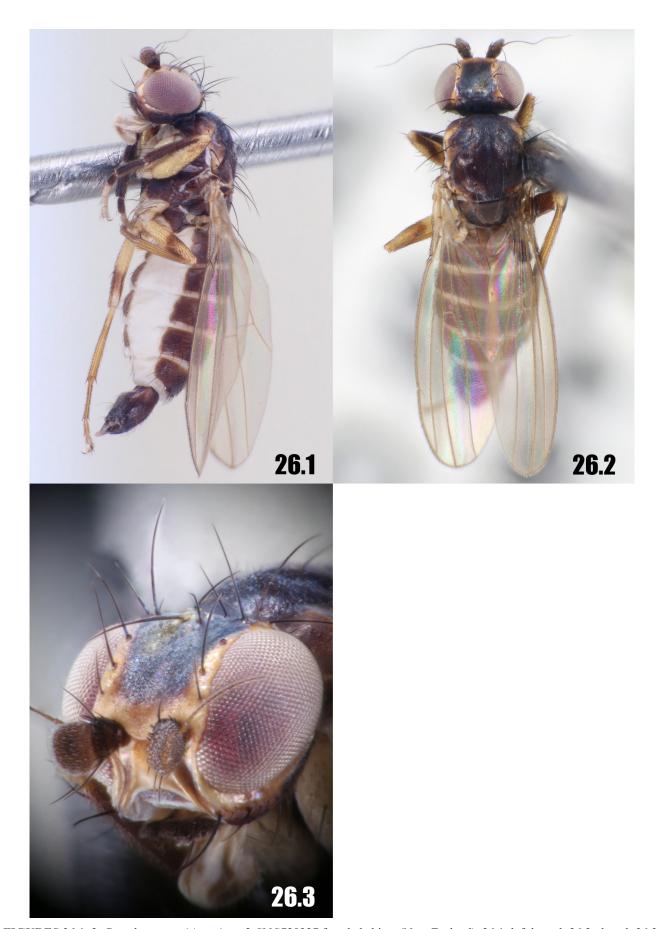
NZAC); **Chatham Islands:** South East Island, Ex. broadbilled prion burrow, xi.1979, P.F. Jenkins (2♀, NZAC).

Comments: Pseudopomyza nigritarsis resembles P. flavitarsis in external appearance, mainly differing in the presence of a small anterior fronto-orbital seta and the dark fore tarsus. Pseudopomyza flavitarsis is widely distributed on the north and south islands of New Zealand, but P. nigritarsis is only known from widely separated outer islands east of the main islands. Both species are known from the Mercury Islands, where P. flavitarsis is found on Green Island and P. nigritarsis on Korapuki Island.

Subgenus Dete McAlpine

Dete McAlpine, 1994: 183 (as subgenus). Type species Pseudopomyza collessi McAlpine, 1994 (original designation). McAlpine, 1994: 182 (keyed).

Dete McAlpine was described as a monotypic subgenus of Pseudopomyza with P. collessi as the type species. This basal lineage (putative sister species to the rest of the genus) remains monotypic with this revision.



FIGURES 26.1–3: *Pseudopomyza* (*Apops*) sp. 2 CNC729327 female habitus (New Zealand). 26.1, left lateral; 26.2, dorsal; 26.3, head. (Undescribed species known only from a female in the subgenus *Apops*, included in Key to species of *Pseudopomyza* Strobl).

Diagnosis

Two fronto-orbital setae; desclerotization of face not reaching ventral point of sub-antennal depression; pedicel both dorsally and ventrally with one long seta; subvibrissa absent; anterior intra-alar seta absent; 3 marginal scutellar setae; scutum and pleuron mostly glossy; katepisternal seta reduced; length of S6 shorter than width and extensions from arcuate sclerotization anteriorly subquadrate.

Pseudopomyza (Dete) collessi McAlpine (Figs. 27.1–3, 28.1–6, 29.1–3)

Pseudopomyza (Dete) collessi McAlpine, 1994:182.—McAlpine, 2019: 88.

Description

Body length 2.2–2.4 mm (males), 2.2–3 (females).

Head: Frons dark brown to black, lighter at anterior margin, fronto-orbital plates paler. Length of 1st fronto-orbital seta 0.7× 2nd. Antenna yellow except first flagellomere distally brown; setae on medial surface of pedicel at most half the length of medioventral long seta. Face entirely yellow; desclerotization at anteromedial margin well below ventral point of sub-antennal depression; carina dorsally pruinose, ventrally glossy; facial plates well developed and sclerotized. Gena mostly yellow, dark brown restricted to postocular area; gena glossy, postgena pruinose; genal height 0.2× eye height; postgena with 2–3 setae at lower margin. Sub-vibrissa absent or indifferentiable from background setulae.

Thorax: Scutum dark brown and glossy. Acrostichal setae small indifferentiable from background setulae. Anterior intra-alar absent; postsutural supra-alar $0.8 \times$ presutural supra-alar, postalar seta subequal presutural supra-alar. Intrapostalar seta small, similar in length to background setulae. Scutellum with 3 marginal setae. Pleuron mostly glossy except katatergite and anatergite pruinose. Katepisternal seta reduced.

Leg: Fore and hind coxae yellow, mid coxa lightly tan; all trochanters yellow. Fore femur brown on distal quarter and dorsal surface, tibia and basal 3 tarsomere brown, tarsomere 4 and 5 white to creamy white. Mid and hind legs yellow. Fore coxae glossy but posterolateral surface ventrally with lines indicating spots of microtrichia.

Male terminalia (Figs. 28.1–6): S6 relatively flat, length shorter than width, with arcuate strip of sclerotization going through middle of sclerite, area anterior to sclerotization subquadrate, sensory setulae at anterior corners, lateral margins with a pair of setae, area posterior to sclerotization weakly sclerotized to membranous. Ventral band of S7+8 without apparent protuberance, thin but very well sclerotized, weakly connected to right of S7+8 forming an asymmetrical and open-ringed sclerite; left side of S7+8 with cleft indicating boundaries of S7 and S8; postspiracular sclerite well sclerotized. Epandrium glossy, uniform in width; width $0.8 \times$ length; posteroventral corners extended posteriorly. Cercus tapering distally. Surstylus claw-like,

posterior lobe apically with scattered setulae. Subepandrial sclerite broad, rounded to subquadrate; anterior and posterior seta subequal in length, setae positioned on posterior quarter of sclerite.

Phallapodeme slightly arched ventrally, phallic guide reduced to a triangular extension from phallapodeme. Ventral bridge of hypandrium somewhat short; dorsal surface of dorsal bridge extended posteriorly; phallic plate straight, flat, wide and encompassing most of phallus, distally with a membranous protuberance. Pregonites connected until mid-length, straight, sensory setulae on distal half of sclerite length. Apex of postgonite paw-like, posteroapical lobe only slightly protruding. Basal distiphallus flat, asymmetrical, distally spatulated with strong nub-like sclerotization leaning to right side, distal distiphallus with tab-like base and sheet-like body, twisted, and apically membranous.

Female terminalia: S6 weakly sclerotized and quarter size of S5, with 1–2 pairs of setae. oviscape arrow-head-shaped, S7 bulbous anteromedially and with scattered setae. Spermathecae mushroom or bowl-shaped, with few tiny indentations.

Type specimens (not examined): Holotype: \emptyset : **AUSTRALIA: New South Wales:** Wentworth Falls, Blue Mountains, 22.xi.1960, D.K. McAlpine (AMSA).

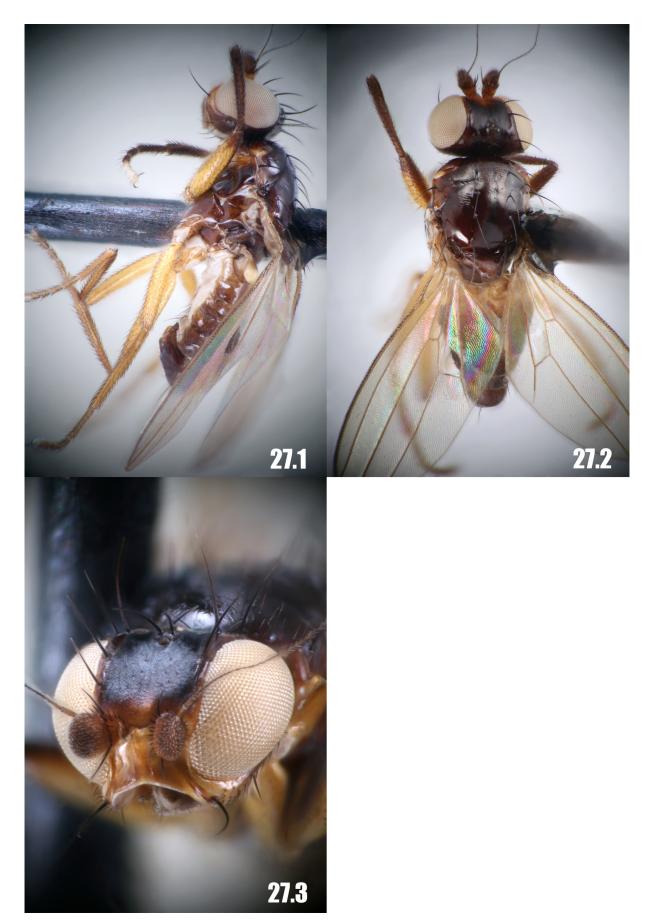
Paratypes: **AUSTRALIA:** Australian Capital Territory: Black Mountain, Canberra, v, ix, x. 1962–1981, I.F. Common & J. Cardale $(2 \, \circlearrowleft, 3 \, \updownarrow, \text{ANIC})$; Blundell's Creek, Brindabella Mts., 3 km E and 6km NE of 'Piccadilly Circus' ii, ix, x.1984–1985, Weir, Lawrence and Johnson $(8 \, \circlearrowleft, 4 \, \updownarrow, \text{ANIC}, \text{CNC}, \text{ some in alcohol})$; **New South Wales:** Mount Wilson, Blue Mountain, ix.1974, D.K. McAlpine $(1 \, \circlearrowleft, \text{AMSA})$; Wentworth Falls, xi.1959–1960, D.K. McAlpine $(3 \, \circlearrowleft, 2 \, \updownarrow, \text{CNC}, \text{AMSA})$.

Other material examined: **AUSTRALIA: Australian Capital Territory:** Black Mountain, Malaise trap, 23.x.1981 (1\$\sqrt{2}\$, AM); Blundells Creek, 3km E of Piccadilly Circus, 850 m, ACT, i.1984, Weir, Lawrence & Johnson (5\$\sqrt{2}\$, 2\$\sqrt{2}\$, AM); Wombat Creek, 6kmNE, Piccadilly Circus, 750 m, flight intercept window/trough trap, iii.1984, Weir, Lawrence & Johnson (1\$\sqrt{2}\$, AM); **New South Wales:** Monga State Forest, 19–24.i.1984, LM (4\$\sqrt{3}\$, 4\$\sqrt{2}\$, CNC); ditto, 23.i.1984 (1\$\sqrt{2}\$, CNC); Mount Wilson, 12.ix.1974, D.K. McAlpine (1\$\sqrt{2}\$, AM); Werrikimbe National Park, Cobcrofts, Carabeen Creek, 31.229S 152.166E, 1060 m, yellow pans, creek bed, c, 16–17.i.2018, D. Bickel (1\$\sqrt{2}\$, AM); **Tasmania:** Waratah, 8 km SW, 41°29'04"S 145°27'41"E, rainforest, pans, 20–21.xii.2003, SAM (1\$\sqrt{2}\$, DEBU).

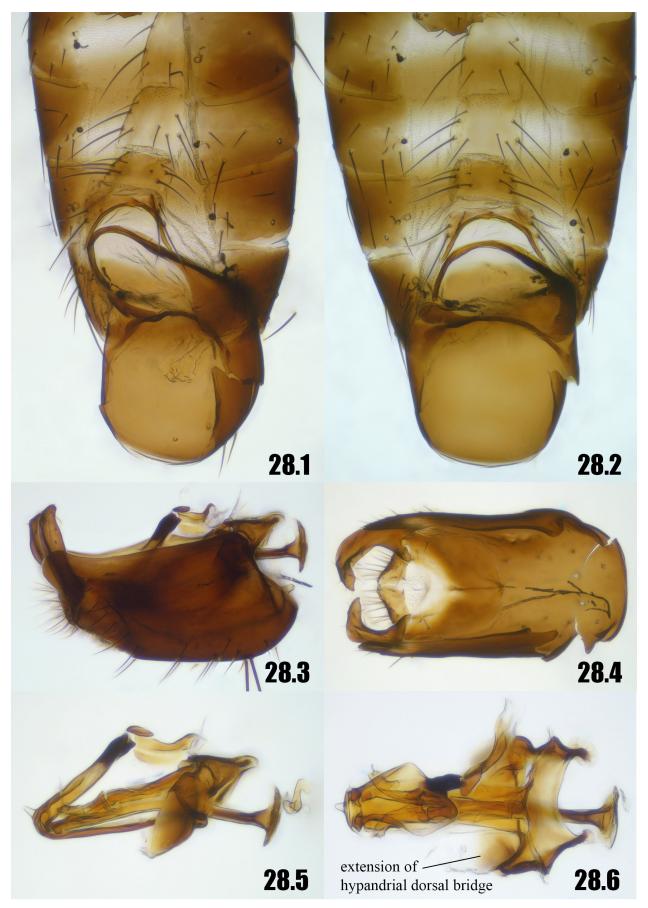
Subgenus Heluscolia (Harrison) revised status

Heluscolia Harrison, 1959: 119 (as subgenus of Heloclusia Malloch). Type species Heloclusia (Heluscolia) antipoda Harrison, 1955 (original designation). Harrison, 1959: 119 (keyed, diagnosis), 121 (key to species); McAlpine, 1966: 683 (synonymy).

Pseudopomyza antipoda and P. brevis were previously



FIGURES 27.1–3: Pseudopomyza (Dete) collessi male habitus (Australia). 27.1, left lateral; 27.2, dorsal; 27.3, head.



FIGURES 28.1–6: *Pseudopomyza (Dete) collessi* male abdomen (Australia). 28.1, terminalia left ventrolateral; 28.2, terminalia ventral; 28.3, epandrium left lateral; 28.4, epandrium ventral; 28.5, phallus and associated structures left lateral; 28.6, phallus and associated structures ventral.



FIGURES 29.1–3: *Pseudopomyza (Dete) collessi* female abdomen (Australia). 29.1, terminalia ventral; 29.2, terminalia left lateral; 29.3, spermathecae and associated structures.

included in the subgenus *Pseudopomyza* McAlpine (Diptera: Pseudopomyzidae) but the two species share unique synapomorphies not found in other *Pseudopomyza* taxa and lack the synapomorphies of the subgenus *Pseudopomyza* (shortened subvibrissa and prescutellar acrostichal setae or setulae). They are therefore here treated as a separate subgenus *Heluscolia* (first described as a monotypic subgenus of *Heloclusia*), reinstated from synonymy with *Pseudopomyza s.s.*. At least one character (a posteriorly positioned subvibrissa) suggests that the subgenus *Heluscolia* is related to *Apops*.

Diagnosis

Synapomorphies unique to this clade include the lengthened anterior extension from the arcuate sclerotization of S6, the sharp perpendicular posteroventral corner of the epandrium, the elongated base of the setae of subepandrial sclerite and the prominent dorsomedial ridge on the anterior half of the phallic plate. In addition to the above synapomorphies, this group is also diagnosable by the following character combination: Head with three frontoorbital setae; subvibrissa strong, at least $0.5 \times$ length of vibrissa and positioned at the posterior limit of vibrissal angle or posterior to vibrissal angle; face desclerotized dorsal to ventral point of sub-antennal depression; two pairs of marginal scutellar setae, base of basal scutellar seta without any setulae.

Description

Body length 1.9–2.5 mm (males), 2.0–2.6 mm (females). Head: With 3 reclinate fronto-orbital setae. Antenna yellow; first flagellomere tan on distal half; arista arising dorsoapically, pubescent, as long as head width; pedicel with at least one large seta medial to medioventral long seta. Vibrissa distinct, subvibrissa at least 0.5× vibrissa length, gena with setulae scattered along ventral 2/3, postgena with 3 setae at lower margin. Colour patterns and pruinosity on gena variable. Genal height 0.18–0.25× eye height. Facial carina pollinose. Ventromedial desclerotization of face surpassing ventral point of subantennal depression; sub-antennal depression reduced, inner face reduced, outer face well sclerotized.

Thorax: Presutural and postsutural acrostichal setae aligned in a single median row, prescutellar acrostichal setae absent. Anterior intra-alar seta sometimes present, if present length inconsistent but often small; presutural and postsutural supra-alar setae present; postalar setae always longer than intra-alar and supra-alar setae. Intrapostalar seta small. Scutellum with 2 pairs of marginal setae. Katepisternal seta well developed.

Legs: All coxae and trochanters yellow. Remaining leg colour patterns variable. Fore coxae pruinosity variable.

Male terminalia (Figs. 31.1–6, 34.1–5): S6 horseshoeshaped (or U-shaped), length subequal or longer than width; extension from arcuate sclerotization widest anteriorly; posterior apices articulating with S7+8. S7+8 dorsally pruinose, asymmetrical, left side of S7+8 with cleft indicating boundaries of S7 and S8; postspiracular

sclerite present. Epandrium with pair of outstanding setae in addition to numerous shorter setae; ventroposterior corner sharply perpendicular. Surstylus simple rod-like, apex tapering. Cerci fused below anal opening; inner surface only with few setulae, outer surface setose. Subepandrial sclerite sheet-like, thin, V-shaped, setae not contiguous but crowded at posterolateral corner of sclerite, anterior seta 2.5× posterior seta. Dorsal bridge of hypandrium short; anterior half of phallic plate with prominent dorsomedial ridge; ventral bridge short, well sclerotized, medially connected to independent, elongated, relatively straight but slightly outwardly bowed pregonites that are sitting ventral to phallapodeme. Pregonites with sensory setulae on five-sixth of length. Postgonite with 2 points and a rounded lobe. Phallapodeme straight, strongly spatulate on distal third, phallic guide present on mid-length. Distiphallus asymmetrical, skewed to the right; basal distiphallus long, half phallapodeme length, extremely sclerotized apically; distal distiphallus well sclerotized basally and membranous on apical half.

Female terminalia: S6 weakly sclerotized with 2 pairs of setae.

Pseudopomyza (Heluscolia) antipoda (Harrison) (Figs. 30.1–4, 31.1–6, 32.1–4)

Heloclusia (Heluscolia) antipoda Harrison, 1955: 215.—Harrison, 1959: 122.—Harrison, 1964: 311.

Protoborborus antipodus (Harrison)—Harrison, 1976: 145.

Pseudopomyza antipoda (Harrison)—Mathis, 1989: 470.—McAlpine, 1994: 182.

Diagnosis

Face yellow except outer face somewhat tan. Gena yellow except ventrally with tan to brown triangular marking, posterior corner of postocular area brown through to occiput, brown colour sometimes extending to ventral margin. Anepisternum glossy except posterodorsal corner. Katepisternum mostly glossy but area posterior to katepisternal seta pruinose.

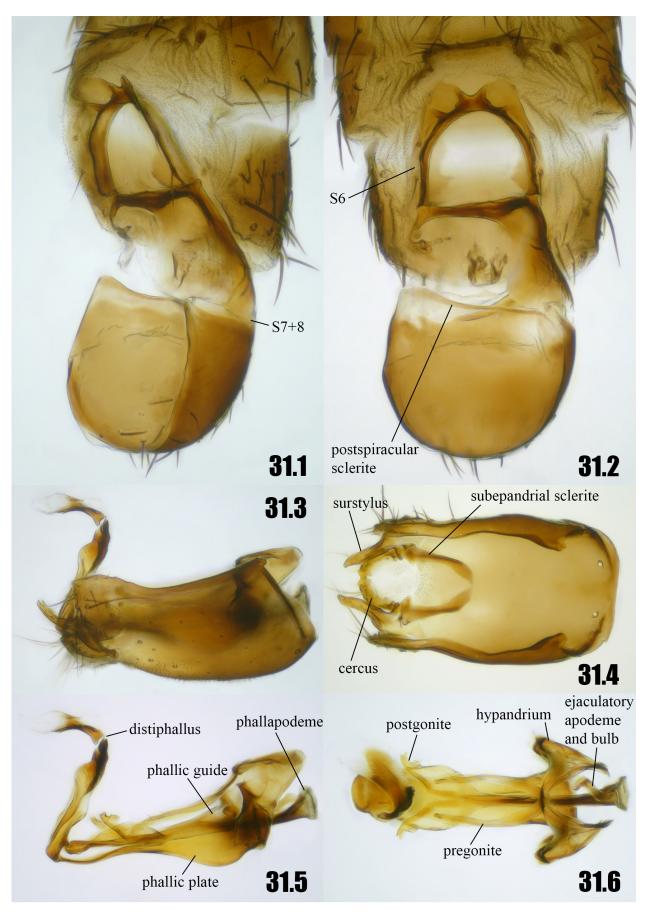
Description

Body length 1.9-2.5 mm (males) (head to wing tip = 2.8-3.3 mm), 2.0-2.6 mm (females) (head to wing tip = 2.8-3.3 mm).

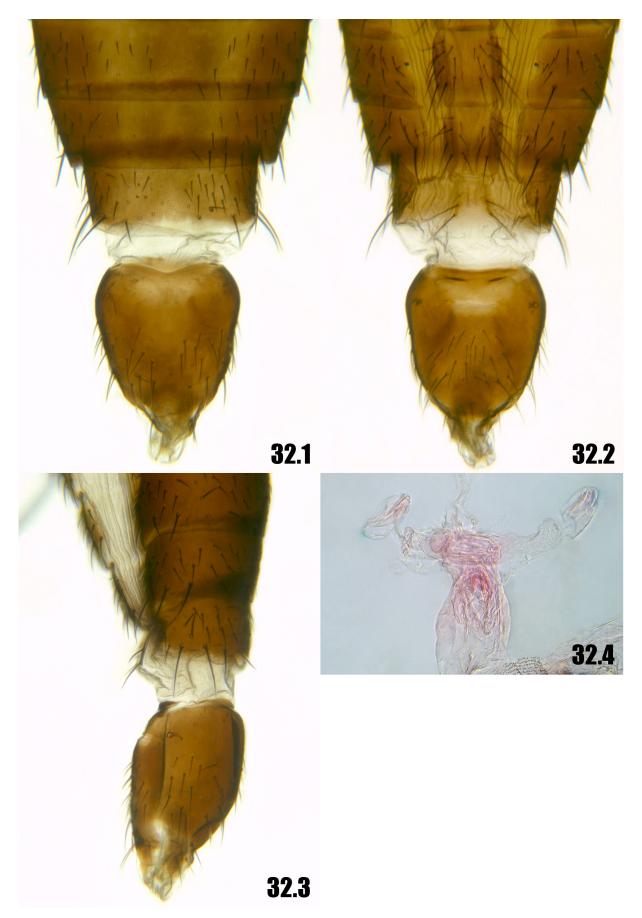
Head: Frons brown, gradually paler towards yellow anterior margin, fronto-orbital plates paler than frons. Length of first fronto-orbital seta 0.6×2^{nd} , 2^{nd} 0.88×3^{rd} . Antenna yellow except outer surface and apex of inner surface of first flagellomere brown. Face yellow except outer face somewhat tan. Gena yellow except ventrally with tan to brown triangular marking, posterior corner of postocular area brown through to occiput, brown colour sometimes extend to ventral margin; uniformly pruinose; genal height $0.25 \times$ eye height. Subvibrissa $0.64 \times$ vibrissa and positioned at the posterior limit of vibrissal angle or posterior to vibrissal angle.



FIGURES 30.1–4: *Pseudopomyza (Heluscolia) antipoda* male habitus (New Zealand). 30.1, left lateral (Campbell Island); 30.2, left lateral (colour variant with anterior intra-alar seta absent) (Adams Island); 30.3, dorsal (Campbell Island); 30.4, head (Campbell Island).



FIGURES 31.1–6: *Pseudopomyza (Heluscolia) antipoda* male abdomen (Campbell Island, New Zealand). 31.1, terminalia left ventrolateral; 31.2, terminalia ventral; 31.3, epandrium left lateral; 31.4, epandrium ventral; 31.5, phallus and associated structures left lateral; 31.6, phallus and associated structures ventral.



FIGURES 32.1–4: *Pseudopomyza (Heluscolia) antipoda* female abdomen (Campbell Island, New Zealand). 32.1, terminalia dorsal; 32.2, terminalia ventral; 32.3, terminalia left lateral; 32.4, spermathecae and associated structures.

Thorax: Scutum brown to dark brown except postpronotum yellowish-brown posteroventrally; uniformly pruinose. Presutural acrostichal setae only slightly longer and thicker than background setulae, 0.2× postsutural acrostichal setae. Anterior intra-alar sometimes present, if present length inconsistent but often small. Presutural supra-alar seta 2× postsutural supra-alar seta and 0.87× postalar seta. Intrapostalar seta subequal postsutural supra-alar seta. Anepisternum glossy except posterior to katepisternal seta pruinose.

Legs: Foreleg dark brown except base and apex of femur. Mid and hind femur mostly brown to dark brown, basal quarter and apical extremities yellow; tibia yellow to tan (an almost imperceptible band at second and distal quarter may appear at different viewing angles or lighting); tarsi yellow except last tarsomere often slightly darker. Fore coxa with medial surface pruinose, anterolateral surface pruinose on anterior, dorsal and ventral margin, posterolateral surface ventrally with sparse lines of pruinosity.

Male terminalia (Figs. 31.1–6): Length and width of S6 subequal, anteromedially shortened, with 2 widely spaced setae along length of extension, sclerite medially sometimes with slightly more sclerotized wing patches. Ventral arm of S7 tapering off past right articulation with S6, apex connected to right side of S7+8 by membrane; postspiracular sclerite thickened and broadly connected to right side of S7+8. Epandrium medially pruinose; width 0.77× length, width uniform. Base of posterior seta on subepandrial sclerite elongated. Ejaculatory apodeme simple, with acutely bent ejaculatory bulb.

Female terminalia: S6 slightly more sclerotized at base of 2 (sometimes 3) setae. S7 with sclerotized pair of sub-marginal strip, and a narrow horizontal band at anterior quarter; setae mainly restricted to mid-section of sclerite. T7 posterior two thirds setose. Spermathecae (1+1) membranous, cup-shaped and smooth.

Type specimens (not examined): Holotype: ♀: NEW ZEALAND: Antipodes Islands: Antipodes Island: Ringdove Bay, on plateau, 8.xi.1950, R.K. Dell (MONZ).

Paratype: **NEW ZEALAND: Campbell Islands:** Campbell Island, 1943, 1 ex., J.H. Sorensen $(1^{\circ}, NZAC)$.

Other material examined: NEW ZEALAND: Antipodes Islands: Antipodes Island, Reef point, 1.ii.1969, G. Kuschel (1♀, NZAC); ditto, 80 m, 8.ii.1969 (1♀, NZAC); Auckland Islands: Adams Island, Fairchild Garden, 20.i.1966, G. Kuschel (1♂, 2♀, NZAC); Enderby Island, Sandy Bay, in tent, 12.ii.1973, D.S. Horning (1♂, 1♀, NZAC); Enderby Island, w. of Sandy Bay, around shag nest on cliff faces, 26.ii.1973, D.S. Dugdale (1♀, NZAC); Campbell Islands: Campbell Island, Lookout Bay, 14–23.i.1969, G. Kuschel (1♂, NZAC); ditto, sealion wallow (2♀, NZAC); Campbell Island, Lyall-St Col Ridge, *Diomedea epomophora* (albatross) nest reared 81/27 em 16.iv.1981, 26.ii.1981, G.W. Ramsay & T.K. Crosby (1♂, 1♀, NZAC); ditto, *Diomedea epomophora* (albatross) nest reared 81/27 em 8.iv.1981 (1♀, NZAC);

Snares Islands: Biological Station, sweeping *Poa annua* and *Carex trifida*, 23.ii.1974, D.S. Horning $(1 \capp2, NZAC)$; ditto, *Stellaria media*, 6.ii.1972 $(1 \capp2, NZAC)$; ditto, sweeping *Stellaria media*, *Poa annua* and *Carex trifida*, 12.i.1977, J.W. Early $(1 \capp2, NZAC)$; North Island, E. end S.W. Promontory Razorback, foliage of *Lepidium oleraceum*, 20.ii.1972, C.J. Horning $(1 \capp2, NZAC)$; Sinkhole Flat, sweeping *Poa tennantiana*, 20.i.1977, J.W. Early $(1 \capp2, NZAC)$.

Comments: Pseudopomyza antipoda is known only from isolated oceanic islands south of New Zealand's South Island. There are minor differences in gena and leg colouration between species from different island groups (Figs. 30.1, 30.2); however, structural characteristics are mostly consistent with the exception of the presence and size of the anterior intra-alar seta, which can differ between specimens and even between left and right body halves of a specimen.

Pseudopomyza (Heluscolia) brevis (Harrison) (Figs. 33.1–3, 34.1–5)

Protoborborus brevis Harrison, 1976: 144. Pseudopomyza brevis (Harrison)—Mathis, 1989: 470.—McAlpine, 1994: 182.

Diagnosis

Face entirely yellow. Gena entirely yellow. An episternum and katepisternum pruinose or pollinose. Brachypterous.

Description (males only)

Body length 1.9–2.2 mm. General colour light tan to brown.

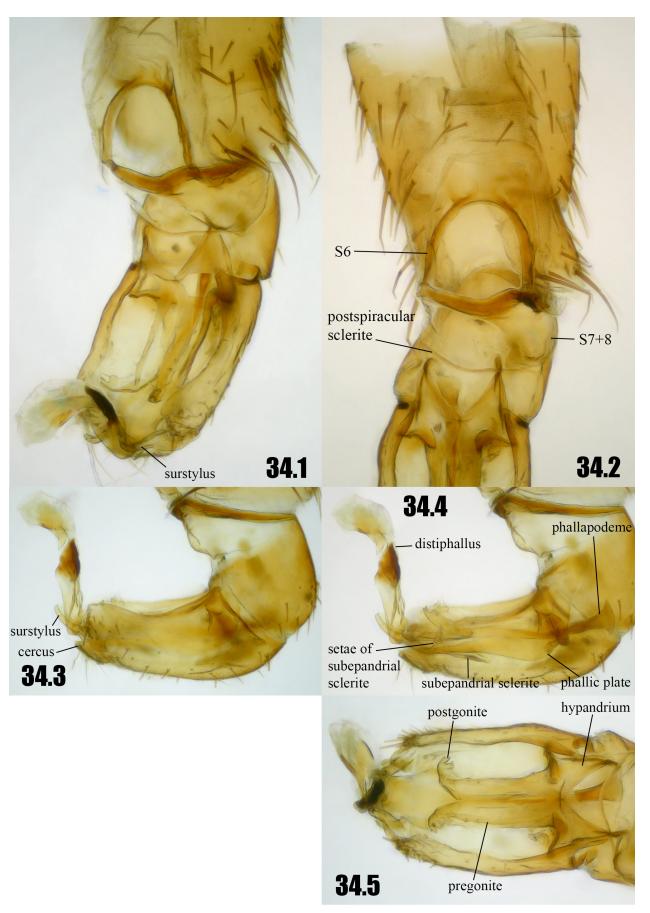
Head: Frons tan, gradually paler towards yellow margin, fronto-orbital plates paler, ocellar triangle darkest. Length of first fronto-orbital seta 0.35×2^{nd} , 2^{nd} 0.9×3^{rd} . Antenna yellow with minimal tan colour on apex of first flagellomere. Face entirely yellow. Gena entirely yellow, uniformly pollinose, genal height $0.18 \times$ eye height. Subvibrissa $0.5 \times$ vibrissa and positioned posterior to vibrissal angle.

Thorax: Scutum margins yellow to tan, medially brown, uniformly pruinose or pollinose. Presutural acrostichal setae only slightly longer and thicker than background setulae, 0.5× postsutural acrostichal setae. Anterior intra-alar present but only slight longer and thicker than background setulae. Presutural supra-alar seta 2× postsutural supra-alar seta and 0.83× postalar seta. Intrapostalar seta 0.66–0.75× postalar seta (chaetotaxy incomplete in available specimens). Anepisternum and katepisternum pruinose or pollinose.

Legs: Fore femur and tibia basal quarter to third and distal extremity yellow, remaining tan to brown (lighter on tibia); basal and distal ends of fore tarsomeres yellow, remaining tan. Mid leg yellow except tarsomere 5 slightly darker. Hind leg yellow except tan band on 2nd quarter and brown tarsomere 5. Fore coxae sparsely pruinose.



FIGURES 33.1–3: Pseudopomyza (Heluscolia) brevis male habitus (New Zealand). 33.1, left lateral; 33.2, dorsal; 33.3, head.



FIGURES 34.1–5: *Pseudopomyza (Heluscolia) brevis* male abdomen (New Zealand). 34.1, terminalia left ventrolateral; 34.2, terminalia ventral; 34.3, epandrium left lateral; 34.4, phallus and associated structures left lateral; 34.5, phallus and associated structures ventral.

Wing: brachypterous, wing length slightly shortened, wing width only half of body width. M_1 and M_4 shortened past r-m, CuA+CuP highly reduced or absent, dm-m absent.

Male terminalia (Figs. 34.1–5): S6 longer than wide, with 1–2 setae (if 2, anterior seta small and widely spaced from posterior seta). Ventral arm of S7 wavy, protruding on left articulation with S6, truncated immediately past right articulation with S6 and connected to right side of S7+8 by weak sclerotization and membrane; postspiracular sclerite uniformly thin. Epandrium medially pruinose; width 0.9× length, width uniform along length. Base of both setae on subepandrial sclerite elongated.

Type specimens: Holotype: ♂: **NEW ZEALAND: Snares Islands:** under dead seabirds, 7–12.i.1973, D.S. & C.J. Horning (NZAC).

Paratypes (not examined): **NEW ZEALAND: Snares Islands:** Same collection data as holotype $(9 \, \circlearrowleft, 16 \, \circlearrowleft, NZAC)$; Comma Bay, under dead *Puffinus griseus*, 12.i.1973, C.J. Horning $(1 \, \circlearrowleft, NZAC)$; Sinkhole Flat, dead leaves and litter of *Poa tennantiana*, 26.i.1972 $(1 \, \circlearrowleft, NZAC)$; Penguin Creek, in wet litter of *Olearia lyallii*, 26.i.1972 $(1 \, \circlearrowleft, NZAC)$; Southwest Promontory, in litter under *Stibocarpa robusta*, 13.ii.1972, D.S. Horning $(1 \, \circlearrowleft, NZAC)$; Station Point, nest of *Pterodroma inexpectata*, 6.ii.1967, J. Warham $(1 \, \backsim, NZAC)$; *Olearia* logs, 10.i.1967, P.M. Johns $(1 \, \backsim, NZAC)$.

Other material examined: NEW ZEALAND: Snares Islands: Sinkhole, *Durvillea* beach drift, 30.i.1967, P.M. Johns (13, NZAC).

Comments: The brachypterous *P. brevis*, like the closely related macropterous *P. antipoda*, is found on the outer islands south of New Zealand.

Subgenus Pseudopomyza Strobl

Protoborborus Malloch, 1933: 261. Type species Protoborborus neozelandicus Malloch, 1933 (original designation). Harrison, 1959: 254 (diagnosis); McAlpine, 1966: 682 (synonymy); Hennig, 1969: 591 (keyed); Hennig, 1971: 1 (discussion of synonymy, phylogenetic discussion); Harrison, 1976: 144 (discussion of synonymy, key to species).

Rhinopomyzella Hennig, 1969: 596 (as genus). Type species Rhinopomyzella nigrimana Hennig, 1969 (original designation). Hennig, 1969: 591 (keyed), 596 (diagnosis, relationships), 598 (key to species); Krivosheina, 1979: 187 (phylogenetic notes), 188 (keyed); Prado, 1984: 1 (Neotropical catalog); McAlpine, 1994: 182 (reduced to subgenus, keyed), 183 (status, diagnosis); Buck & McAlpine, 2010: 824 (as subgenus, keyed).

Macalpinella Papp, 2005: 189 (as genus). Type species Macalpinella brevifacies Papp, 2005 (original designation). Papp, 2005; 189 (description, illustr); Buck & McAlpine, 2010: 823 (reduced to subgenus).

The subgenus *Pseudopomyza* McAlpine was previously considered one of five subgenera of *Pseudopomyza* and included *P. atrimana* (Meigen), *P. antipoda* (Harrison), *P. aristata* (Harrison), *P. brevicaudata* (Harri

brevis (Harrison) and *P. neozelandica* (Malloch). Two of these species are here transferred to the reinstated subgenus *Heluscolia*, and the species formerly placed in *Macalpinella* syn. n. (*P. brevifacies*) and *Rhinopomyzella* syn.n. (*P. nigrimana*, *P. albimana*) are here transferred to a redefined subgenus *Pseudopomyza*.

The subgenus *Pseudopomyza* now consists of the type species *P. atrimana* (Palaearctic), *P. aristata* (New Zealand), *P. brevifacies* (Palaearctic/Oriental boundary in Bhutan, Japan and Taiwan), *P. neozelandica* (New Zealand), *P. nigrimana* (Neotropical), *P. albimana* (Neotropical) and 15 new Neotropicalspecies.AllNeotropicalspecies in the subgenus are in the *P. nigrimana* species group (the Neotropical clade of the former subgenus *Rhinopomyzella*). An additional species from New Zealand (sp.n. 1 CNC729345), known from a single female, remains undescribed.

Diagnosis

Three fronto-orbital setae; subvibrissa present but at most 0.3× length of vibrissa or only 2× length of background setulae and positioned on vibrissal angle; pedicel with several moderately long ventral setae. Anterior intra-alar seta distinct; prescutellar acrostichal chaetotaxy present, either a distinct pair of setae or scattered setulae. Phallic plate relatively flat and straight.

Description

Body length 1.5–2.8 mm (males), 1.5–3.1 mm (females).

Head: With 3 reclinate fronto-orbital setae. Antenna colour variable; arista arising dorsoapically, pubescent, at least as long as head width; pedicel with at least one large seta medial to medioventral long seta. Vibrissa distinct, subvibrissa at most $0.3 \times$ length of vibrissa or only $2 \times$ length of background setulae and positioned on vibrissal angle; gena with setulae scattered along ventral 2/3; postgena with 3 setae at lower margin. Colour patterns and pruinosity on gena variable. Genal height $0.23-0.58 \times$ eye height. Facial carina pollinose. Ventromedial desclerotization of face variable, but often not surpassing ventral point of sub-antennal depression; facial plates usually well developed and sclerotized (except more basal lineages).

Thorax: Presutural and postsutural acrostichal setae aligned in a single median row, prescutellar acrostichal setae (or sometimes just setulae) present. Anterior intra-alar seta present; presutural and postsutural supra-alar setae present (except the Neotropical *P. angustifrons*); postalar setae always longer than intra-alar and supra-alar setae. Intrapostalar seta small. Scutellum with 2 pairs of marginal setae, more derived lineages often with 3 minute setulae at base of basal seta. Katepisternal seta well developed.

Legs: Colour patterns variable. Fore coxae pruinosity variable.

Male terminalia (Figs. 36.1–5, 39.1–5, 42.1, 45.1–6, 53.1–3): S6 horseshoe-shaped (or U-shaped) or H-shaped; posterior apices articulating with S7+8. S7+8 dorsally

pruinose, either asymmetrical and left side of S7+8 with cleft indicating boundaries of S7 and S8, or symmetrical and without cleft; postspiracular sclerite present or absent. Epandrium with pair of anterior outstanding setae and rarely second pair of posterior setae differentially larger than the numerous shorter setae; posteroventral corner sometimes extended posteriorly. Surstylus variable. Cerci fused at posterior margin of anal opening; inner surface only with few setulae, outer surface setose. Subepandrial sclerite sheet-like, narrow or broad, setae usually not contiguous or crowded at posterolateral corner of sclerite, anterior seta often larger than posterior seta. Dorsal bridge of hypandrium short; phallic plate relatively flat and straight; ventral bridge long or short, well sclerotized, medially connected to pregonites. Pregonites independent of each other and relatively straight or fused and strongly arched; position of sensory setulae on pregonites variable. Postgonite shape variable. Phallapodeme straight or strongly arched, sometimes distally spatulate, phallic guide often present. Distiphallus symmetrical or asymmetrical (skewed to the right); basal distiphallus of various lengths and form, sometimes extremely sclerotized apically but more often uniformly sclerotized and tubular; distal distiphallus variable but always membranous apically.

Female terminalia: S6 weakly sclerotized usually with 1–2 pairs of setae. Sclerotization pattern of S7 variable. Spermathecae shape and texture variable but usually well sclerotized and symmetrical.

Pseudopomyza (Pseudopomyza) aristata (Harrison) (Figs. 35.1–3, 36.1–5, 37.1–3)

Heloclusia (Heluscolia) aristata Harrison, 1959:121, 123.

Pseudopomyza aristata (Harrison)—Mathis, 1989: 470.—
McAlpine, 1994:182.

Diagnosis

Eye large. Pedicel brown and first flagellomere uniformly brown. Facial desclerotization not passing ventral point of sub-antennal depression. Medial acrostichal setae well-developed. Pleuron pruinose or pollinose; katepisternum with a row of 5 setulae ventral to katepisternal seta; scutellum with no setulae. Legs with variegated yellow and brown colour patterns. Male S7+8 asymmetrical, weakly sclerotized on right lateral; left side of S7+8 with cleft indicating boundaries of S7 and S8; postspiracular sclerite weak and broken. Surstylus without lamella.

Description

Length 1.9–2.8 mm (males), 1.8–2.8 mm (females).

Head: Frons dark brown to black, lighter at anterior margin, fronto-orbital plates paler. Length of first fronto-orbital seta 0.3×2^{nd} , 2^{nd} subequal to 3^{rd} . Antenna entirely brown. Carina and outer face tan remaining face yellow; desclerotization at anteromedial margin of face almost reaching ventral point of sub-antennal depression. Gena mostly yellow, dark brown restricted to posterior corner

of postocular area; gena and postgena pruinose; genal height $0.26 \times$ eye height. Sub-vibrissa $0.33 \times$ vibrissa and positioned on or at posterior limit of vibrissal angle.

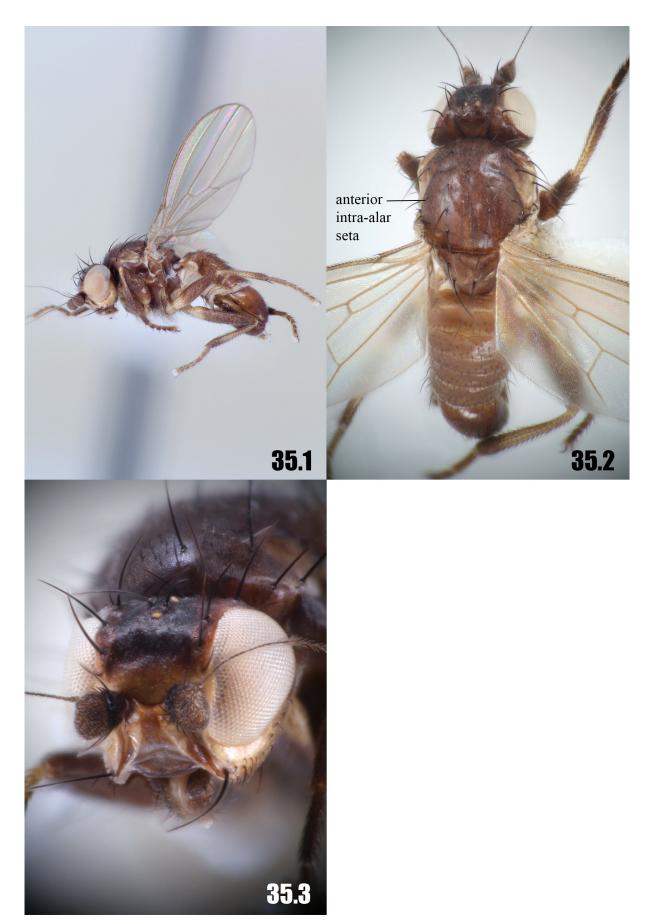
Thorax: Scutum brown; uniformly pruinose. Presutural acrostichal setae small indifferentiable from background setulae, postsutural acrostichal setae only slightly longer than background setulae. Anterior intraalar 0.4× presutural supra-alar seta, postsutural supra-alar 0.6× presutural supra-alar, postalar seta 1.1× presutural supra-alar. Intrapostalar seta subequal anterior intraalar. Scutellum with 2 marginal setae. Pleuron entirely pruinose. Katepisternum with a row of 5 setulae ventral to katepisteral seta.

Legs: Fore coxa medially brown, remaining yellow, mid coxa dorsally tan to brown, hind coxa yellow; all trochanter yellow. Fore coxae medial and anterolateral surface pruinose/ pollinose, anterodorsal corner of posterolateral surface pruinose, ventrally with sparse lines of pruinosity. Foreleg brown except basal quarter of femur and basal half of tibia yellow. Mid and hind femur brown except basal quarter yellow; tibia yellow except distal quarter tan (very light tan band at second quarter may appear at different viewing angles or lighting); tarsus yellow.

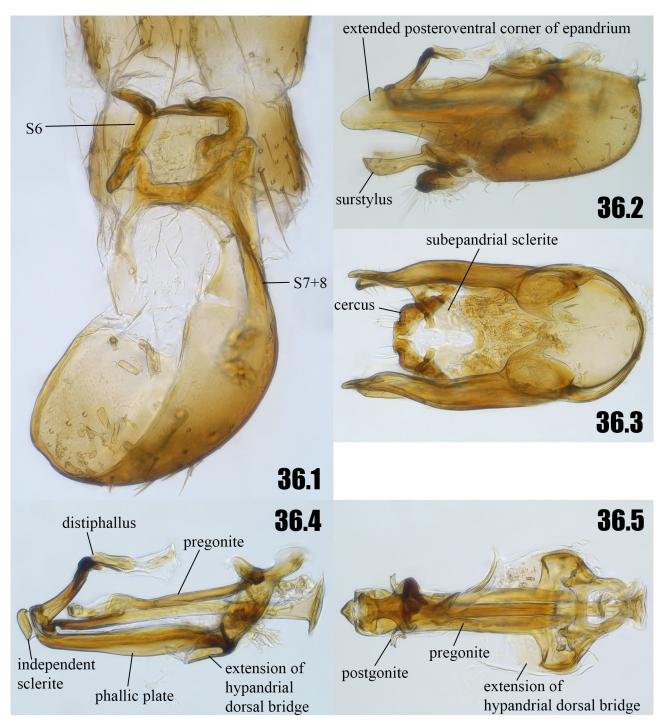
Male terminalia (Figs. 36.1-5): S6 H-shaped, anterolateral arms bent ventrally and with sensory setulae on mid-length, posterolateral arms thicken at mid-length and with seta on inner surface. Anterolateral corners of S7+8 strongly protuberant, articulating with S6; S7 weakened past right protuberance and weakly connected to right side of S7+8; "ring" of S7+8 stretched long (possibly to accommodate long epandrium); left side of S7+8 with cleft indicating boundaries of S7 and S8; postspiracular sclerite weak and broken. Epandrium uniformly pruinose, uniform in width; anteroventral corners dilated, articulating points with hypandrium close to medial line; posteroventral corners strongly extended posteriorly. Cercus truncated apically. Surstylus straight, slightly dilated distally, distally with scattered setulae. Subepandrial sclerite narrow, V-shaped; anterior and posterior seta closely paired at posterior edge, anterior seta 2.5× posterior seta.

Phallapodeme relatively straight, phallic guide reduced to a triangular extension from phallapodeme. Ventral bridge of hypandrium short; outer surface of dorsal bridge with sheet-like extension; phallic plate relatively straight, deep trough-like, apex with independent sclerite; dorsal surface of dorsal bridge extended posteriorly. Pregonites mostly independent of each other; relatively straight; sensory setulae on distal half of sclerite length; apex extended dorsally, L-shaped. Postgonite small, forked and trilobate. Distiphallus skewed to the right, basal distiphallus tubular, distally spatulate and heavy on the right, distal distiphallus strongly curved, basally with leaf-like sclerite, distally with smaller and weaker leaf-like sclerite in middle of membranous mass.

Female terminalia: S6 weakly sclerotized, with 2 pairs of setae, anterior pair shorter than posterior pair. S7 laterally bulbous at base, ventrally with a pair of triangular well sclerotized protuberances, and a medial hourglass-



FIGURES 35.1–3: *Pseudopomyza (Pseudopomyza) aristata* male habitus (New Zealand). 35.1, left lateral; 35.2, dorsal; 35.3, head.



FIGURES 36.1–5: *Pseudopomyza* (*Pseudopomyza*) *aristata* male abdomen (New Zealand). 36.1, terminalia left ventrolateral; 36.2, epandrium left lateral; 36.3, epandrium ventral; 36.4, phallus and associated structures left lateral; 36.5, phallus and associated structures ventral.

shaped sclerotization. Spermathecae smooth, weakly sclerotized and of flattened mushroom-shape.

Type specimen: Holotype: ♂: **NEW ZEALAND: Auckland:** Little Barrier Island, Kauri Gulley and tracks, 24.xi.1954, R.A. Harrison (NZAC).

Other material examined: **NEW ZEALAND: North Island: Auckland:** Moerangi, 38.54S 175.36E, 625 m, podocarp forest, window trap, 4–9.iv.1980, A. Newton & M. Thayer (1&\circ\), DEBU); **Bay of Plenty:** Kaimai range,

Old Kaimai Rd. MT near summit, 22.xii.1970, J. Gillespie (1\$\tilde{\cappa}\$, 1\$\varphi\$, NZAC); **Hawke's Bay:** Puketitiri, Little Bush, MT, 25.ix.1986, T.H. Davies; **Manawatū-Whanganui:** Mt. Ruapehu, Ohakune, Blyth track, MT, 7–8.ii.1970, J. Gillespie (1\$\tilde{\cappa}\$, NZAC); ditto, Rimu track, 700 m, 18.viii.1999, SAM (2\$\tilde{\cappa}\$, DEBU); **Northland:** Waipoua SF., near Forest hq, 35.9S 173.3W, 90 m, Podocarpbroadleaf, 11–15.iv.1980, A. Newton & M. Thayer (1\$\tilde{\cappa}\$, DEBU); **Waikato:** Pirongi, West Road nr Oparau





FIGURES 37.1–3: *Pseudopomyza (Pseudopomyza) aristata* female abdomen (New Zealand). 37.1, terminalia ventral; 37.2, terminalia left lateral; 37.3, spermathecae and associated structures.

R, 7.xi.1970, J. Gillespie (1♀, NZAC); **South Island: Canterbury:** Canterbury Castle Hill, 80k N Christchurch, 43.32S 172.38E, grass, 22.ii.1999, SAM (1♀, DEBU); **West Coast:** Punakaiki, *Nothofagus* forest, on limestone, MT, 29.xii–3.i.1984, LM (5♂, 3♀, CNC); Punakaiki, MT nr fungi, 29.xii–3.i.1984, LM (1♂, DEBU); Sunny Bright Shore Lake Kaniere, 135 m, 42.518S 171.09W, podocarp forest, window trap, 15–17.iii, 1980, A. Newton & M. Thayer (1♂, NZAC).

Pseudopomyza (Pseudopomyza) atrimana (Meigen) (Figs. 38.1–3, 39.1–5, 40.1–4)

Opomyza atrimana Meigen, 1830: 106.—Macquart, 1835: 557.— Schiner, 1864: 55.

?Dichrochira atrimana (Meigen)—Becker, 1905: 58.

Pseudomyza atrimana (Meigen)—Frey, 1952: 8 (genus name correct on page 7, but erroneous at the species description and below the Figure on page 8).

Pseudopomyza atrimana (Meigen)—Chandler, 1983: 89.—
Krivosheina, 1984: 49.—McAlpine, 1994: 182.—Greve & Jonassen, 1995: 131.—Shatalkin, 1995: 142, 143.—Merz, 1998: 132.—Papp, 1998: 122.—Krivosheina, 1999: 503.—Papp, 2001: 268.—Skibińska & Chudzicka, 2007: 198.—Tschirnhaus, 2008: 67, 87.—Zuijlen, 2009: 1.—Ventura Pérez, 2010: 308.—Beuk, 2013: 1.—Andrade & Gonçalves, 2014: 168.—Kahanpää & Stuke, 2014: 254.—Chandler, 2021: 271.

Pseudopomyza nitidissima Strobl, 1893: 284.—Hendel, 1902: 264 (synonymized with atrimana)—Becker, 1905: 251.—Chvála, 2008: 196.

Diagnosis

Eye large. Facial desclerotization not passing ventral point of sub-antennal depression. Pedicel yellow, first flagellomere bicoloured. Prescutellar acrostichal setae absent, prescutellar area with only scattered setulae. Pleuron mostly glossy. Scutellum with a cluster of 3 setulae at base of basal seta. Legs with variegated yellow and brown colour patterns. Male S7+8 symmetrical; left side of S7+8 without cleft indicating boundaries between S7 and S8; postspiracular sclerite absent. Surstylus with lamella. Ventral bridge of hypandrium long. Distiphallus strongly asymmetrical.

Description

Length 2–2.4 mm (males), 2.2–2.9 mm (females).

Head: Frons dark brown to black, except thick yellow band at anterior margin, fronto-orbital plates (rarely ocellar triangle) paler. Length of first fronto-orbital seta 0.75× 2nd, 2nd subequal to 3rd. Antenna yellow except first flagellomere distally brown. Face entirely yellow; desclerotization at ventromedial margin reaching ventral point of sub-antennal depression. Gena mostly yellow, sometimes with minimal brown under eye, dark brown restricted to postocular area; glossy on anterior half, pruinose on posterior half and through to postgena; genal

height 0.23× eye height. Subvibrissa 0.37× vibrissa and positioned on vibrissal angle.

Thorax: Scutum dark brown; uniformly pruinose. Presutural acrostichal setae small but differentiated, half as long as postsutural acrostichal setae. Anterior intra-alar and supra-alar (1+1) setae subequal, half as long as postalar seta. Intrapostalar seta small but differentiated, 2× background setulae. Scutellum with 2 pairs of marginal setae and 3 minute setulae at base of basal seta. Anepisternum glossy, Katepisternum anterior half glossy, posterior half pruinose.

Legs: All coxae and trochanters yellow. Fore coxae pruinose but pruinosity of posterolateral surface relatively sparse compared to medial and anterolateral surfaces. Foreleg dark brown except basal quarter of femur yellow. Base and apex of mid femur yellow, mid-section yellowish-brown; tibia and tarsus yellow. Hind femur dark brown except basal half or less yellow; hind tibia and tarsus yellow.

Male terminalia (Figs. 39.1-5): S6 apparently Hshaped, lateral extensions from sclerotization extending lateral sides extend ventrally, sensory setulae on apex of anterolateral arms, 2 long setae on body of anterolateral arms, anterior area connecting anterolateral arms weakly sclerotized. Ventral band of S7+8 without apparent protuberance but thick and very well sclerotized, strongly connected to right of S7+8 forming a symmetrical and closed ring sclerite; left side of S7+8 without cleft indicating boundaries between S7 and S8; postspiracular sclerite absent. Epandrium mostly pruinose except anteromedial area; width 0.65× length, slightly widened medially. Cercus somewhat tapered. Surstylus strongly bent anteriorly, inner lamella wider than body of surstylus, apex truncate. Subepandrial sclerite large and broad, rounded to almost subquadrate; anterior seta 2.5× posterior seta and displaced laterally, setae well-spaced on posterior half of sclerite, not crowded at posterior corner.

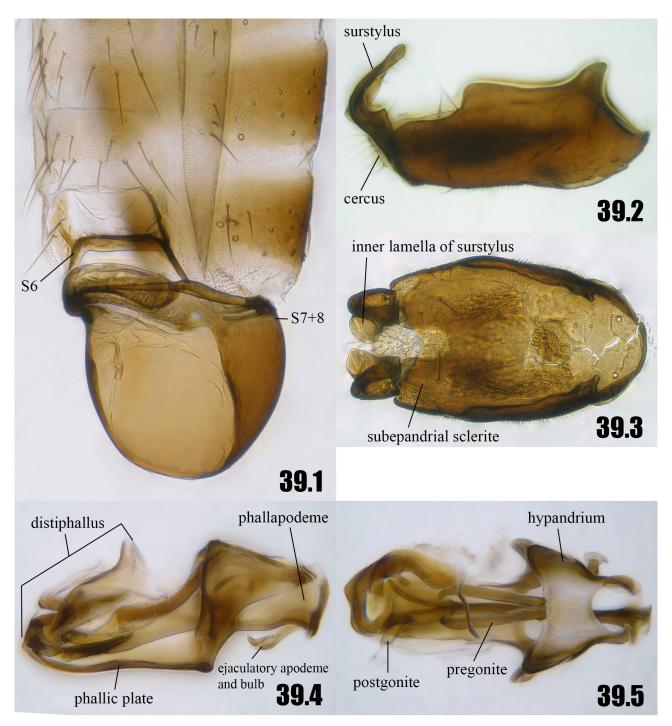
Terminalia proportionally shorter when compared to epandrium length, barely reaching anterior margin of anal opening (when distiphallus is deflexed forward). Phallapodeme relatively straight, phallic guide reduced to a triangular extension from phallapodeme. Ventral bridge of hypandrium long, phallic plate flat, straight, wide and encompassing most of phallus. Pregonites mostly independent of each other; gently curved dorsal-ventrally, but not bowed laterally; sensory setulae on distal half of sclerite. Postgonite short, shallowly forked and weakly trilobate, posterodorsal lobe apically acute. Distiphallus strongly skewed to the right, basal distiphallus thick, open-ringed, heavy on right side, distal distiphallus basally thick, flat and twisted, sitting on right side of basal distiphallus, distally membranous and covering distal half of terminalia.

Female terminalia: S6 weakly sclerotized, with 2 pairs of setae. S7 protuberant at base and posterolaterally to sensory setulae; area posterior to protuberance with 3 stripes of sclerotization. Spermathecae smooth, weakly sclerotized and bulbous with distal depression.

Type specimens (not examined): Opomyza atrimana Meigen, 1830: The type locality was in the vicinity of



FIGURES 38.1–3: Pseudopomyza (Pseudopomyza) atrimana male habitus (Russia). 38.1, left lateral; 38.2, dorsal; 38.3, head.

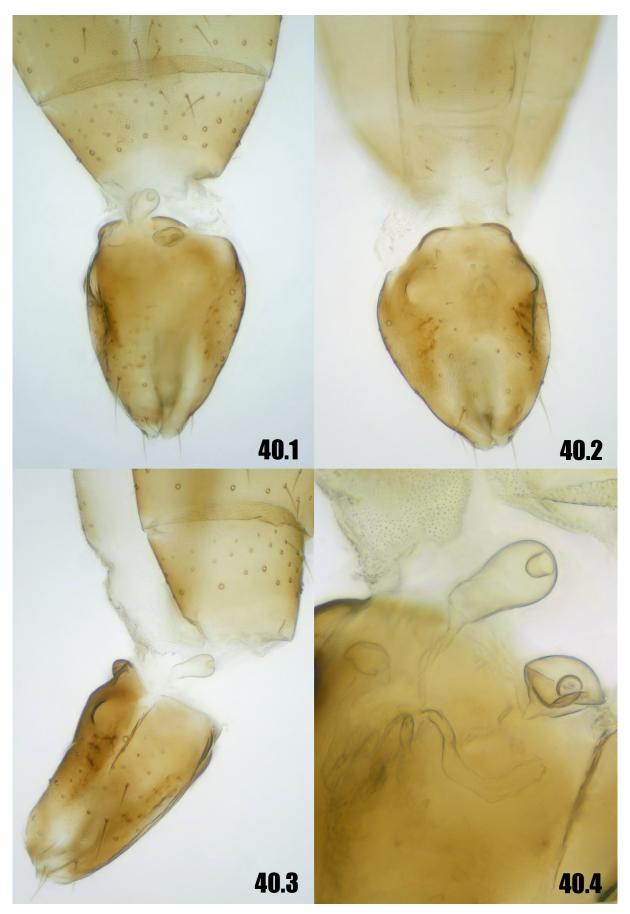


FIGURES 39.1–5: *Pseudopomyza (Pseudopomyza) atrimana* male abdomen (Russia). 39.1, terminalia left ventrolateral; 39.2, epandrium left lateral; 39.3, epandrium ventral; 39.4, phallus and associated structures left lateral; 39.5, phallus and associated structures ventral.

Aachen, West Germany. Hendel (1902) mentioned that Thalhammer had collected it in Transylvania (Rumania). Type depository unknown. Becker (1902) was unable to find the types. *Pseudopomyza nitidissima* Strobl, 1893: The type locality was in Seitenstentten, Austria. Female type probably lost (Chvála, 2008), but four other Strobl specimens are found in NMBA.

Other material examined: JAPAN: Iwate: Mt. Hayachine, 39°33'29.01"N 41°29'20"E, 400 m, MT, 20–27.vi.1989, H. Makihara & M. Sharkey (1♀, CNC);

Shikoku: Ishizuchi Mt. N.P. Tsuchigoya, 1400 m, 11–18.viii.1980, S. Peck (1♂, DEBU); RUSSIA (USSR): Siberia: Altai Region, Teletskoye Lake, 10–20.vii.1991, SAM (4♂, 5♀, DEBU); carrion trap, 11–15.vii.1991 (2♂, 2♀, DEBU); ditto, carrion trap 11–16.vii.1991 (3♂, DEBU); ditto, carrion/FIT, 8–11.vii.1991 (10♂, 15♀, DEBU); ditto, pans along river, 10–16.vii.1991 (4♂, 1♀, DEBU); ditto, pans along river, 16–20.vii.1991 (1♂, 4♀, DEBU); ditto, meadow pan traps, 8–16.vii.1991 (1♂, 2♀, DEBU); ditto, pans in wet meadow, 16–20.vii.1991 (2♂,



FIGURES 40.1–4: *Pseudopomyza (Pseudopomyza) atrimana* female abdomen (Russia). 40.1, terminalia dorsal; 40.2, terminalia ventral; 40.3, terminalia left lateral; 40.4, spermathecae.

3♀, DEBU); ditto, pans in wet meadow nr. piles of old slash, 15–19.vii.1991 (1 \circlearrowleft , 1 \updownarrow , DEBU); ditto, pan traps in poplar grove, 16–20.vii.1991 (40° , 49° , DEBU); ditto, pan traps in poplar grove, 16–28.vii.1991 (4%, DEBU); ditto, pan traps in poplar litter, 11-15.vii.1991 (213, 10, DEBU); ditto, pan traps in pine grove, 11-15.vii.1991 (50, 59, DEBU); ditto, pine grove, pan traps & FIT, 10– 20.vii.1991 (40, 39, DEBU); ditto, pine grove, pan traps & FIT, 16–20.vii.1991 (3♂, 3♀, DEBU); ditto, pan traps in field/forest edge, 11-15.vii.1991 ($1 \stackrel{?}{\circlearrowleft}$, $1 \stackrel{?}{\hookrightarrow}$, DEBU); ditto, pans in lake drift line, 15–20.vii.1991 (1\(\frac{1}{2}\), DEBU); ditto, swept over mud, 16.vii.1991 (26, DEBU); ditto, pans in wet area flooded, nettles, sand, 16-20.vii.1991 (13, 19, DEBU); ditto, dry area among ferns, nettles, pan traps, 16–20.vii.1991 (1♀, DEBU); Altai Region, 1500 m, under conifer branches, 12.vii.1991, SAM (1♀, DEBU); ditto, sweep/MT nr. cabin, 16.vii.1991 (2\,\tilde{Q}\), DEBU); Altai Region, ca. 20km S. Teletskove Lake, bulldozed vegetation, 19.vii.1991, SAM (3\delta, DEBU); Altai Region, ca. 50km SE of Teletskoye Lake, 1500 m, pans in balsam liter (fresh), (Abies), 11-16.vii.1991, SAM (7 $\stackrel{?}{\circ}$, $12\stackrel{?}{\circ}$, DEBU); ditto, sweep/ MT nr. cabin, 10.vii.1991 (23, DEBU); ditto, sweep/MT nr. cabin, 16.vii.1991 (13, DEBU); ditto, around hunting cabin, pine, balsam FIT/ MT, 11-16.vii.1991, SAM (13, 12, DEBU); ditto, wet area, 13-15.vii.1991 (16, DEBU); Gorno Altai, under pine tree by roadside, 8.vii.1991, SAM ($1 \circlearrowleft$, $3 \circlearrowleft$, DEBU); Novosibirsk Region, Cherny Mis, aspirated in ferns nr. dung, 26.vi.1991, SAM (1♂, DEBU); ditto, poplar forest, dung traps in ferns, 24-25.vi.1991 (16, DEBU); ditto, fallen poplar, 27.vii.1991 (2 \circlearrowleft , 3 \circlearrowleft , DEBU); ditto, poplar litter, in pines, 25.vi.1991(26, DEBU); ditto, aspirated among sedge roots, 28.vi.1991 (16, DEBU); ditto, pan traps in pines, 20–30.vi.1991 (2♂, DEBU); Novosibirsk Region, Old Botanical Garden, FIT/MT head, 15.vi-15.vii.1991, SAM (1&, DEBU).

Comments: Although the specimens examined here are mostly from Russia, *Pseudopomyza atrimana* is widespread across the Palaearctic and can be abundant. Its sister group relationship to the *P. nigrimana* species group is supported by synapomorphies including the inner lamella of the surstylus and the long ventral bridge of the hypandrium.

Pseudopomyza (Pseudopomyza) brevicaudata (Harrison)

(Figs. 41.1–3, 42.1, 43.1–4)

Heloclusia (Heluscolia) brevicaudata Harrison, 1964: 312.

Protoborborus brevicaudatus (Harrison)—Harrison, 1976: 144, 145.

Pseudopomyza brevicaudata (Harrison)—Mathis, 1989b: 470.—McAlpine, 1994: 182.

Diagnosis

Eye small. Antenna entirely brown to black. Facial desclerotization past ventral point of sub-antennal depression. Medial acrostichal setae well developed.

Anepisternum and katepisternum pruinose. Legs all brown; fore coxae entirely pruinose. Male S7+8 asymmetrical, weakly sclerotized on right lateral; left side of S7+8 with cleft indicating boundaries of S7 and S8. Surstylus without lamella.

Description

Body length 2.2 mm (male) (head to wing tip = 3.7 mm), 3.1 mm (female) (head to wing tip = 3.9 mm).

Head: Frons dark brown to black, lighter at anterior margin, fronto-orbital plates paler. Length of first fronto-orbital seta 0.75×2^{nd} , $2^{nd} \cdot 0.9 \times 3^{rd}$. Antenna entirely brown to black. Face tan; desclerotization at anteromedial margin of face reaching ventral point of sub-antennal depression. Gena yellow with light splotches of tan colour anteriorly and brown from postocular area through to occiput; uniformly pruinose; genal height $0.58 \times$ eye height. Subvibrissa $0.26 \times$ vibrissa and positioned on vibrissal angle.

Thorax: Scutum brown to drak brown; uniformly pruinose. Presutural acrostichal setae similar to background setulae, 3 postsutural medial acrostichal setae of similar length followed by 3 pairs of acrostichal increasing in length, prescutellar pair large. Anterior intra-alar present, 0.5× presutural supra-alar seta. Presutural supra-alar seta 1.3× postsutural supra-alar seta and 0.75× postalar seta. Intrapostalar seta subequal to intra-alar seta. Scutellum with 2 pairs of marginal. Anepisternum and katepisternum pruinose.

Legs: All brown to dark brown. Fore coxae entirely pruinose.

Male terminalia (Fig. 42.1): S6 horseshoe-shaped, length subequal width, with 4 large setae arranged more or less in diagonal pairs. S7+8 weak on right side, left side of S7+8 with cleft indicating boundaries of S7 and S8. Epandrium uniformly pruinose; width subequal to length, width uniform along length. Surstylus straight, simple rod-like, tapering apically. Phallus surpassing posterior margin of cercus a great length. Basal distiphallus long.

Female terminalia: S6 weakly sclerotized, with 3 pairs of setae, anterior pair shortest. S7 dorsally with a trapezoidal desclerotization below sensory setulae. Spermathecae straited, well sclerotized, with distal depression, basal opening as wide as spermathecal width.

Type specimens: Holotype: ♂: **NEW ZEALAND: Campbell Islands:** Campbell Island, Beeman camp, 2–50 m, chicken yard ddr., 6–11.xii.1961, J.L. Gressitt (NZAC).

Paratypes (not examined): Same collection data as holotype $(2 \circlearrowleft, 3 \circlearrowleft, NZAC)$

Other material examined: NEW ZEALAND: Auckland Islands: Auckland Island (N), Ranui Cove, 2 m, MT, 30.xii.1962, J.L. Gressitt (12, NZAC).

Comments: *P. brevicaudata* and the undescribed sp. 1 CNC729345 (Figs. 48.1–3) are characterized by small eyes (also in *P. brevifacies*), all brown legs, densely pruinose fore coxa, large pair of prescutellar acrostichal setae, and extensive desclerotization of the ventromedial



FIGURES 41.1–3: *Pseudopomyza (Pseudopomyza) brevicaudata* female habitus (New Zealand). 41.1, left lateral; 41.2, dorsal; 41.3, head.



FIGURE 42.1. *Pseudopomyza* (*Pseudopomyza*) *brevicaudata* male abdomen (New Zealand). 42.1, terminalia left lateral. Holotype photographed undissected.

margin of the face (surpassing the ventral point of the sub-antennal depression) relative to other species of the *Pseudopomyza s.s.*. The two can be easily distinguished by the number of scutellar setae (*P. brevicaudata* has two pairs; sp. 1 CNC729345 has three pairs). Male genitalia differences could not be assessed because dissections were avoided on the male holotype of *P. brevicaudata*, and males of sp. 1 CNC729345 remain unknown.

Pseudopomyza (Pseudopomyza) brevifacies (Papp) (Figs. 44.1–3, 45.1–6, 46.1–4)

Macalpinella brevifacies Papp, 2005: 191.

Diagnosis

Eye small. Face and carina protruding, facial desclerotization not passing ventral point of sub-antennal depression. Subvibrissa absent. Antenna yellow except first flagellomere distally brown. Medial acrostichal setae well developed. Anepisternum and katepisternum mostly glossy. Scutellum with a cluster of 3 setulae at base of

basal seta. Legs with variegated yellow and brown colour patterns. Fore coxa flattened, mostly pruinose. Male S7+8 symmetrical; left side of S7+8 without cleft indicating boundaries between S7 and S8; postspiracular sclerite absent. Surstylus without lamella.

Description

Length 1.8–2.1mm (males), 1.6–2 (females).

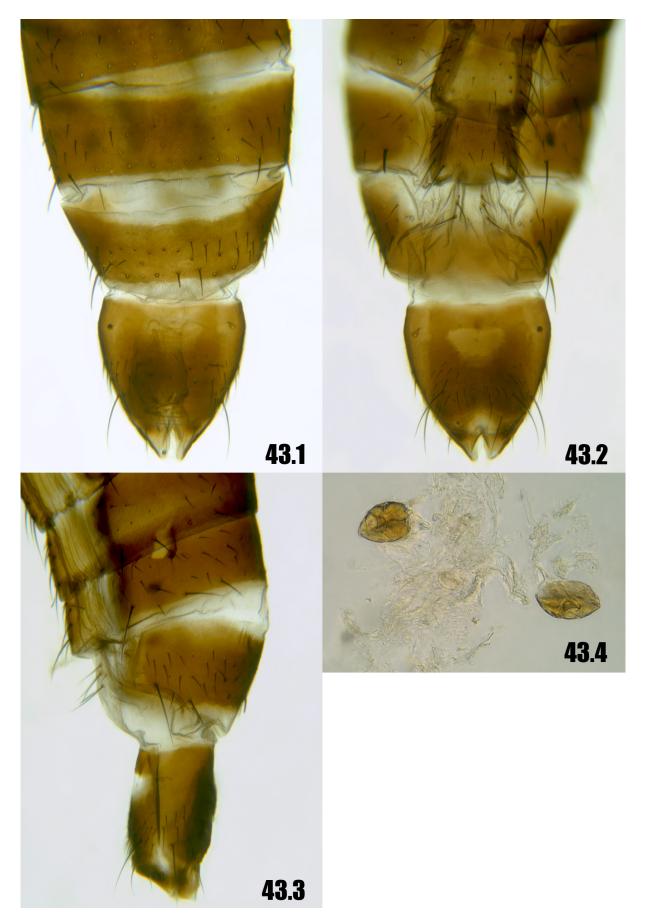
Head: Frons dark brown to black, fronto-orbital plates rarely paler. Length of second fronto-orbital seta $0.6 \times 1^{\text{st}}$. Antenna yellow except first flagellomere distally brown. Face entirely brown, carina often darker; face well sclerotized, desclerotization at anteromedial margin well below ventral point of sub-antennal depression, carina protruding. Gena entirely brown to dark brown, pruinose, genal height $0.4 \times$ eye height. Sub-vibrissa absent or indifferentiable from background setulae.

Thorax: Scutum dark brown to black; uniformly pruinose. Presutural acrostichal setae small but differentiated, half as long as postsutural acrostichal setae. Anterior intra-alar subequal to supra-alar (1+1) setae and 0.5× postalar seta. Intrapostalar seta small, only slightly longer than background setulae. Scutellum with 2 pairs of marginal setae and 3 minute setulae at base of basal seta. Anepisternum glossy; katepisternum mostly glossy except posterodorsal corner.

Legs: All coxae brown; all trochanters tan to yellow. Fore coxae flattened, medial surface pruinose, medioventral corner of anterolateral surface pruinose, dorsally with a small patch of pruinosity, posterolateral surface pruinose ventrally and on posterior margin. Foreleg brown to dark brown. Mid femur brown except extremity, tibia and tarsus yellow. Hind femur brown, tibia and tarsus yellow.

Male terminalia (Figs. 45.1-6): S6 with strongly arcuate hood-like anterior band, posteroventral corners with inwardly curling extensions and membranous wings extending into cavity of hood; posterodorsal corners articulating with S7+8. S7+8 symmetrical and closeringed; left side without cleft indicating boundaries of S7 and S8; postspiracular sclerite absent. Epandrium uniformly pruinose; uniform in width, width subequal length; posteroventral corners extended posteriorly, extension almost as long as body of epandrium. Cercus distally dilated, apically truncated; fused edge of cerci long. Surstylus crab-claw-like, base of distal lobe with weakened connection, allowing some movement. Subepandrial sclerite broad, V-shaped; anterior seta 2.5× posterior seta and displaced laterally, setae well-spaced on posterior third of sclerite.

Phallus proportionally shorter, barely reaching anterior margin of anal opening (when distiphallus is deflexed forward). Phallapodeme relatively straight, phallic guide reduced to a triangular extension from phallapodeme. Ventral bridge of hypandrium somewhat short, phallic plate relatively straight and flat. Pregonites mostly independent of each other, relatively straight, sensory setulae on basal half of sclerite length. Postgonite forked. Basal distiphallus tubular, symmetrical, slightly



FIGURES 43.1–4: *Pseudopomyza (Pseudopomyza) brevicaudata* female abdomen (New Zealand). 43.1, terminalia dorsal; 43.2, terminalia ventral; 43.3, terminalia left lateral; 43.4, spermathecae and associated structures.



FIGURES 44.1–3: Pseudopomyza (Pseudopomyza) brevifacies male habitus (Japan). 44.1, left lateral; 44.2, dorsal; 44.3, head.



FIGURES 45.1–6: *Pseudopomyza (Pseudopomyza) brevifacies* male abdomen (Taiwan). 45.1, terminalia left ventrolateral; 45.2, terminalia ventral; 45.3, epandrium ventrolateral; 45.4, epandrium ventral; 45.5, phallus and associated structures left lateral; 45.6, phallus and associated structures ventral.



FIGURES 46.1–4: *Pseudopomyza* (*Pseudopomyza*) *brevifacies* female abdomen (Taiwan). 46.1, terminalia dorsal; 46.2, terminalia ventral; 46.3, terminalia left lateral; 46.4, spermathecae.

widened distally, distal opening at an acute angle, distal distiphallus with elongated tapering dorsal sclerite and ventral membranous mass, apex curly.

Female terminalia: S6 weakly sclerotized, half the width of S5, with 3–4 pairs of subequal setae. T7 with medial spot of sclerotization at anterior margin; S7 with bracket-like sclerotization pattern. Spermathecae straited and bulbous, well sclerotized, slightly compressed dorsal-ventrally, with deep distal depression.

Type specimens (not examined): Holotype: ♂: TAIWAN: Nantou: Shuili, forest undergrowth, 30.ix.2000, L. Papp (HNHM).

Other material examined: BHUTAN: Sarpang: 13km NW Gelephu, 26°58'5"N 90°33'32"E, 1200 m, MT, 25–27.viii.2017, Hauser & Borkent, NPPC team (1 \circlearrowleft , CNC); TAIWAN: Wushe: 1150 m, flight trap, 16.iii.1983, H. & M. Townes (8 \updownarrow , DEBU); ditto, 23.iii.1983 (12 \circlearrowleft , 9 \updownarrow , DEBU); JAPAN: Ibaraki: Tsuchiura City, (Marsh) pan traps, 26–29.viii.1989, M.J. Sharkey (1 \updownarrow , CNC).

Pseudopomyza (Pseudopomyza) neozelandica (Malloch)

(Figs. 47.1-5)

Protoborborus neozelandicus Malloch, 1933: 262.—Harrison, 1959: 254

Pseudopomyza neozelandica (Malloch)—Mathis, 1989: 470.—McAlpine, 1994: 182.

McAlpine (1994) suspected that *P. neozelandica* was a synonym of *P. antipoda*, which it somewhat resembles in coloration and patterning. *Pseudopomyza neozelandica*, however, has the antenna uniformly brown, the gena mainly yellow without tan to brown triangular marking at the ventral margin, and the hind tibia with a distinct band at distal quarter. *Pseudopomyza neozelandica* is morphologically more similar to *P. aristata* in having a well-developed anterior intra-alar seta, pruinose/pollinose pleuron, and a row of five setulae ventral to the katepisternal seta. However, *P. neozelandica* differs from *P. aristata* in having strong medial acrostichal setae instead of reduced medial acrostichal setae.

Diagnosis

Eye large. Pedicel brown and first flagellomere uniformly brown. Facial desclerotization not passing ventral point of sub-antennal depression. Legs with variegated yellow and brown colour patterns. Medial acrostichal setae well developed. Pleuron pruinose or pollinose; katepisternum with a row of 5 setulae ventral to katepisternal seta; scutellum with only marginal setae.

Type specimens: Holotype (not examined): ♀: **NEW ZEALAND: North Island: Manawatū-Whanganui:** Wanganui, M.N. Watt (NHMUK).

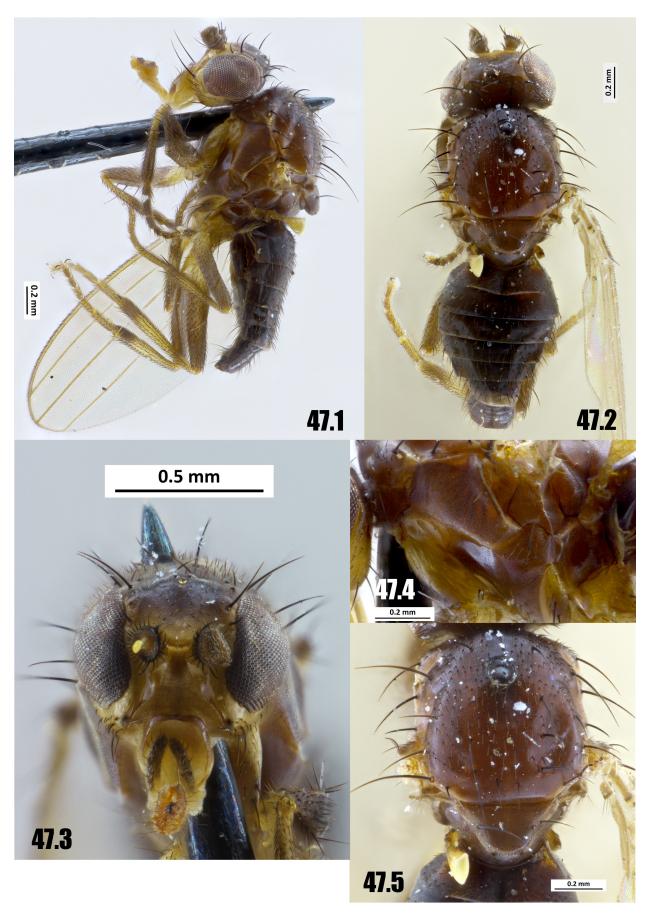
Paratype (examined by photographs only): **NEW ZEALAND: South Island: West Coast:** Otira, 10.ii.1922, A.L. Tonnoir (1° , CMNZ).

Pseudopomyza (s.s.) nigrimana species group

subgenus Rhinopomyzella Hennig (Diptera: Pseudopomyzidae) was described for *P. nigrimana* Hennig and P. albimana Hennig and was previously treated as one of the five subgenera of Pseudopomyza. Rhinopomyzella renders Pseudopomyza s.s. paraphyletic and is now included in the subgenus Pseudopomyza and treated as the P. nigrimana species group. This clade furthermore includes fifteen newly described Neotropical species, P. adunca (South America), P. albimana (Hennig) (Central and South America, Caribbean), P. ampliata (Guatemala), P. angustifrons (Mexico, Guatemala), P. binaevia (Costa Rica), P. brunneicacumen (Guatemala, Costa Rica, Venezuela), P. cordata (Costa Rica, Peru), P. cyathiformis (Costa Rica), P. flavicacumen (Costa Rica, Venezuela, Ecuador), P. gambiformis (Ecuador), P. inflexa (Costa Rica), *P. machaera* (Guatemala), *P. nigrimana* (Hennig) (Central and South America, Caribbean), P. parabinaevia (Venezuela, Peru), *P. proboscis* (Costa Rica, Guatemala), P. prolata (Ecuador), P. simulatrix (Bolivia). The P. nigrimana-group is the sister group to P. atrimana, supported by synapomorphies including the inner lamella of the surstylus and long ventral bridge of the hypandrium. Other character states shared by *P. atrimana* and the P. nigrimana-group include an H-shaped S6 (also found in P. aristata), a symmetrical S7+8 (also found in P. brevifacies and P. medianentis) and the absence of a faint defining break on the left side indicating the boundaries of the fused S7 and S8 (a similar state is found in P. brevifacies).

Diagnosis

The *P. nigrimana* species group ranges from southern Mexico and the Caribbean to northern Argentina at a wide range of elevations (from sea level to 2800m). Species in this group are characterized by medially fused and dorsally arched pregonites (Buck & McAlpine, 2010), an equally arched phallapodeme and a symmetrical distiphallus. In addition to the above synapomorphies, the species group is also distinguishable from other Pseudopomyza by the following characters: Head with three fronto-orbital setae; subvibrissa present but at most 0.3× length of vibrissa or only 2× length of background setulae and positioned on vibrissal angle; facial plates broad and well sclerotized, carina at least sclerotized past ventral point of sub-antennal depression. Pedicel with several moderately long ventral setae. Anterior intra-alar seta present, scutellum with two marginal setae and 3 minute setulae at base of basal seta. S7+8 symmetrical and close-ringed, without cleft on left side indicating



FIGURES 47.1–5: *Pseudopomyza (Pseudopomyza) neozelandica* female habitus (New Zealand). 47.1, left lateral; 47.2, dorsal; 47.3, head; 47.4, thorax left lateral; 47.5, thorax dorsal. Images provided by the Canterbury Museum, photographed by Johnathon Ridden.



FIGURES 48.1–3: *Pseudopomyza* (*Pseudopomyza*) sp.1 CNC729345 female habitus (New Zealand). 48.1, left lateral; 48.2, dorsal; 48.3, head. (Undescribed species known only from a female in the subgenus *Pseudopomyza*, included in Key to species of *Pseudopomyza* Strobl).

boundaries of S7 and S8, postspiracular sclerite absent. Surstylus with inner lamella. Subepandrial sclerite broad, setae not contiguous or crowded at posterolateral corner of sclerite. Ventral bridge of hypandrium long, phallic plate relatively flat and straight.

Description

Body length 1.5–2.5 mm (males), 1.5–2.9 mm (females). Head: With 3 reclinate fronto-orbital setae. Antenna yellow; first flagellomere tan on distal half; arista arising dorsoapically, pubescent, as long as head width. Vibrissa distinct, subvibrissa at most 0.3× vibrissa length, gena with setulae scattered along ventral 2/3, postgena with 2 setae at lower margin. Colour patterns and pruinosity on gena variable (Fig. 50). Genal height 0.2–0.4× eye height. Facial carina pollinose. Face mostly sclerotized, ventromedial desclerotization reaching ventral point of sub-antennal depression. Facial colour patterns highly variable with some sexual dimorphism, usually darker in females (Fig. 49).

Thorax: Postpronotum yellowish-brown posteroventrally, notopleuron ventrally yellowish-brown to various degrees. Presutural and postsutural acrostichal setae aligned in a single median row, except prescutellar acrostichal setae paired. Anterior intra-alar seta present, usually with one presutural and one postsutural supra-alar setae, of various lengths; postalar setae always longer than intra-alar and supra-alar setae. Intrapostalar seta small. Scutellum with 2 pairs of marginal setae and 3 minute setulae at base of basal seta.

Legs: Fore and hind coxae yellow or creamy white, mid coxa dorsally brown, ventrally yellow. All trochanters yellow. Remaining leg colour patterns variable with minimal, if any, sexually dimorphic differences on fore tarsus (Fig. 51). Fore coxa pruinose but pruinosity of posterolateral surface relatively sparse compared to medial and anterolateral surfaces.

Wing: Wing interference patterns consistent within the group and as in Figure 87.

Male terminalia (Figs. 53.1–3, 55.1–3, 58.1–3, 61.1– 3, 66.1–3, 69.1–3, 72.1–3, 75.1–3, 78.1–3, 81.1–3, 84.1– 3, 88.1-3, 91.1-3, 94-3, 97.1-3, 100.1-3): S6 usually with pair of anterolateral arms, arms sometimes with thin connecting sclerite bridging between, sensory setulae often at apices of arms; posterolateral angles of S6 apically articulating with S7+8. S7+8 dorsally pruinose, ring-like and completely symmetrical, left side of S7+8 without cleft indicating boundaries of S7 and S8; postspiracular sclerite absent. Epandrium with pair of outstanding setae in addition to numerous shorter setae. Surstylus well sclerotized, with inner lamella. Cerci apices appear to be merely touching on outer surface but fused on surface facing phallus. Subepandrial sclerite sheet-like, broad, sometimes raised at spots (Fig. 53.3), posterolateral setae not contiguous or crowded at posterior margin of sclerite. Hypandrium shield-like; ventral bridge long, medially connected to fused, elongated, strongly arched pregonites running below phallapodeme. Apex of phallic

plate articulating with base of basal distiphallus/ remnant of basiphallus. Phallapodeme strongly arched; phallic guide usually present. Postgonite shape variable. Basal distiphallus variable but usually tubular; distal distiphallus variable but mainly membranous.

Female terminalia: S6 weakly sclerotized or membranous, usually with 1–2 pairs of setae, rarely bare or with additional setulae. Sclerotization pattern of S7 variable. Spermathecae variable in shape and texture but usually well sclerotized and symmetrical.

Pseudopomyza (Pseudopomyza) adunca Yau and Marshall sp. nov.

(Figs. 49k, 50k, 51q, 52.1-4, 53.1-3)

Diagnosis

Frons almost entirely dark brown, with at most very narrow yellow anterior margin. Face at least partially yellow on sub-antennal depression and most of facial ridge. Gena with a dark brown band no more than half genal height below lower eye margin, continuous with dark brown posterior half of gena, remainder yellow or tan. Fore tarsus bicoloured; mid femur yellow. Anterolateral arms of male S6 apically tapered. Apex of surstylus tapered and curved medially, slightly hooked; inner lamella narrow. Subepandrial sclerite with strong protuberance anterior to setae. Postgonite spatulate. Basal distiphallus short, bent ventrally.

Description

Body length 1.9–2.2 mm (males).

Head: Frons black or dark brown, fronto-orbital plates sometimes paler than frons. Length of first fronto-orbital seta 0.85×2^{nd} , 2^{nd} subequal to 3^{rd} . Male face mostly yellow, each side with dark brown marking on outer face. Gena dark brown band below lower eye margin continuous with dark brown posterior half of gena; glossy on anterior half or more, pruinose on posterior half and through to postgena and lower occiput; genal height 0.3×2^{rd} eye height.

Thorax: Scutum dark brown, uniformly pruinose expect glossy band anterior to and no wider than scutellum. Presutural acrostichal setae small but differentiated, length a third of postsutural setae, prescutellar pair of acrostichal setae absent. Presutural supra-alar seta slightly longer than subequal anterior intra-alar and postsutural supra-alar setae, and 2/3 of postalar seta. Anepisternum and katepisternum glossy.

Legs: Basal third of fore femur yellow, distal two thirds dark brown; fore tibia dark brown; tarsomere 1 dark brown, tarsomere 2 dark brown except creamy white apex, remaining tarsal segments creamy white. Mid leg yellow. Hind femur apically and distodorsally starting at basal third dark brown, distoventrally usually tan, remaining yellow; hind tibia and tarsus yellow.

Male terminalia (Figs. 53.1–3): Anterolateral arms of S6 short, apically tapered; connecting sclerite between

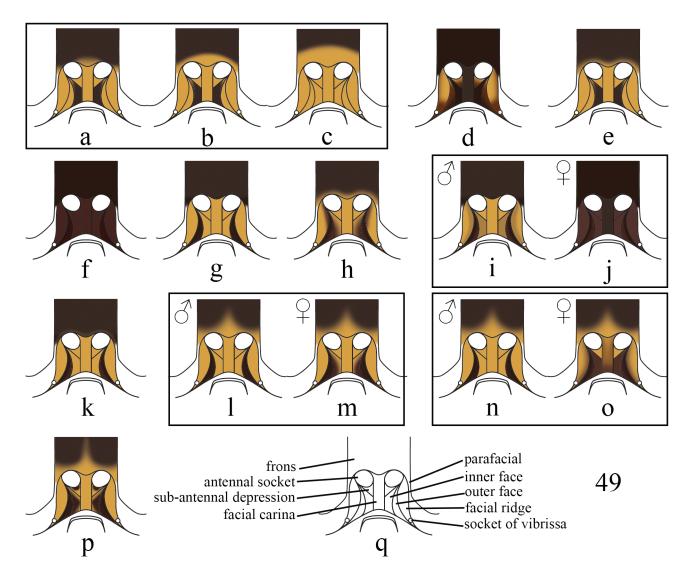


FIGURE 49. Pseudopomyza nigrimana species group, face and frons colour patterns (species arranged in phylogenetic order). 49a–c, *P. nigrimana* (a, typical form (southern Brazil and northern Argentina); b, widespread form (central and most of South America); c, Puerto Rican form); d, *P. proboscis*; e, *P. prolata*; f, *P. albimana, angustifrons, cordata* and simulatrix; g, *P. ampliata* and gambiformis; h, *P. machaera*; i, *P. brunneicacumen* and flavicacumen male; j, *P. brunneicacumen* and flavicacumen female; k, *P. adunca*; l, *P. inflexa* male; m, *P. inflexa* female; n, *P. cyathiformis* male; o, *P. cyathiformis* female; p, *P. binaevia* and parabinaevia; q, morphology of face and frons.

arms absent; mid-section of sternite curved anteriorly. Ventrolateral corners of S7+8 protruding and connected by a ledge. Epandrium entirely glossy; wider at mid-length, width 0.7×100 length. Cercus uniform in width. Surstylus of uniform width, apex medially curved to appear hooked; inner lamella narrow, extending relatively straight from body of surstylus. Subepandrial sclerite rounded, with strong protuberance anterior to setae; anterior seta distinctly longer than posterior seta and placed more laterally.

Phallapodeme laterally compressed towards apex; length beyond phallic plate $0.55\times$ sheathed length; phallic guide width $2.3\times$ height. Postgonite spatulate. Basal distiphallus short, bent ventrally, length $1.6\times$ width; distal distiphallus with forked sclerite within membranous portion, length $1.17\times$ length of basal distiphallus. Female unknown.

Etymology: The name refers to the medially hooked surstylus (Latin 'aduncus': bent inwards, hooked, aquiline).

Type specimens: Holotype: \circlearrowleft : **ECUADOR**: **Pichincha:** Quito, 10km NW, Valley nr. Hostería San Jorge, pans in grass pile, 23.x.1999, SAM, debu00115559 (QCAZ).

Paratypes: **BOLIVIA**: **La Paz**: Zongo, 16°6'32"N 68°4'30"W, roadside, sweep cut foliage, 18.iv.2001, SAM (2\$\frac{1}{2}\$, CBFC, DEBU). **ECUADOR**: **Napo**: above Papallacta, paramo & elfin forest, 4000 m, ii.1983, M. Sharkey & LM (1\$\frac{1}{2}\$, DEBU); SierrAzul Reserve, 14km W Cosanga, 0°40'55"S 77°56' 9"W, tree fall, 2200 m, yellow pans, 10–11.v.2002, SAM & S. Paiero (1\$\frac{1}{2}\$, DEBU). **VENEZUELA**: **Mérida**: Sta. Rosa Trail, along spring, ca 1500 m, FIT, 24–30.iv.1988, SAM (1\$\frac{1}{2}\$, MIZA); **Trujillo**:

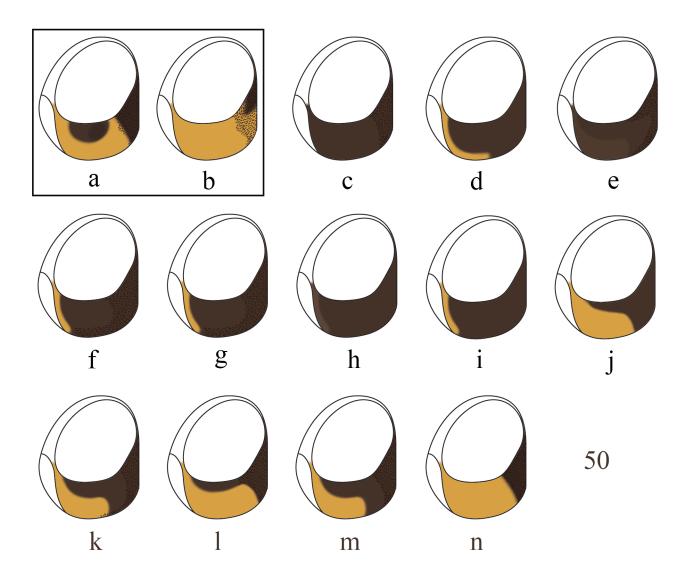


FIGURE 50. Pseudopomyza nigrimana species group, gena colour patterns and pruinosity (species arranged in phylogenetic order) (pruinosity indicated by short brown strokes). 50a-b, *P. nigrimana* (a, widespread form (specimens from continental Central and South America and Caribbean excluding Puerto Rico); b, specimens from main island of Puerto Rico) c, *P. proboscis*; d, *P. prolata*; e, *P. cordata*; f, *P. ampliata*; g, *P. machaera*; h, *P. albimana*, *P. angustifrons* and *simulatrix*; i, *P. brunneicacumen* and *flavicacumen*; j, *P. gambiformis*; k, *P. adunca*; l, *P. inflexa*; m, *P. cyathiformis*; n, *P. binaevia* and *parabinaevia*.

Guaramacal National Park, 14 km NE Boconó, 2000 m, 25.viii.−1.ix.1992, LM (1♂, DEBU).

Comments: The holotype and most of the paratypes of *Pseudopomyza adunca* were collected at relatively high elevations. It seems to be associated with elfin forests or high cloud forest habitats.

Pseudopomyza (Pseudopomyza) albimana (Hennig) (Figs. 49f, 50h, 51g, h, 54.1–4, 55.1–3, 56.1–4)

Rhinopomyzella albimana Hennig, 1969: 598. Pseudopomyza (Rhinopomyzella) albimana (Hennig)—McAlpine, 1994: 183.

Diagnosis

Frons, face and gena brown. Fore tarsus bicoloured; mid

femur yellow. Apex of anterolateral arms of male S6 posteriorly curved. Surstylus long, slender, laterally flared at distal quarter before tapering to apex; inner lamella narrow. Subepandrial sclerite relatively flat. Postgonite spatulate. Basal distiphallus slightly bent ventrally. Female S7 basally with slender X-shaped sclerotization. Spermathecae short, striate on distal half.

Description

Body length 1.7–2.0 mm (males), 1.7–2.4 mm (females).

Head: Frons brown, fronto-orbital plates paler than remainder of frons. Length of first fronto-orbital seta 0.75×2^{nd} , 2^{nd} subequal to 3^{rd} . Face generally brown, outer face of darkest brown. Gena brown, without markings, rarely tan or tannish yellow on anterior margin; glossy, pruinose at the junction of gena, postgena and lower occiput; genal height $0.23 \times$ eye height.

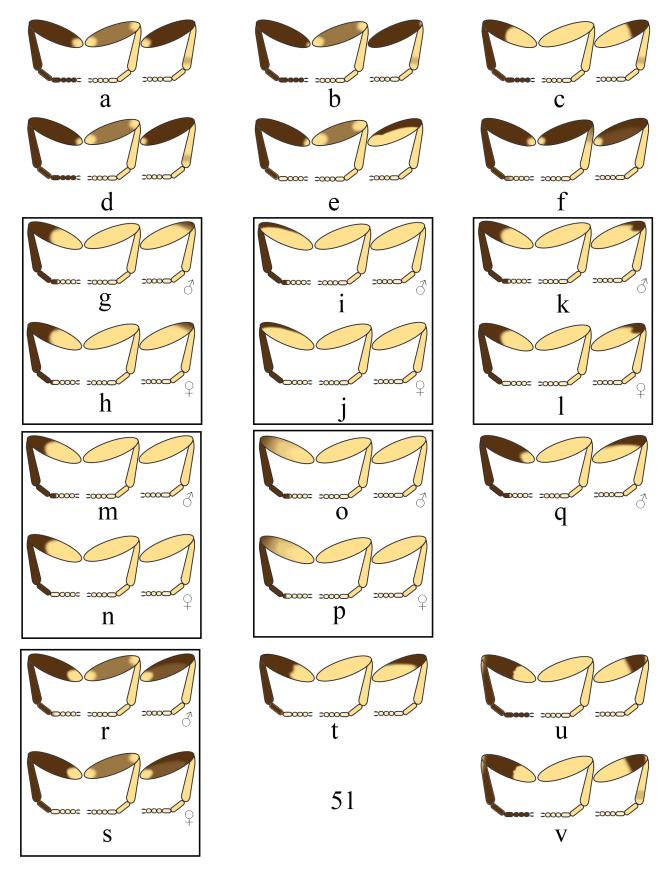
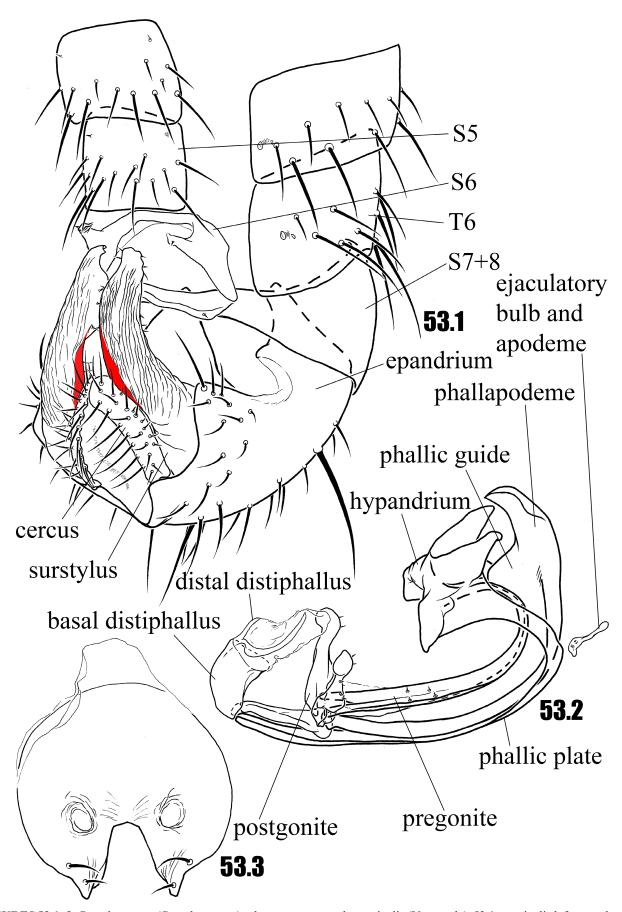


FIGURE 51. Pseudopomyza nigrimana species group, leg colour patterns: foreleg left, mid leg middle, hind leg right (species arranged in phylogenetic order). 51a, P. nigrimana (most of range except typical form from southern Brazil and northern Argentina); b, P. proboscis; c, P. nigrimana typical form (southern Brazil and northern Argentina) and P. prolata; d, P. cordata; e, P. ampliata; f, P. machaera; g-h, P. albimana (g, male; h, female); i-j, P. angustifrons (i, male; j, female); k-l, P. brunneicacumen (k, male; l, female); m-n, P. flavicacumen (m, male; n, female); o-p, P. gambiformis (o, male; p, female); q, P. adunca male; r-s, P. inflexa (r, male; s, female); t, P. cyathiformis; u, P. binaevia; v, P. parabinaevia.



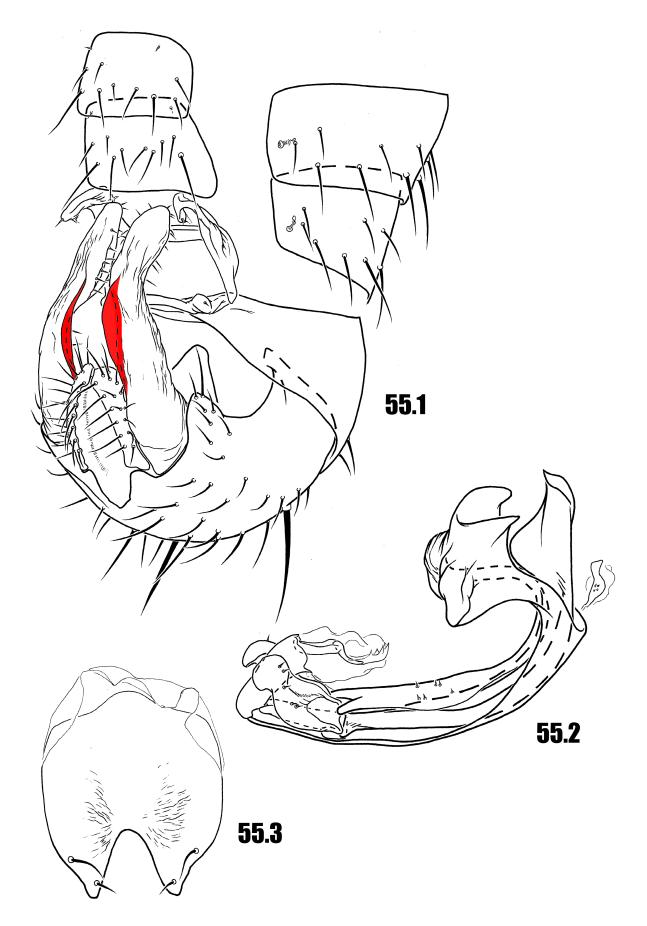
FIGURES 52.1–4: *Pseudopomyza (Pseudopomyza) adunca* **sp. nov.**, male habitus. 52.1, left lateral (Ecuador); 52.2, dorsal (Ecuador); 52.3, head (Ecuador); 52.4, terminalia, ventral (Venezuela).



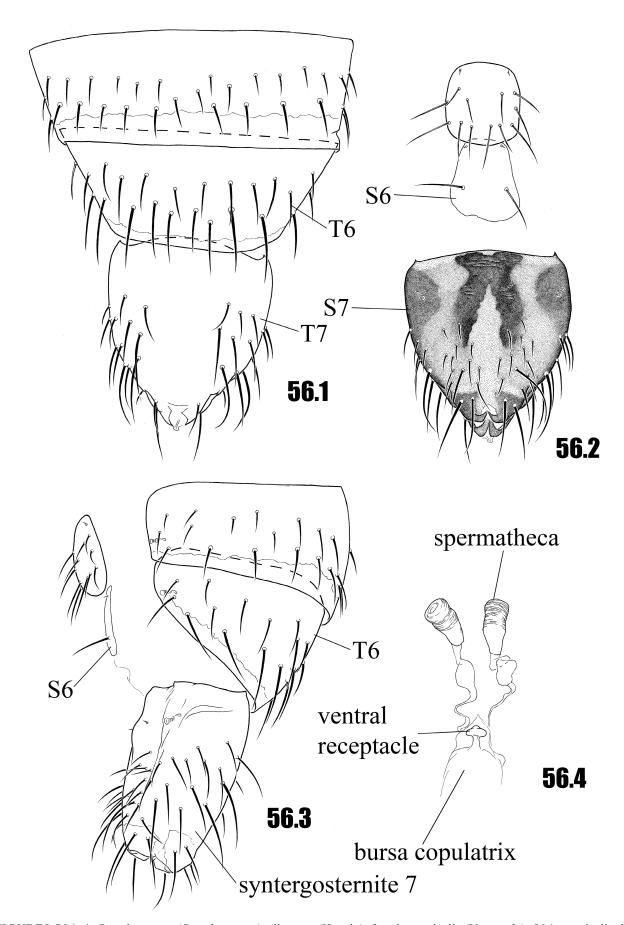
FIGURES 53.1–3: *Pseudopomyza* (*Pseudopomyza*) *adunca* **sp. nov.**, male terminalia (Venezuela). 53.1, terminalia left ventrolateral (inner lamella of surstylus marked red); 53.2, phallus and associated structures left lateral; 53.3, subepandrial sclerite anterior surface. Abbreviations: S5–6, sternites 5–6; S7+8, syntergosternite 7+8; T6, tergite 6.



FIGURES 54.1–4: *Pseudopomyza (Pseudopomyza) albimana* (Hennig), male habitus. 54.1, left lateral (Venezuela); 54.2, dorsal (Dominican Republic); 54.3, head (Dominican Republic); 54.4, terminalia, ventral (Costa Rica).



FIGURES 55.1–3: *Pseudopomyza* (*Pseudopomyza*) *albimana* (Hennig), male terminalia (Venezuela). 55.1, terminalia left ventrolateral (inner lamella of surstylus marked red); 55.2, phallus and associated structures left lateral; 55.3, subepandrial sclerite anterior surface.



FIGURES 56.1–4: *Pseudopomyza* (*Pseudopomyza*) *albimana* (Hennig), female terminalia (Venezuela). 56.1, terminalia dorsal; 56.2, terminalia ventral; 56.3, terminalia left lateral; 56.4, spermathecae and associated structures ventral. Abbreviations: S6, sternite 6, S7, sternal portion of oviscape.

Thorax: Scutum reddish brown, uniformly pruinose except for glossy band anterior to and no wider than scutellum. Presutural acrostichal setae small but differentiated, ½ as long as postsutural acrostichals; prescutellar pair of acrostichal setae absent. Anterior intra-alar and supra-alar (1+1) setae subequal, ½ as long as postalar seta. Anepisternum and katepisternum glossy.

Legs: Basal half or more of fore femur yellow, distal half or more dark brown; fore tibia dark brown; tarsomere 1 dark brown, tarsomere 2 brown except creamy white apex, remaining tarsal segments creamy white. Mid leg yellow. Hind femur mainly yellow, but distal 1/3 sometimes tan; hind tibia and tarsus yellow.

Male terminalia (Figs. 55.1–3): Apex of anterolateral arms of S6 posteriorly curved; mid-section of sternite anteriorly curved. Ventrolateral corners of S7+8 with nublike protuberance connected by a ledge. Epandrium almost entirely glossy except pruinose at extreme posterolateral corners adjacent to lateral margin; widest at mid-length, width $0.7 \times$ length. Cerci uniform in width. Surstylus long, slender, laterally flared at distal quarter before tapering to apex; inner lamella narrow, outwardly bent from surface of surstylus. Subepandrial sclerite trapezoidal with anterior margin shallowly arcuate, surface relatively flat; anterior seta distinctly longer than posterior seta and placed more laterally.

Phallapodeme laterally compressed towards apex; length beyond phallic plate $0.5\times$ sheathed length; phallic guide width $2.8\times$ height. Postgonite spatulate. Basal distiphallus slightly bent ventrally at distal 1/3, length $2.3\times$ width; distal distiphallus membranous, except thin basal sclerite, length subequal to basal distiphallus.

Female terminalia: S6 weakly sclerotized, with a pair of setae. S7 basally with slender X-shaped sclerotization. Spermathecae cylindrical, striate on distal half.

Type specimens: Holotype (not examined): ♂: "27°11'S., 52°23'W., Nova Teutônia, **Brazil**, 300–500 m, VIII. 1961, F. Plaumann. Type number 9952" (CNC).

Paratypes: 3: "Same collection data as holotype. Type number 9952" (CNC) (1 not examined).

Other material examined: BRAZIL: Rio de Janeiro: Teresópolis, trail to Pedra do Sino, 1500–2000 m, 14.iii.1990, SAM (23, MZUSP); Santa Catarina: Nova Teutônia, 27°11'S 52°23'W, 300-500 m, viii.1964, F. Plaumann (2♂, 1♀, CNC); São Paulo: São Carlos, Canchin Farm, MT, 4–6.i.1996, M.J. Sharkey (3 $\stackrel{?}{\circ}$), MZUSP). BOLIVIA: La Paz: near Mapiri Arroyo Tuhiri, 15.2805, 68.25°W, 500 m, MT (upper), 9-12.iv.2004, B. Brown (16, CSCA). COSTA RICA: Cartago: Dulce Nombre, Vivero Linda Vista, 1400 m, MT, vi-vii.1993, P. Hanson (1♂, DEBU); Hwy 2, 67 km S San José, roadside, 6.viii.1995, SAM (1&, DEBU); **Puntarenas**: Coto Brus. Zona Protectora, Las Tablas. Est. Biol. Las Alturas, 1500-1600 m, MT, 13–14.x.2012 (1♀, MNCR); San José: Behind Hotel Bougainvillea, compost pile, 6.viii.1995, SAM (3\langle, 1\top, DEBU); Moravia, Zurquí de Moravia, north pasture, 1600 m, yellow pan trap, 24.ii.2013 (12, MNCR). DOMINICAN REPUBLIC: Pedernales: Cabo Rojo, Alcoa Road km26, pans, 17-20.i.1989, SAM & J. Swann (23, DEBU); Puerto Plata, La Cumbre, 400

m, 21.iii.1978, LM (3♂, 2♀, CNC). **ECUADOR**: **Napo**: Río Palenque, Ex. Heliconia, 27.ii.1979, SAM (13), DEBU); Pichincha: Maquipucuna Biological Reserve main trail, ca. 1300 m, 27.x.1999, SAM (12, DEBU); Nanegalito, 7 km SE, trout farm 'San José', riverine forest, tree fall, 1500 m, sweep, 27-30.x.1999, SAM (1♀, DEBU). **GRENADA**: **Saint Andrews**: Grand Etang Mount Qua Qua, 3.i.1995, SAM (2♂, DEBU); ditto, sweep (1\int, DEBU); **Saint John**: Concord Falls, Nutmeg plantation, 4.i.1995, SAM (1 \circlearrowleft , DEBU). **HONDURAS**: Francisco Morazán: El Zamorano, black light trap, xi–xii.1970, G.F. Freytag (1♀, DEBU). **PARAGUAY**: Itapúa: Karonay, 17 km W San Rafael Res., 26°45'53"S 55°50'37"W, 90-110 m, FIT, 18-21.xi.2000, Z.H. Falin (13, DEBU). VENEZUELA: Aragua: Maracay, Pozo del Diablo, MT, 11.vi.1996, M.J. Sharkey (13♂, 8♀, DEBU); Maracay, Pozo del Diablo, FIT, 11.vi.1996, M.J. Sharkey (18, DEBU); **Trujillo:** Boconó-Guaramacal Rd, wet litter, 2130 m, sweep, 3.iii.1995, SAM (1♀, DEBU); Zulia: El Tucuco, Sierra de Perija, 1ºrainforest, 200 m, 20–23.iv.1981, H. Townes & LM (1♂, DEBU).

Comments: Pseudopomyza albimana, like P. proboscis, has relatively short setae on the scutum compared to other described species (10-20% shorter). Most other external characters of P. albimana are extremely similar to P. brunneicacumen and P. flavicacumen, but these species are easily differentiated by facial colour. The male genitalic structures are also very similar to P. brunneicacumen and P. flavicacumen but the dimensions of the basal distiphallus differentiate the three species: P. albimana is never as "stubby" as P. brunneicacumen (Fig. 66.2) and the ventral edge of the basal distiphallus is twice as long. The width of the basal distiphallus of *P. albimana* continuously increases distally, but never thickens and then constricts at distal 1/3 as in P. flavicacumen (Fig. 75.2). Also, P. albimana surstyli are long, slender and laterally flared at distal quarter before tapering to the apex unlike the truncate, paddle-shaped surstyli of *P. brunneicacumen* and P. flavicacumen.

Pseudopomyza (Pseudopomyza) ampliata Yau and Marshall sp. nov.

(Figs. 49g, 50f, 51e, 57.1–4, 58.1–3)

Diagnosis

Frons black or dark brown. Face mostly yellow, with brown marking on outer face. Gena generally dark brown, except anterior margin yellow to tan. Fore tarsus bicoloured; mid femur brown except base and apex. Anterolateral arms of male S6 long, twisted medially, apical margin parallel to posterior margin of S5. Surstylus paddle-shaped. Subepandrial sclerite relatively flat. Postgonite spatulate. Basal distiphallus with wide distal opening.

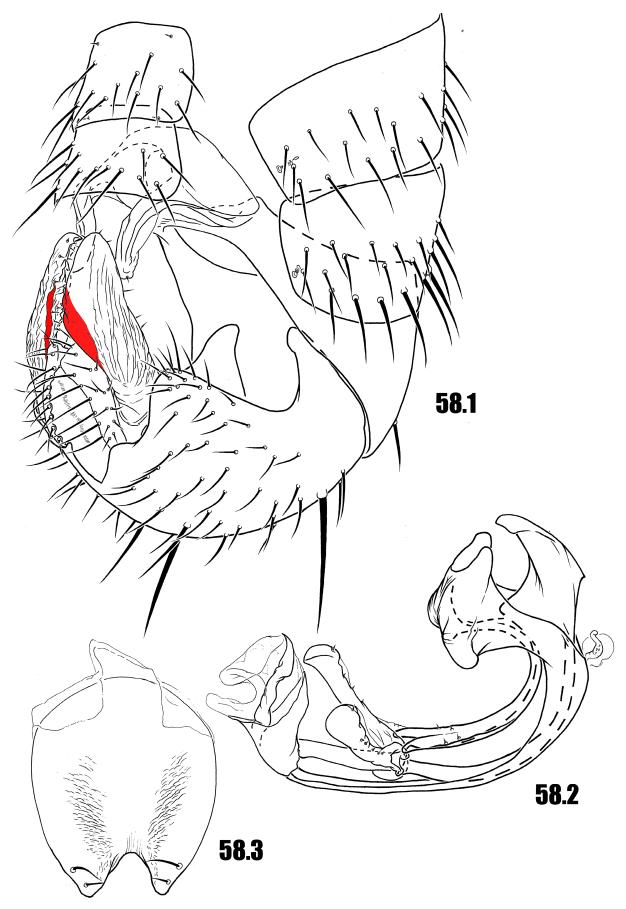
Description

Body length 1.9 mm (male).

Head: Frons black or dark brown, fronto-orbital plates



FIGURES 57.1–4: *Pseudopomyza (Pseudopomyza) ampliata* **sp. nov.**, male habitus (Guatemala). 57.1, left lateral; 57.2, dorsal; 57.3, head; 57.4, terminalia, ventral.



FIGURES 58.1–3: *Pseudopomyza* (*Pseudopomyza*) *ampliata* **sp. nov.**, male terminalia (Guatemala). 58.1, terminalia left ventrolateral (inner lamella of surstylus marked red); 58.2, phallus and associated structures left lateral; 58.3, subepandrial sclerite anterior surface.

and ocellar triangle slightly paler. Head macrochaetae damaged, chaetotaxy not observed. Face mostly yellow, each side with brown marking on outer face. Gena generally dark brown, except anterior margin yellow to tan; anterodorsally glossy, pruinose elsewhere; genal height $0.3 \times$ eye height.

Thorax: Scutum dark brown, pruinose only anterior to anterior dorsocentral seta and on posterolateral edge, area lateral to supra-alar setae glossy and corrugated, remaining scutum smooth and glossy. Macrochaetae damaged, chaetotaxy not observed. Anepisternum and katepisternum glossy.

Legs: Fore femur dark brown except base yellow; fore tibia dark brown; tarsomere 1 dark brown, remaining tarsal segments white or creamy white. Basal and apical ¼ of mid femur yellow, mid-section brown; mid tibia and tarsus yellow. Hind femur apically and distodorsally dark brown, remaining yellow; hind tibia and tarsus yellow.

Male terminalia (Figs. 58.1–3): Anterolateral arms of S6 long, uniform width, twisted medially, apical margin parallel to posterior margin of S5; mid-section of sternite anteriorly curved. Epandrium mostly glossy except pruinose at posterolateral surfaces; width 0.75×10^{-5} length, widest at mid-length. Cercus uniform in width. Surstylus paddle-shaped; inner lamella outwardly bent from surface of surstylus. Subepandrial sclerite rounded, surface relatively flat; anterior seta distinctly longer than posterior seta and placed more laterally.

Phallapodeme laterally compressed towards apex; length beyond phallic plate 0.4× sheathed length; phallic guide width 2.6× height. Postgonite spatulate. Basal distiphallus with wide distal opening, length 0.95× width; distal distiphallus with long, well-sclerotized sclerite at base of membranous portion, length 1.1× length of basal distiphallus.

Etymology: The name refers to the widening basal distiphallus (Latin 'ampliare': to enlarge, expand, widen).

Type Specimen: Holotype: ♂: **GUATEMALA**: **El Progreso:** Cerro Pinalón, 15°5'1"N 89°56'42"W, 2575 m, treefall gap edge in cloud forest, MT, 29.iv–5.v.2009, debu00347819 (UVGC).

Pseudopomyza (Pseudopomyza) angustifrons Yau and Marshall sp. nov.

(Figs. 49f, 50h, 51i, j, 59.1-4, 60.1-2, 61.1-3, 62.1-4)

Diagnosis

Frons dark brown. Face brown to yellowish-brown. Gena generally brown, except anterior margin yellow to tan. Fore tarsus bicoloured; mid femur yellow. Anterolateral arms of male S6 distally rounded and slightly bulbous on posterior edge. Surstylus paddle-shaped, inner lamella large. Subepandrial sclerite relatively flat. Postgonite sock-shaped. Basal distiphallus short. Female S7 with medial protuberance. Spermathecae smooth with no striation, base not constricted.

Description (typical specimens)

Body length 1.9-2.6 mm (males), 2.7 mm (female).

Head: Frons dark brown, fronto-orbital plates and ocellar triangle rarely paler. Length of first fronto-orbital seta $0.5 \times 2^{\rm nd}$, $3^{\rm rd} 0.75 \times 2^{\rm nd}$. Face generally brown to yellowish-brown, frontogenal suture and outer face of darkest brown. Gena generally brown, except anterior margin yellow to tan; gena and postgena glossy, occiput pruinose; genal height $0.2 \times$ eye height.

Thorax: Scutum dark reddish brown, pruinose medial to supra-alar row, pruinose only anterior to anterior dorsocentral seta and on posterolateral edge, area ventral to supra-alar setae glossy and corrugated, remaining scutum glossy with some micro-ridging. Acrostichal setulae of uniform size. Anterior intra-alar seta always present, half as long as postalar seta; presutural supra-alar seta absent; postsutural supra-alar seta present or absent. Intrapostalar seta as small as background setulae. Anepisternum and katepisternum glossy.

Legs: Fore femur apically and distodorsally dark brown, remainder yellow; fore tibia dark brown; tarsomere 1 dark brown, tarsomere 2 dark brown except creamy white apex, remaining tarsal segments creamy white. Mid and hind legs yellow.

Male terminalia (Figs. 61.1–3): Anterolateral arms of S6 distally rounded and slightly bulbous on posterior edge; mid-section of sternite anteriorly curved. Epandrium mostly glossy except pruinose at posterolateral corners adjacent to lateral margin; uniform width, width 0.75×10^{-5} length. Cercus uniform in width. Surstylus paddleshaped; inner lamella large, outwardly bent from surface of surstylus. Subepandrial sclerite trapezoidal, surface relatively flat; anterior seta distinctly longer than posterior seta and placed more laterally.

Phallapodeme laterally compressed towards apex; length beyond phallic plate 0.7× sheathed length; phallic guide width 6× height. Postgonite sock-shaped. Basal distiphallus short, length 1.3× width; distal distiphallus with long, well-sclerotized sclerite at base of widening membranous complex, length 1.6× length of basal distiphallus.

Female terminalia: S6 weakly sclerotized, with one pair of setae. S7 medial protuberance sloping posterolaterally. Spermathecae smooth with no striation (Figure drawn when spermathecae collapsed; striation represents an artefact); base not constricted.

Etymology: The name refers to the narrow face and frons (Latin 'angustus': narrow, tight, slender, thin; Latin 'frons': brow, forehead, fore part of anything).

Type specimens: Holotype: ♂: **GUATEMALA**: **Zacapa:** 7km N San Lorenzo, 2000 m, dung, 10–17.vi.1993, B. Gill (UVGC).

Paratypes: **GUATEMALA**: **Quetzaltenango**: 8km SE Zunil, 2630 m, FIT #4, 17–19.vi.1993, J. Ashe & R. Brooks (1 \circlearrowleft , DEBU); 8km SE Zunil, 2650 m, FIT #6, 17–19.vi.1993, J. Ashe & R. Brooks (1 \circlearrowleft , 1 \updownarrow , DEBU), Same collection data as holotype (1 \updownarrow , DEBU). **MEXICO**: **Chiapas:** Cerro Huitepec (Pico), ca. 5km W San Cristóbal, 2750 m, cloud forest litter, 18.ix.1991, R.S. Anderson (1 \updownarrow , UNAM).



FIGURES 59.1–4: *Pseudopomyza (Pseudopomyza) angustifrons* **sp. nov.** (typical form), male habitus (Guatemala). 59.1, left lateral; 59.2, dorsal; 59.3, head; 59.4, terminalia, ventral.



FIGURES 60.1–2: *Pseudopomyza (Pseudopomyza) angustifrons* **sp. nov.** (atypical form), male habitus (Guatemala). 60.1, left lateral; 60.2, dorsal.

Pseudopomyza (Pseudopomyza) binaevia Yau and Marshall sp. nov.

(Figs. 49p, 50n, 51u, 63.1–3, 64.1–4)

Diagnosis

Frons yellow at anterior margin and with medial yellow stripe. Face mostly yellow, with brown marking on outer face and most of inner face, dorsal half of sub-antennal depression with dark brown marking. Anterior ½ to 3/4 of gena yellow, remainder dark brown. Fore tarsus brown; mid femur yellow. S7 with a pair of pouch-like protuberances. Spermathecae elongated, striate along entire length but weakly so basally.

Description (females only)

Body length 2.9 mm.

Head: Frons dark brown to black, yellow at anterior margin and with medial yellow stripe down entire length of frontal vitta. Fronto-orbital plates paler than frons. Length of first fronto-orbital seta 0.87×2^{nd} , 2^{nd} subequal to 3^{rd} . Face mostly yellow, with brown marking on outer face and most of inner face, dorsal half of sub-antennal

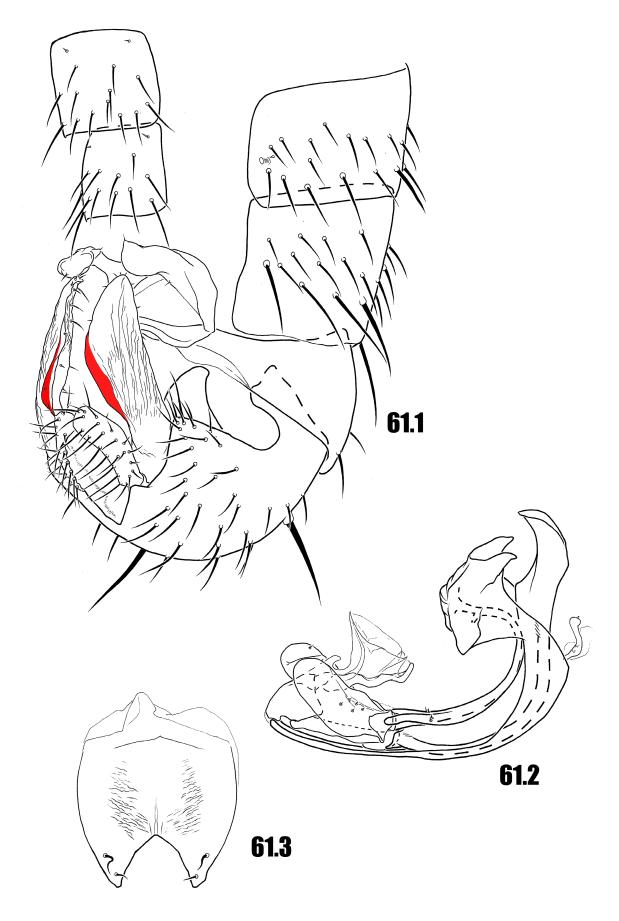
depression with dark brown marking. Anterior ½ to 3/4 of gena yellow, remainder dark brown; glossy on anterior 1/2 to 3/4, remaining pruinose and through to occiput and postgena; genal height 0.3× eye height.

Thorax: Scutum dark brown, uniformly pruinose except for glossy band posterior to prescutellar acrostichal setae, band no wider than scutellum. Presutural acrostichal setae small and hardly differentiated from surrounding scutal setulae, only 1/3 as long as postsutural and prescutellar acrostichal setae. Anterior intra-alar and supra-alar (1+1) setae subequal, 2/3 as long as postalar seta. Anepisternum and katepisternum glossy.

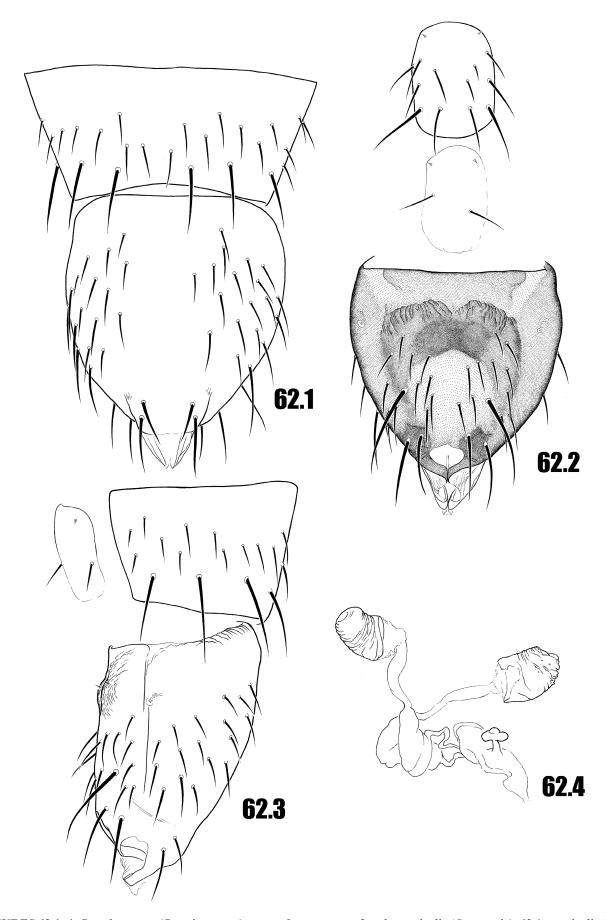
Legs: Fore femur yellow on basal half or less, distal half dark brown; base of fore tibia yellow, remainder of tibia and tarsus brown. Mid leg yellow. Hind femur with basal half or more yellow, distal half dark brown; tibia and tarsus yellow.

Female terminalia: S6 membranous, with two pairs of setae, anterior pair weak. S7 with a pair of pouch-like protuberances. Spermathecae elongated, striate along entire length but weakly so basally.

Etymology: The name *binaevia* refers to the two pairs of dark markings on the face (Latin '*bi*-': double, two; Latin '*naevius*': with a mole, birthmark).



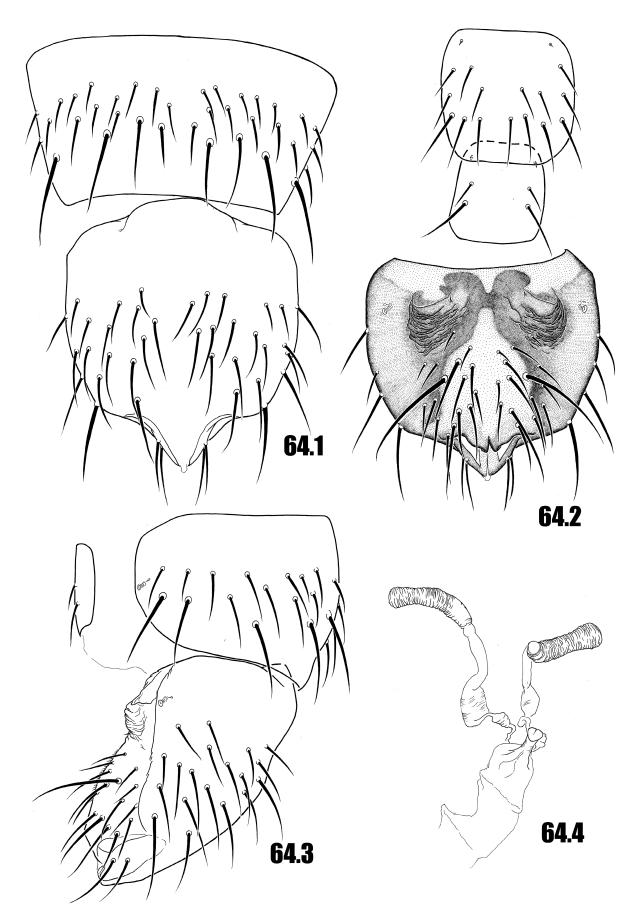
FIGURES 61.1–3: *Pseudopomyza (Pseudopomyza) angustifrons* **sp. nov.**, male terminalia (Guatemala). 61.1, terminalia left ventrolateral (inner lamella of surstylus marked red); 61.2, phallus and associated structures left lateral; 61.3, subepandrial sclerite anterior surface.



FIGURES 62.1–4: *Pseudopomyza (Pseudopomyza) angustifrons* **sp. nov.**, female terminalia (Guatemala). 62.1, terminalia dorsal; 62.2, terminalia ventral; 62.3, terminalia left lateral; 62.4, spermathecae and associated structures ventral.



FIGURES 63.1–3: *Pseudopomyza (Pseudopomyza) binaevia* **sp. nov.**, female habitus (Costa Rica). 63.1, left lateral; 63.2, dorsal; 63.3, head.



FIGURES 64.1–4: *Pseudopomyza (Pseudopomyza) binaevia* **sp. nov.**, female terminalia (Costa Rica). 64.1, terminalia dorsal; 64.2, terminalia ventral; 64.3, terminalia left lateral; 64.4, spermathecae and associated structures ventral.

Type specimens: Holotype: ♀: **COSTA RICA**: **Cartago**: Tapantí National Park, treefall, 1550 m, pan trap, 7–12.x.1999, SAM & M. Buck, debu00104431 (MNCR).

Paratypes: Same collection data as holotype (2♀, DEBU); Paraíso, Tapantí National Park, 1600 m, MT, 30.iii.—7.iv.2013 (1♀, MNCR); **Puntarenas**: Monteverde Reserve, cloud forest, 1500 m, ii.1980, W. Mason (1♀, CNC); **San José**: Moravia, Zurquí de Moravia, tower path, 1600 m, MT, 12–19.vii.2013 (1♀, MNCR).

Comments: This species is very similar to *P. parabinaevia*, which is found in South America (Venezuela, Peru), with regard to colour markings of the face, gena and legs, but the thoracic pruinosity differentiates it clearly from *P. parabinaevia*. The female S7 of *P. binaevia* also has a stronger pair of pouch-like protuberances when compared to *P. parabinaevia*. Male genitalic differences could not be assessed because males are unknown for *P. binaevia*.

Pseudopomyza (Pseudopomyza) brunneicacumen Yau and Marshall sp. nov.

(Figs. 49i, j, 50i, 51k, l, 65.1–4, 66.1–3, 67.1–4)

Diagnosis

Frons black or dark brown. Male face mostly yellow, with dark brown marking on outer face; female face brown. Gena dark brown except anterior margin narrowly yellow. Fore tarsus bicoloured; mid femur yellow. Apex of anterolateral arms of male S6 posteriorly curved. Surstylus paddle-shaped, inner lamella narrow. Subepandrial sclerite relatively flat. Postgonite spatulate. Basal distiphallus short, apex obliquely truncate in lateral view. Female S7 with wide set X-shaped sclerotization. Spermathecae cylindrical, striate on distal half.

Description

Body length 1.5–1.8 mm (males), 1.8–2.2 mm (females). Head: Frons black or dark brown, fronto-orbital plates rarely paler than frons. Length of first fronto-orbital seta 0.8× 2nd, 2nd subequal to 3rd. Male face mostly yellow, each side with dark brown marking on outer face, inner face and dorsal-inner margin of facial ridge sometimes tan; female face generally brown, outer face and sometimes facial carina of darkest brown. Gena dark brown except anterior margin narrowly yellow; glossy, pruinose at junction of gena, postgena and lower occiput; genal height 0.3× eye height.

Thorax: Scutum dark brown, uniformly pruinose expect for glossy band anterior to and no wider than scutellum. Presutural acrostichal setae not differentiated from remainder of scutal setulae; postsutural acrostichal setae subequal; prescutellar pair of acrostichal setae absent. Presutural supra-alar seta slightly longer than subequal anterior intra-alar and postsutural supra-alar setae, and 2/3 as long as postalar seta. Anepisternum and katepisternum glossy.

Legs: Basal half of fore femur yellow, distal half dark brown; fore tibia dark brown; tarsomere 1 dark brown, tarsomere 2 dark brown except creamy white apex, remaining tarsal segments creamy white. Mid leg yellow. Hind leg yellow, except for brown distal quarter of hind femur.

Male terminalia (Figs. 66.1–3): apex of anterolateral arms of S6 posteriorly curved; mid-section of sternite anteriorly curved. Ventrolateral corners of S7+8 nub-like. Epandrium mostly glossy except pruinose at posterolateral corners adjacent to lateral margin; slightly longer than wide, widest at mid-length. Cercus slightly wider at midlength. Surstylus paddle-shaped, of uniform width; inner lamella narrow, outwardly bent from surface of surstylus. Subepandrial sclerite trapezoidal, surface relatively flat; anterior seta distinctly longer than posterior seta and placed more laterally.

Phallapodeme laterally compressed towards apex; length beyond phallic plate $0.3\times$ sheathed length; phallic guide width $2.5\times$ height. Postgonite spatulate. Basal distiphallus short, apex obliquely truncate in lateral view, length $1.8\times$ width; distal distiphallus membranous, except slight basal sclerotization, length subequal to basal distiphallus.

Female terminalia: S6 weakly sclerotized, with a pair of setae. S7 with wide set X-shaped sclerotization. Spermathecae cylindrical, striate on distal half.

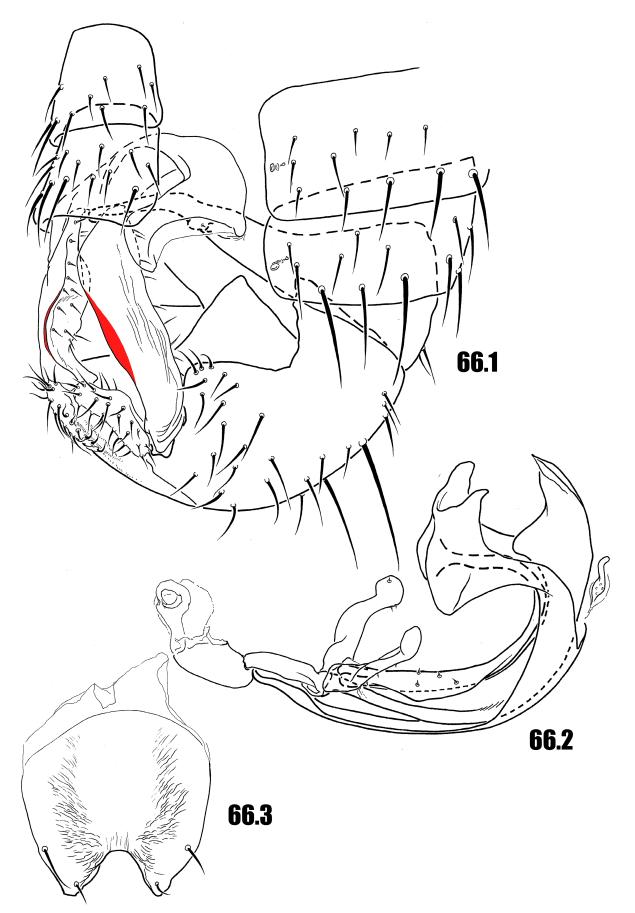
Etymology: This name refers to the brown distal quarter of the hind femur (Latin 'brunneus': brown; Latin 'cacumen': extreme point, end).

Type specimens: Holotype: ♂: **COSTA RICA**: **Puntarenas**: Monteverde Biological Reserve, tree fall and trail, 1500 m, sweep, 14.vi.2000, M. Buck, debu00126777 (MNCR).

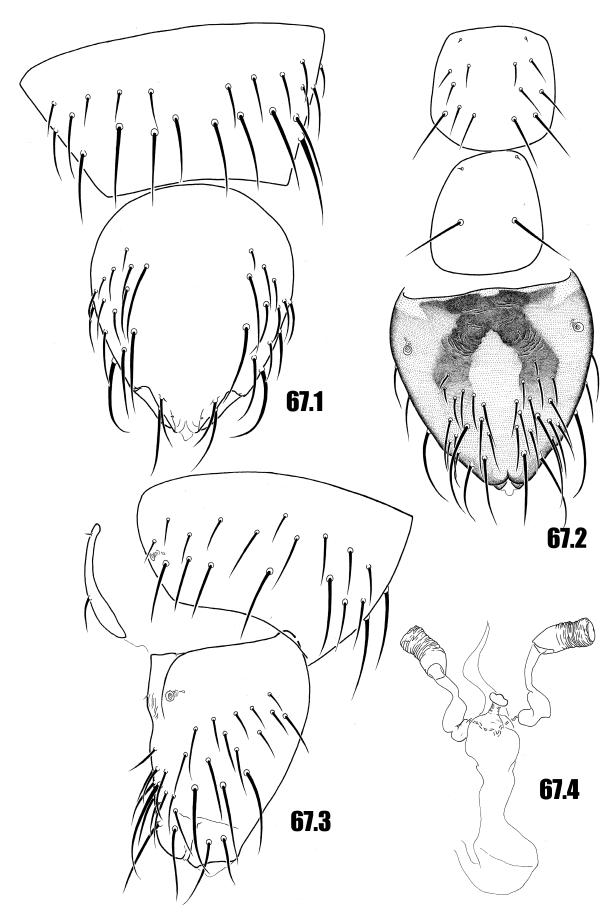
Paratypes: BOLIVIA: La Paz: Cumbre Alto Beni, vicinity of Caranavi, 15°40'19"S 67°29'35"W, 1685 m, MT, 15–21.iv.2004, S.D. Gaimari & M. Hauser (50, 59, 59)CSCA). Cartago: Paraíso, Tapantí National Park, 1600 m, MT, 21–29.ix.2013 (2♀, MNCR); ditto, 10–17.ii.2013 (1♀, MNCR); Tapantí National Park, tree fall, 1550 m, pan trap, 7–12.x.1999, SAM & M. Buck (20, 32, DEBU); Tapantí National Park, 4.x.1999, SAM & M. Buck (1♀, DEBU); **Puntarenas**: Coto Brus. Zona Protectora Las Tablas. Est. Biol. Las Alturas, 1500-1600 m, MT, 5–13.viii, 2013 (1♀, MNCR); Same collection data as holotype (3\infty, DEBU); Monteverde Biological Reserve, tree fall, 1500 m, sweep and pan trap, 14.vi.2000, M. Buck (3♂, 1♀, DEBU); Monteverde Reserve, 1500 m,15– 20.viii.1986, LM (1♂, 5♀, DEBU); ditto, 15–20.vii.1986 (1♀, DEBU); Monteverde Biological Reserve, 1500 m, 15–20.viii.1986, LM (3♀, DEBU); San José: Moravia, Zurquí de Moravia, 1600 m, MT, 28.ii.–8.iii.2013 (1♀, MNCR); ditto, 12–19.vii.2013 (2 \circlearrowleft , 2 \updownarrow , MNCR); ditto, 2–9.viii.2013 (2 $^{\circ}$, 1 $^{\circ}$, MNCR); ditto, 9–16.viii.2013 (1♀, MNCR); ditto, 16–23.viii.2013 (1♂, MNCR); ditto, 13–20.ix.2013 (16, MNCR); Creek 2, 17–23.xi.2012 $(1 \, \mathcal{Q}, \, \text{MNCR})$; ditto, Tower path, 30.iii.-6.iv.2013 $(1 \, \mathcal{Q}, \, \text{MNCR})$ MNCR). GUATEMALA: Baja Verapaz: Biotopo Quetzal, 15°12'46"N 90°12'56"W, cloud forest, 1720 m, MT, 7–10.v.2009 (1 \circlearrowleft , UVGC). **VENEZUELA**: **Aragua:**



FIGURES 65.1–4: *Pseudopomyza (Pseudopomyza) brunneicacumen* **sp. nov.**, male habitus (Costa Rica). 65.1, left lateral; 65.2, dorsal; 65.3, head; 65.4, terminalia, ventral.



FIGURES 66.1–3: *Pseudopomyza (Pseudopomyza) brunneicacumen* **sp. nov.**, male terminalia (Costa Rica). 66.1, terminalia left ventrolateral (inner lamella of surstylus marked red); 66.2, phallus and associated structures left lateral; 66.3, subepandrial sclerite anterior surface.



FIGURES 67.1–4: *Pseudopomyza (Pseudopomyza) brunneicacumen* **sp. nov.**, female terminalia (Costa Rica). 67.1, terminalia dorsal; 67.2, terminalia ventral; 67.3, terminalia left lateral; 67.4, spermathecae and associated structures ventral.

Parque Nac. Henri Pittier Hwy. Maracay-Choroní, km19, creek, 1330 m, s.s., 15.iv.1994, LM (13, MIZA)

Comments: *Pseudopomyza brunneicacumen* can be easily confused with *P. flavicacumen*. These species differ externally only in colour of the hind femur and pruinosity of the scutum. The basal distiphallus of *P. brunneicacumen* is distinctly shorter than that of *P. flavicacumen* (Fig 75.2). The dimensions of the phallic guide and the curvature of the "spoon handle" of the postgonite also differ between the two species.

Pseudopomyza (Pseudopomyza) cordata Yau and Marshall sp. nov.

(Figs. 49f, 50e, 51d, 68.1–4, 69.1–3, 70.1–4)

Diagnosis

Frons dark brown. Face and gena brown. Fore tarsus brown; mid femur yellowish-brown except base and apex. Anterolateral arms of male S6 short, flat, apically tapering. Surstylus broad, paddle-shaped; inner lamella broad spindle-shaped with convex inner margin. Subepandrial sclerite relatively flat. Postgonite heart-shaped. Basal distiphallus flared distally. Female S7 with broad medial protuberance on basal third; apex of oviscape with small pair of hook-like processes. Spermathecae elongated, with striation along entire length except apex.

Description

Body length 1.7 mm (males), 1.7–1.8 mm (females).

Head: Frons dark brown, fronto-orbital plates and ocellar triangle paler. Length of first fronto-orbital seta 0.4×2^{nd} , $3^{rd} 0.8 \times 2^{nd}$. Face generally brown, outer face of darkest brown. Gena generally brown, without markings, sometimes anteroventral half slightly lighter brown; mostly glossy ventral to lower eye margin, posteroventrally pruinose, postocular area, occiput and postgena pruinose; genal height $0.35 \times$ eye height.

Thorax: Scutum dark brown; uniformly pruinose except for glossy band posterior to prescutellar acrostichal setae, band no wider than scutellum. Presutural acrostichal setae small but differentiated, half as long as postsutural acrostichal setae and half as long as to slightly shorter than prescutellar acrostichals. Presutural supra-alar and anterior intra-alar setae subequal, slightly longer than postsutural supra-alar seta, $0.78\times$ postalar seta. Anepisternum and katepisternum glossy.

Legs: Foreleg dark brown except yellow base of femur. Base and apex of mid femur yellow, mid-section yellowish-brown; tibia and tarsus yellow. Hind femur dark brown except base; tibia and tarsus yellow.

Male terminalia (Figs. 69.1–3): Anterolateral arms of S6 short, flat, apically tapering; lateral margin of S6 with 1–2 long setae. Ventrolateral corners of S7+8 with nublike protuberances connected by ledge. Epandrium mostly glossy except with pruinose lateral patch at mid-length of each side; width of epandrium uniform, subequal to length. Cercus of uniform width. Surstylus broad, paddle-

shaped; inner lamella broad spindle-shaped with convex inner margin, extending relatively straight from body of surstylus. Subepandrial sclerite crescent-shaped, surface relatively flat; anterior seta distinctly longer than posterior seta and in slightly more lateral position.

Phallapodeme long and thin on basal half; broad, laterally compressed on distal half; length beyond phallic plate $0.38\times$ sheathed length; phallic guide width $4.4\times$ height. Postgonite flat, heart-shaped, weakly sclerotized distally. Basal distiphallus flared distally, length $1.7\times$ width; distal distiphallus membranous apically tapering, length $1.9\times$ length of basal distiphallus.

Female terminalia: S6 weakly sclerotized, with pair of stronger setae and a few small setae. S7 with broad medial protuberance on basal third; apex of tergal portion of oviscape with small pair of hook-like processes. Spermathecae elongated, with striation along entire length except apex.

Etymology: The name refers to the heart-shaped postgonite (Latin '*cordatus*': heart-shaped).

Type specimens: Holotype: ♂: **COSTA RICA**: **Puntarenas**: Monteverde Biological Reserve, tree fall and trail, 1500 m, sweep, 14.vi.2000, M. Buck, debu00126775 (MNCR).

Paratypes: **BOLIVIA:** La Paz: Cumbre Alto Beni, vicinity of Caranavi, 15°40'19"S 67°29'35"W, 1685 m, MT, 15–21.iv.2004, S.D. Gaimari & M. Hauser (1♂, CSCA). **COSTA RICA:** Puntarenas: Monteverde Biological Reserve, tree fall, 1500 m, sweep and pan trap, 14.vi.2000, M. Buck (1♀, DEBU); Monteverde Biological Reserve, 1500 m, 15–20.viii.1986, LM (1♂, DEBU); Monteverde Reserve, 1500 m, 15–20.viii.1986, LM (3♂, DEBU); Monteverde Reserve, 1550 m, 15–20.viii.1986, LM (1♂, DEBU).

Other material examined: **PERU**: **Cusco**: Cock-of-the-Rock Lodge, NE Paucartambo, 13°3'18"S 71°32'42"W, 1120 m, FIT, 4–9.xi.2007, D. Brzoska (1♀, DEBU).

Comments: The pair of hook-like processes on the apex of the oviscape (Figs. 70.1–2) is unique to this species. One Peruvian female specimen (see above) is excluded from type series due to the outlying locality and the significantly longer hook-like process on the apex of the oviscape although it seems otherwise identical to typical specimens.

Pseudopomyza (Pseudopomyza) cyathiformis Yau and Marshall sp. nov.

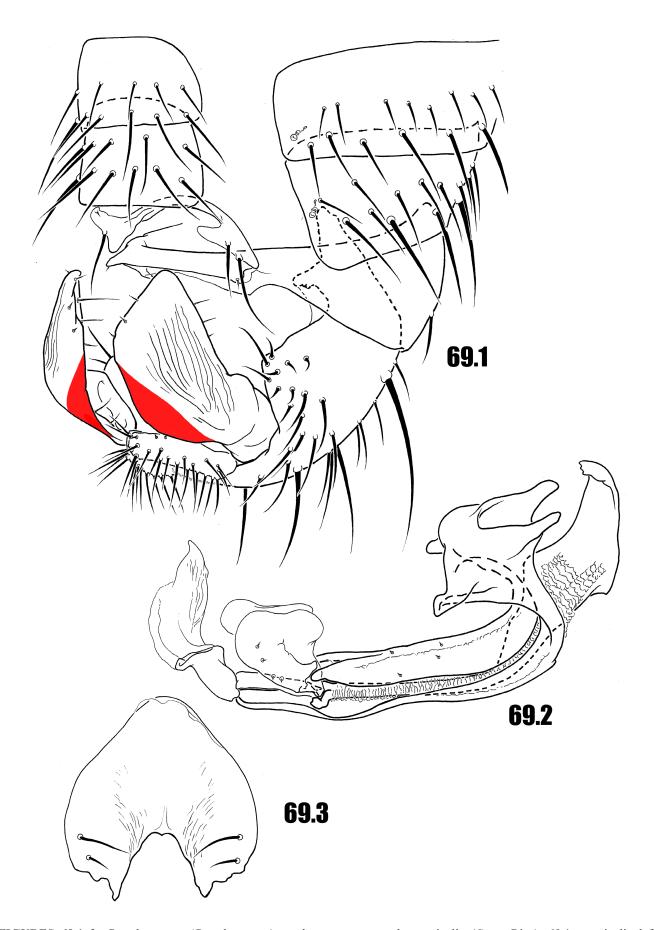
(Figs. 49n, 50m, 51t, 71.1-4, 72.1-3, 73.1-4)

Diagnosis

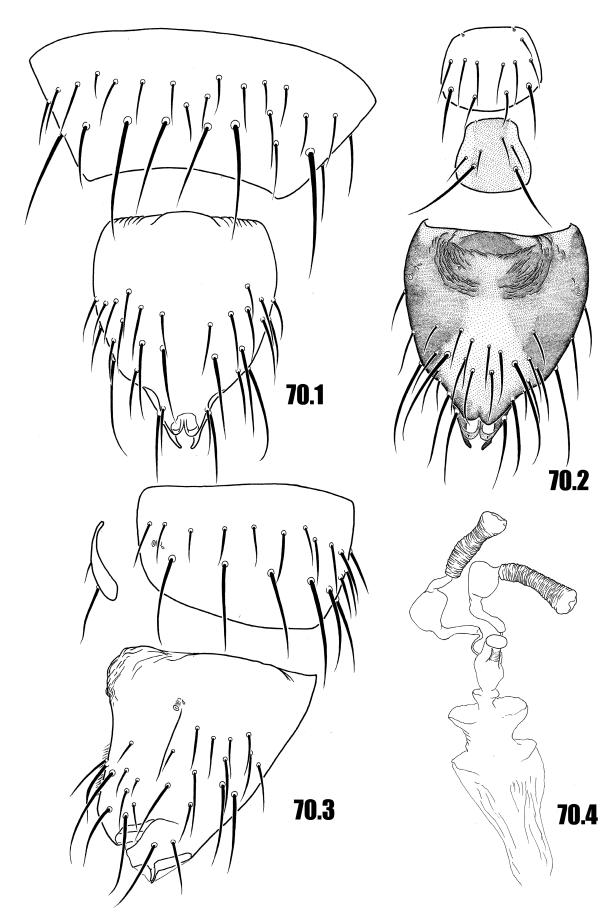
Frons dark brown to black. Male face mostly yellow, each side with dark brown marking on outer face; female inner and outer face brown, facial carina tan. Gena with a dark brown band below lower eye margin, continuous with dark brown posterior half of gena, remainder yellow or tan. Fore tarsus bicoloured, mid femur yellow. Anterolateral arms of male S6 twisted medially, apical margin parallel to posterior margin of S5, apex flattened and expanded.



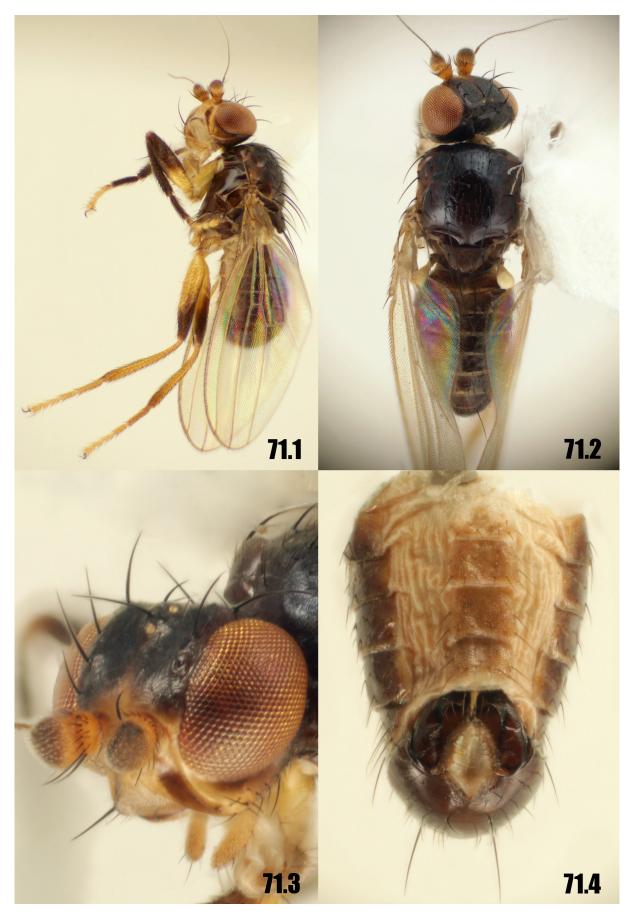
FIGURES 68.1–4: *Pseudopomyza (Pseudopomyza) cordata* **sp. nov.**, male habitus (Costa Rica). 68.1, left lateral; 68.2, dorsal; 68.3, head; 68.4, terminalia, ventral.



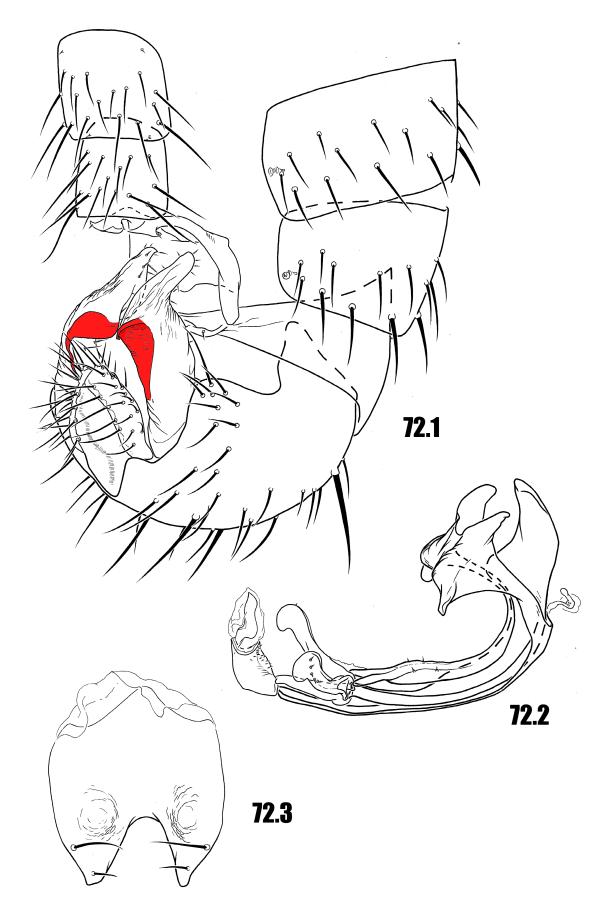
FIGURES 69.1–3: *Pseudopomyza (Pseudopomyza) cordata* **sp. nov.**, male terminalia (Costa Rica). 69.1, terminalia left ventrolateral (inner lamella of surstylus marked red); 69.2, phallus and associated structures left lateral; 69.3, subepandrial sclerite anterior surface.



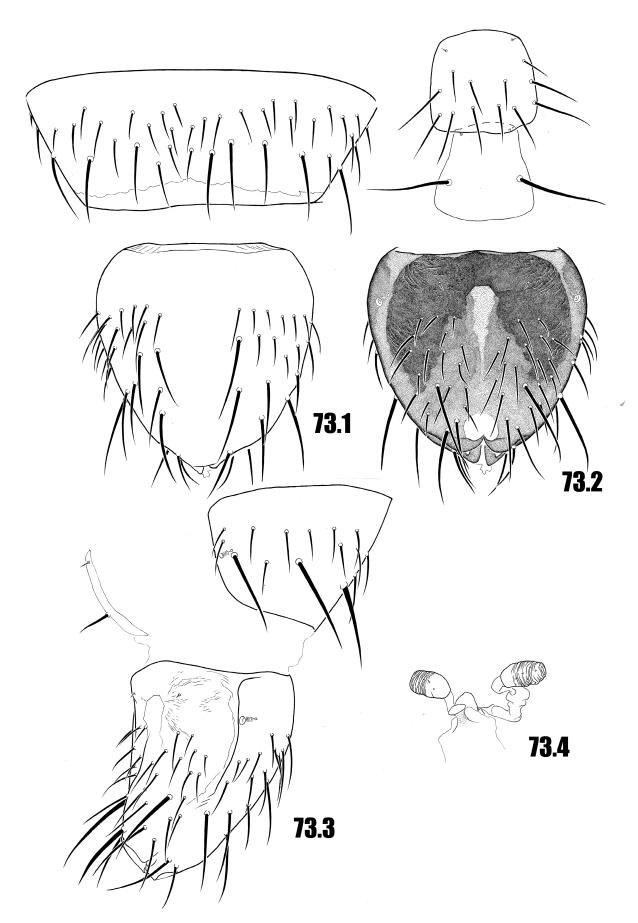
FIGURES 70.1–4: *Pseudopomyza* (*Pseudopomyza*) *cordata* **sp. nov.**, female terminalia (Costa Rica). 70.1, terminalia dorsal; 70.2, terminalia ventral; 70.3, terminalia left lateral; 70.4, spermathecae and associated structures ventral.



FIGURES 71.1–4: *Pseudopomyza (Pseudopomyza) cyathiformis* **sp. nov.**, male habitus (Costa Rica). 71.1, left lateral; 71.2, dorsal; 71.3, head; 71.4, terminalia, ventral.



FIGURES 72.1–3: *Pseudopomyza (Pseudopomyza) cyathiformis* **sp. nov.**, male terminalia (Costa Rica). 72.1, terminalia left ventrolateral (inner lamella of surstylus marked red); 72.2, phallus and associated structures left lateral; 72.3, subepandrial sclerite anterior surface.



FIGURES 73.1–4: *Pseudopomyza (Pseudopomyza) cyathiformis* **sp. nov.**, female terminalia (Costa Rica). 73.1, terminalia dorsal; 73.2, terminalia ventral; 73.3, terminalia left lateral; 73.4, spermathecae and associated structures ventral.

Surstylus bent medially; inner lamella large, extremely convex to form posterior-facing cup. Subepandrial sclerite with round protuberance above anterior seta. Postgonite spatulate. Basal distiphallus short, bent ventrally. Female S7 with thick inverted U-shaped sclerotization. Spermathecae cylindrical, striate on distal 2/3.

Description

Body length 2.3 mm (male), 2.3 mm (female).

Head: Frons dark brown to black, yellow at anterior margin and with medial yellow stripe on frontal vitta from mid-length to anterior margin, fronto-orbital plates and ocellar triangle slightly paler. Length of first fronto-orbital seta 0.67×2^{nd} , 2^{nd} subequal to 3^{rd} . Male face mostly yellow, each side with dark brown marking on outer face; female outer face of darkest brown somewhat bleeding over to inner margin of facial ridge, inner face brown, facial carina tan. Dark brown band below lower eye margin continuous with dark brown colour on posterior half of gena; gena glossy on anterior half, pruinose on posterior half and through to postgena and lower occiput; genal height $0.22 \times$ eye height.

Thorax: Scutum dark brown, pruinose only anterior to anterior dorsocentral seta and lateral to anterior intra-alar setae, area medial to intra-alar setae glossy and corrugated, remaining scutum smooth and glossy. Presutural acrostichal setae small but differentiated, length one third of postsutural setae, prescutellar pair absent. Presutural supra-alar, anterior intra-alar and postsutural supra-alar setae consecutively shorter, anterior intra-alar half as long as postalar seta. Anepisternum and katepisternum glossy.

Legs: Basal half or less of fore femur yellow, distal half dark brown; fore tibia dark brown; tarsomere 1 dark brown, tarsomere 2 dark brown except creamy white apex, remaining tarsal segments creamy white. Mid leg unknown for male specimen, female yellow. Hind femur dark brown apically and distodorsally from end of basal third outward, remainder yellow; hind tibia and tarsus yellow.

Male terminalia (Figs. 72.1–3): Anterolateral arms of S6 twisted medially, apical margin parallel to posterior margin of S5; apex flattened and expanded, sensory setula on outer corner; mid-section of sternite curved dorsally. Ventrolateral corners of S7+8 protruding and connected by a ledge. Epandrium mainly glossy except small strip dorsal to anal opening; wider at posterior half, width 0.92× length. Cercus uniform in width. Surstylus bent medially; inner lamella large, extremely convex to form posterior-facing cup. Subepandrial sclerite trapezoidal with anterior margin shallowly arcuate, with round protuberance above anterior seta; anterior seta distinctly longer than posterior seta and placed more laterally.

Phallapodeme laterally compressed towards apex; length beyond phallic plate 0.38× sheathed length; phallic guide width 2.4× height. Postgonite spatulate. Basal distiphallus short, bent ventrally, ventral surface with minute spikes, length 1.9× width; distal distiphallus with undulate sclerite within membranous portion, length 0.9× length of basal distiphallus.

Female terminalia: S6 weakly sclerotized, with

one pair of setae. S7 with thick inverted U-shaped sclerotization. Spermathecae cylindrical, striate on distal 2/3

Etymology: The name refers to the posterior-facing cup-shaped lamina on the male surstylus (Latin 'cyathus': ladle, cup; Latin 'forma': form, shape, figure).

Type specimens: Holotype: ♂: COSTA RICA: Cartago: Tapantí National Park, La Esperanza del Guarco, 2700 m, 9°42'0"N 83°5'49"W, oak forest, treefall pans, 17–18.viii.2001, SAM, debu00203261 (MNCR).

Paratype: Same collection data as holotype (1 $\stackrel{\bigcirc}{\searrow}$, MNCR).

Pseudopomyza (Pseudopomyza) flavicacumen Yau and Marshall sp. nov.

(Figs. 49i, j, 50i, 51m, n, 74.1–4, 75.1–3, 76.1–4)

Diagnosis

Frons black or dark brown. Male face mostly yellow, with dark brown marking on outer face; female face brown. Gena dark brown except anterior margin narrowly yellow. Fore tarsus bicoloured; mid femur yellow. Apex of anterolateral arms of male S6 posteriorly curved. Surstylus paddle-shaped, inner lamella narrow. Subepandrial sclerite relatively flat. Postgonite spatulate. Basal distiphallus long, widest at distal 1/3 before constricting towards distal opening. Female S7 with thick inverted U-shaped sclerotization. Spermathecae mushroom-shaped, striate on distal half.

Description

Body length 1.5–1.9 mm. External characters similar to *P. brunneicacumen*, except colour generally paler; frontal orbital plates paler than frons; scutum glossy posterolaterally and anterior to scutellum; hind leg yellow.

Male external terminalia characters (Figs. 75.1–3) similar to *P. brunneicacumen*, except epandrium longer than wide and of uniform width.

Phallapodeme laterally compressed towards apex; length beyond phallic plate 0.7× sheathed length; phallic guide width 2× length. Basal distiphallus long, widest at distal 1/3 before constricting towards distal opening, length 2.6× width; distal distiphallus membranous, except for thin arcuate sclerite at base, length 0.7× length of basal distiphallus.

Female terminalia: S6 very weakly sclerotized, with no setae. S7 with thick inverted U-shaped sclerotization. Spermathecae mushroom-shaped, striate on distal half.

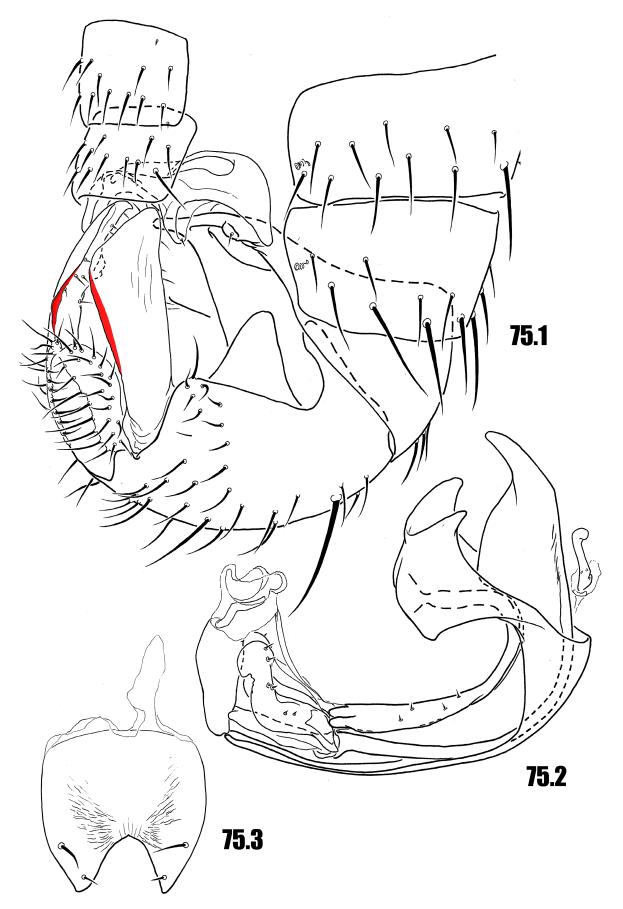
Etymology: This name refers to the yellow distal quarter of the hind femur (Latin '*flavus*': golden-yellow, yellow; Latin '*cacumen*': extreme point, end).

Type specimens: Holotype: ♂: **COSTA RICA**: **Cartago**: Hwy 2, km 67, roadside, 6.viii.1995, SAM (MNCR).

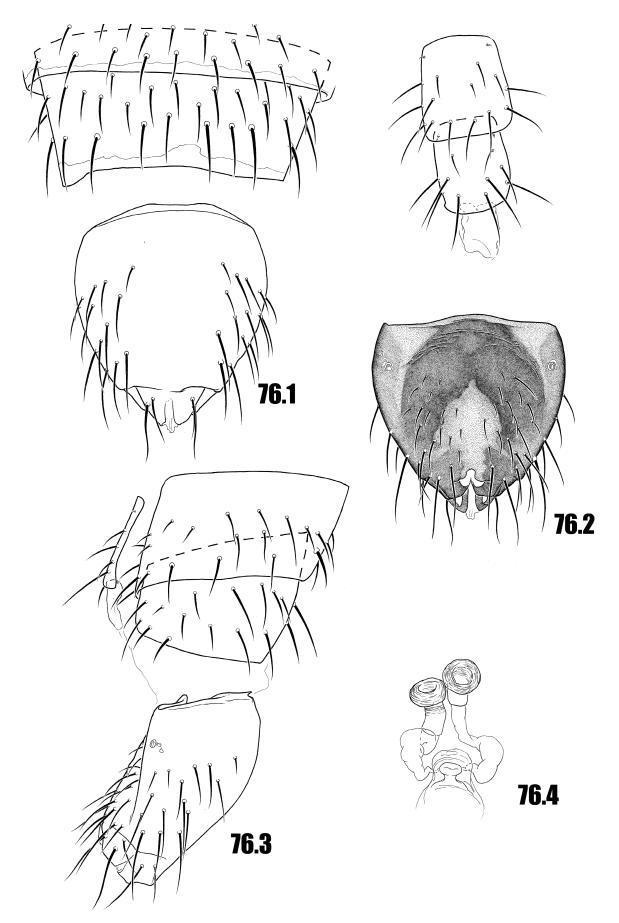
Paratypes: **COSTA RICA**: **Heredia**: 16km SSE La Virgen, 10°16'N 84°5'W, transect, 11–20.ii.2001 (13),



FIGURES 74.1–4: *Pseudopomyza* (*Pseudopomyza*) *flavicacumen* **sp. nov.**, male habitus. 74.1, left lateral (Venezuela); 74.2, dorsal (Venezuela); 74.3, head (Costa Rica); 74.4, terminalia, ventral (Costa Rica).



FIGURES 75.1–3: *Pseudopomyza (Pseudopomyza) flavicacumen* **sp. nov.**, male terminalia (Venezuela). 75.1, terminalia left ventrolateral (inner lamella of surstylus marked red); 75.2, phallus and associated structures left lateral; 75.3, subepandrial sclerite anterior surface.



FIGURES 76.1–4: *Pseudopomyza* (*Pseudopomyza*) *flavicacumen* **sp. nov.**, female terminalia (Venezuela). 76.1, terminalia dorsal; 76.2, terminalia ventral; 76.3, terminalia left lateral; 76.4, spermathecae and associated structures ventral.

DEBU); **Puntarenas**: 2000 m, 12.vii.1995, SAM (13), DEBU); Coto Brus. Zona Protectora Las Tablas. Est. Biol. Las Alturas, 1500-1600 m, MT, 26.xi.-3.xii.2012 (2♂, MNCR); ditto, 13–14.x.2012 (1♀, MNCR); ditto, 25.ii.-5.iii.2013 (1♀, MNCR); San José: behind Hotel Bougainvillea, compost pile, 6.viii.1995, SAM ($1 \stackrel{?}{\circ}$, $1 \stackrel{?}{\circ}$, DEBU); Cerro de la Muerte, 20km S, Empalme, 2800 m, xi.-xii.1989, P. Hanson (1\frac{1}{2}, DEBU); Zurquí de Moravia, 1600 m, iii.1981, P. Hanson (16, DEBU); Zurquí de Moravia, North pasture, 1600 m, MT, 21–29.xii.2012 (13), 1♀, MNCR); ditto, YP, 24.ii.2013 (1♀, MNCR); Zurquí de Moravia, tower path, 1600 m, MT, 21.xii.2012 (13), MNCR); ditto, 29.xii.2012−3.i.2013 (1², MNCR); ditto, 11–18.i.2013 (1 \bigcirc , MNCR); ditto, 28.ii.–8.iii.2013. (1 \bigcirc , MNCR); ditto, 30.iii.-6.iv.2013 (33, 19, MNCR); ditto, 26.vii.−2.viii.2013 (1♂, MNCR); ditto, 2−9.viii.2013 (1♀, MNCR); ditto, 6–13.ix.2013 (2%, MNCR). **ECUADOR**: Pichincha: Tandayapa, 3.5km SE, in green leaf litter (tree fall), 28.x.1999, SAM (1\$\int_0\$, DEBU). VENEZUELA: Lara: Yacambú, cloud forest, 1200 m, 7.v.1981, H. Townes (2♂, 2♀, DEBU); **Trujillo**: 10km E Boconó, "Laguna de Lucerdo" [= Laguna de los Cedros], slash/compost, 1760 m, 3.iii.1995, SAM (20, DEBU); Guaramacal NP, 14km NE Boconó, 2000 m, 25.viii.−1.ix.1992, LM (2♂, 2♀, MIZA; $2 \circlearrowleft$, $2 \circlearrowleft$, CNC; $4 \circlearrowleft$, $3 \circlearrowleft$, DEBU).

Comment: *Pseudopomyza flavicacumen* can easily be confused with *P. brunneicacumen*. For further discussion of the two species, see comments under the latter.

Pseudopomyza (Pseudopomyza) gambiformis Yau and Marshall sp. nov.

(Figs. 49g, 50j, 51o, p, 77.1–4, 78.1–3, 79.1–4)

Diagnosis

Frons black or dark brown. Male face mostly yellow, with dark brown marking on outer face; female face brown. Male gena with dark brown band below lower eye margin in posterior 3/4, merging into dark brown posterior half of gena; female gena brown. Fore tarsus bicoloured; mid femur yellow. Apex of anterolateral arms of male S6 posteriorly bent. Surstylus slightly spatulate with strongly oblique, truncate apex; inner lamella narrow. Subepandrial sclerite relatively flat. Postgonite spatulate. Basal distiphallus apex structurally folded inwards forming an M-shape, ventral margin of opening with small, lip-like projection. Female S7 with thick and wide X-shaped sclerotization. Spermathecae cylindrical, striate on distal half.

Description

Body length 1.7–2.1 mm (males), 2.1–2.2 mm (females). Head: Frons black or dark brown, fronto-orbital plates slightly paler. Length of first fronto-orbital seta $0.6 \times 2^{\rm nd}$,

3rd slightly shorter or subequal to 2nd. Male face mostly yellow, each side with dark brown marking on outer face, inner face and dorsal-inner margin of facial ridge sometimes tan; female face generally brown, with lower margin of antennal socket, outer face and facial carina darker. Male gena with dark brown band below lower eye margin in posterior 3/4, merging into dark brown posterior half of gena; female gena brown; gena glossy, pruinose at junction of gena, postgena and lower occiput; genal height 0.3× eye height.

Thorax: Scutum dark brown, uniformly pruinose expect for glossy band anterior to and no wider than scutellum. Presutural acrostichal setae not differentiated from remainder of scutal setulae; postsutural acrostichal setae subequal; prescutellar pair absent. Presutural supraalar seta slightly longer than subequal anterior intra-alar and postsutural supra-alar setae, and 2/3 of postalar seta. Anepisternum and katepisternum glossy.

Legs: Fore femur mostly yellow, distal end slightly tan; fore tibia dark brown; tarsomere 1 dark brown, tarsomere 2 dark brown except creamy white apex, remaining tarsal segments creamy white. Mid and hind legs yellow.

Male terminalia (Figs. 78.1–3): Apex of anterolateral arms of S6 posteriorly bent; mid-section of sternite anteriorly curved. Ventrolateral corners of S7+8 protruding and connected by ledge. Epandrium mostly glossy except for pruinose posterolateral corner adjacent to lateral margin; width $0.85 \times length$, widest posteriorly. Cercus uniform in width. Surstylus slightly spatulate with strongly oblique, truncate apex; inner lamella narrow, outwardly bent from surface of surstylus. Subepandrial sclerite trapezoidal, surface relatively flat; anterior seta distinctly longer than posterior seta and placed more laterally.

Phallapodeme laterally compressed towards apex; length beyond phallic plate 0.47× sheathed length; phallic guide width 2.7× height. Postgonite spatulate. Basal distiphallus apex structurally folded inwards forming an M-shape, ventral margin of opening with small, liplike projection, length 2.2× width; distal distiphallus membranous, with thin, undulate medial sclerite, length subequal to basal distiphallus.

Female terminalia: S6 weakly sclerotized, with a pair of setae. S7 with thick and wide X-shaped sclerotization. Spermathecae cylindrical, striate on distal half.

Etymology: The name refers to the basal distiphallus, which is similar in shape to the two-toed hooves of many ungulates (Latin 'gamba': hoof; Latin 'forma': form, shape, figure).

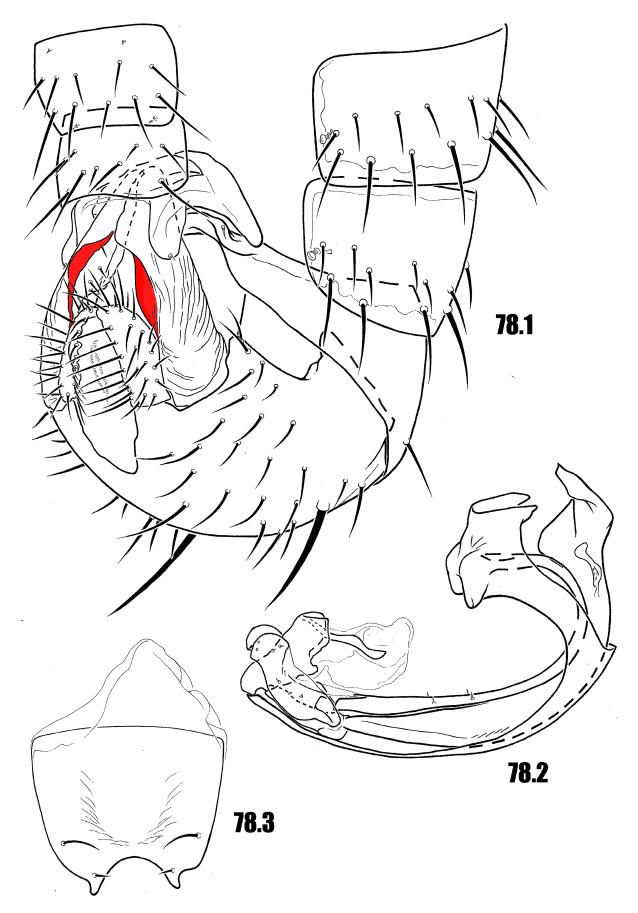
Type specimens: Holotype: \circ : **ECUADOR**: **Chimborazo:** "Linje", Chimborazo, vii.1955, Levi Castillo (USNM)

Paratypes: Same collection data as holotype (10 \circlearrowleft , 3 \circlearrowleft , USNM).

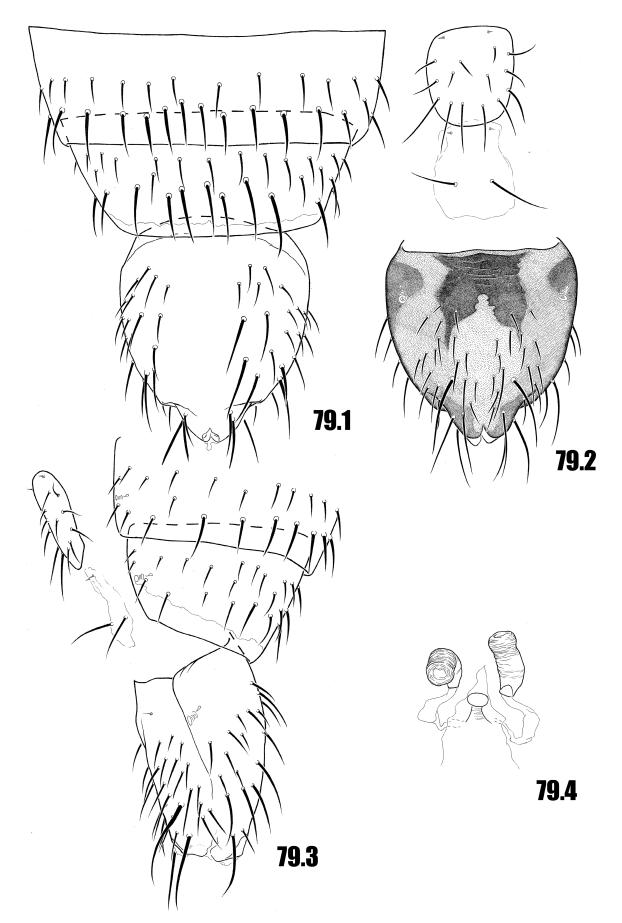
Pseudopomyza (Pseudopomyza) inflexa Yau and



FIGURES 77.1–4: *Pseudopomyza (Pseudopomyza) gambiformis* **sp. nov.**, male habitus (Ecuador). 77.1, left lateral; 77.2, dorsal; 77.3, head; 77.4, terminalia, ventral.



FIGURES 78.1–3: *Pseudopomyza (Pseudopomyza) gambiformis* **sp. nov.**, male terminalia (Ecuador). 78.1, terminalia left ventrolateral (inner lamella of surstylus marked red); 78.2, phallus and associated structures left lateral; 78.3, subepandrial sclerite anterior surface.



FIGURES 79.1–4: *Pseudopomyza (Pseudopomyza) gambiformis* **sp. nov.**, female terminalia (Ecuador). 79.1, terminalia dorsal; 79.2, terminalia ventral; 79.3, terminalia left lateral; 79.4, spermathecae and associated structures ventral.

Marshall sp. nov.

(Figs. 49l, m, 50l, 51r, s, 80.1–4, 81.1–3, 82.1–4)

Diagnosis

Frons dark brown to black, yellow at anterior margin and with medial yellow stripe. Male face mostly yellow, with dark brown marking on outer face; female face brown. Gena with dark brown band below lower eye in posterior 3/4, merging with dark brown posterior half of gena. Fore tarsus bicoloured, mid femur yellowish-brown except base and apex. Anterolateral arms of male S6 distally widened and flattened. Surstylus slightly narrowed at mid-length, rounded distomedially; inner lamella narrow. Subepandrial sclerite with slight protuberance medial to anterior seta. Postgonite spatulate. Basal distiphallus abruptly bent dorsally. Female S7 basally with inverted U-shaped sclerotization. Spermathecae cylindrical, striate on distal half.

Description

Head: Frons dark brown to black, yellow at anterior margin and with medial yellow stripe extending from mid length to anterior margin. Fronto-orbital plates paler than frontal vitta. Length of first fronto-orbital seta 0.8×2^{nd} , 2^{nd} subequal to 3^{rd} . Male face mostly yellow, each side with dark brown marking on outer face, sometimes bleeding into inner face; female face brown, outer face darkest.

Body length 1.9–2.4 mm (males), 2.1–2.6 mm (females).

dark brown marking on outer face, sometimes bleeding into inner face; female face brown, outer face darkest. Gena with dark brown band below lower eye in posterior 3/4, merging with dark brown posterior half of gena; gena glossy on anterior half, pruinose on posterior half through to occiput and postgena; genal height 0.3× eye height.

Thorax: Scutum dark brown, pruinose anterior to first dorsocentral seta and lateral to supra-alar setae; area posterolateral to prescutellar dorsocentral seta glossy and smooth, remaining scutum glossy and corrugated. Presutural acrostichal setae not differentiated from remainder of scutal setulae; postsutural acrostichal setae subequal and slightly longer than prescutellar pair. Presutural supra-alar, anterior intra-alar and postsutural supra-alar setae become consecutively shorter, postsutural supra-alar about half as long as postalar seta. Anepisternum and katepisternum glossy.

Legs: Fore femur dark brown except for yellow base; fore tibia dark brown (basal half may appear yellowish-brown in posterolateral view); tarsomere 1 dark brown, tarsomere 2–4 white or creamy white. Base and apex of mid femur yellow, mid-section yellowish-brown; mid tibia and tarsus yellow. Hind femur dark brown, except basal quarter yellow; hind tibia and tarsus yellow.

Male terminalia (Figs. 81.1–3): Anterolateral arms of S6 distally widened and flattened; mid-section of sternite anteriorly curved. Ventrolateral corners of S7+8 nub-like. Epandrium mostly glossy except pruinose on posterolateral surface; subequal in length and width, widened posteriorly. Cercus uniform in width. Surstylus slightly narrowed at mid-length, rounded distomedially; inner lamella narrow, outwardly bent from surface of

surstylus. Subepandrial sclerite rounded, with slight protuberance or elevation medial to anterior seta; anterior seta distinctly longer than posterior seta and placed more laterally.

Phallapodeme laterally compressed towards apex; length beyond phallic plate $0.7\times$ sheathed length; phallic guide width $3.4\times$ height. Postgonite spatulate. Basal distiphallus abruptly bent dorsally, length $3.4\times$ width; distal distiphallus membranous, with two curved lobes, length $0.7\times$ length of basal distiphallus.

Female terminalia: S6 membranous, with no setae. S7 basally with inverted U-shaped sclerotization. Spermathecae cylindrical, striate on distal half.

Etymology: The species name refers to the bent basal distiphallus (Latin '*inflexus*': bent, curved, bowed).

Type specimens: Holotype: ♂: **COSTA RICA**: **Cartago**: Tapantí-Macizo Cerro de la Muerte National Park, La Esperanza del Guarco, 9°42'0"N 83°51'49"W, oak forest, treefall, 2700 m, pan trap, 17–18.viii.2001, SAM, debu00206819 (MNCR).

Paratypes: Same collection data as holotype (23, 29, DEBU, MNCR); Tapantí National Park, La Esperanza del Guarco, 9°42'0"N 83°51'49"W, oak forest, treefall, 2700 m, pan trap, 17–18.viii.2001, SAM (23, 29, DEBU, MNCR); **Puntarenas**: Las Alturas, trail to Cerro Chai, 1700–2100 m, 13–15.viii.1995, SAM (19, DEBU); **San José:** Cerro de la Muerte, 20km S, Empalme, 2800 m, xi.—xii.1989, P. Hanson (19, DEBU); Moravia, Zurquí de Moravia, 1600 m, MT, 12.ix.2012 (13, MNCR); ditto, Tower path, 30.iii–6.iv.2013 (13, MNCR).

Other examined material: COSTARICA: **Puntarenas**: 2000 m, 12.vii.1995, SAM (4Å, DEBU).

Comments: The stem of the postgonite of *P. inflexa* is of uniform width and less curved than that of *P. flavicacumen* (Fig. 75.2) and *P. albimana* (Fig. 55.2); the elongated posterolateral projections of the hypandrium and the abruptly bent basal distiphallus are also distinctive for *P. inflexa*. All records of this species are from above 1500 m, and most are from over 2000 m.

Pseudopomyza (Pseudopomyza) machaera Yau and Marshall sp. nov.

(Figs. 49h, 50g, 51f, 83.1–4, 84.1–3)

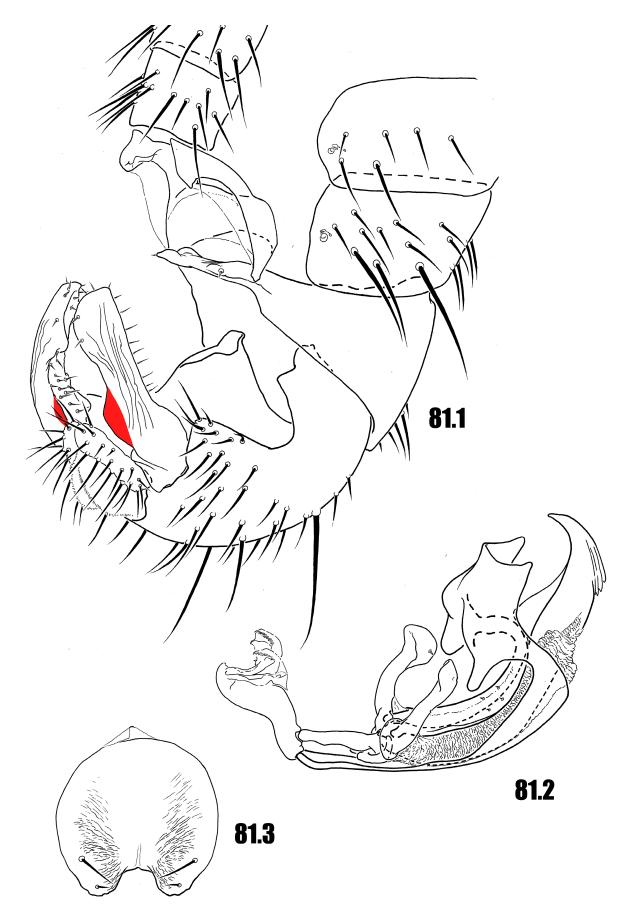
Diagnosis

Frons black or dark brown. Face mostly yellow, with dark brown marking on outer face. Gena brown, except yellow to tan anterior margin. Fore tarsus bicoloured; mid femur brown except for yellow base. Anterolateral arms of male S6 distally dilated and rounded with an anterior point. Surstylus glaive-shaped, long and broadest at mid-width, distally tapered to a point; inner lamella long and wide. Subepandrial sclerite relatively flat. Postgonite spatulate with posteroapical edge excavated to form hook-like point. Basal distiphallus slightly curved, distal opening strongly oblique.

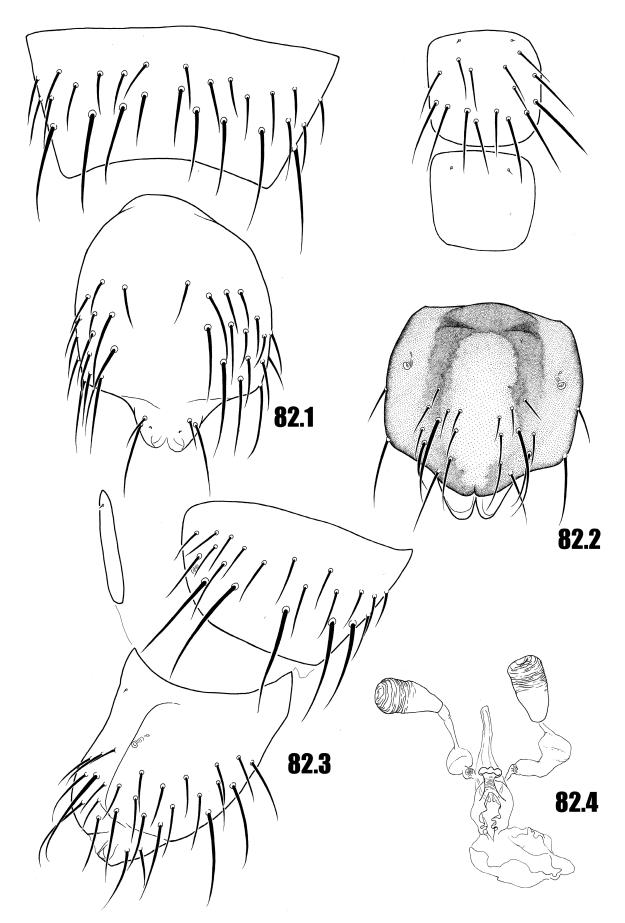
Description (male only)



FIGURES 80.1–4: *Pseudopomyza (Pseudopomyza) inflexa* **sp. nov.**, male habitus (Costa Rica). 80.1, left lateral; 80.2, dorsal; 80.3, head; 80.4, terminalia, ventral.



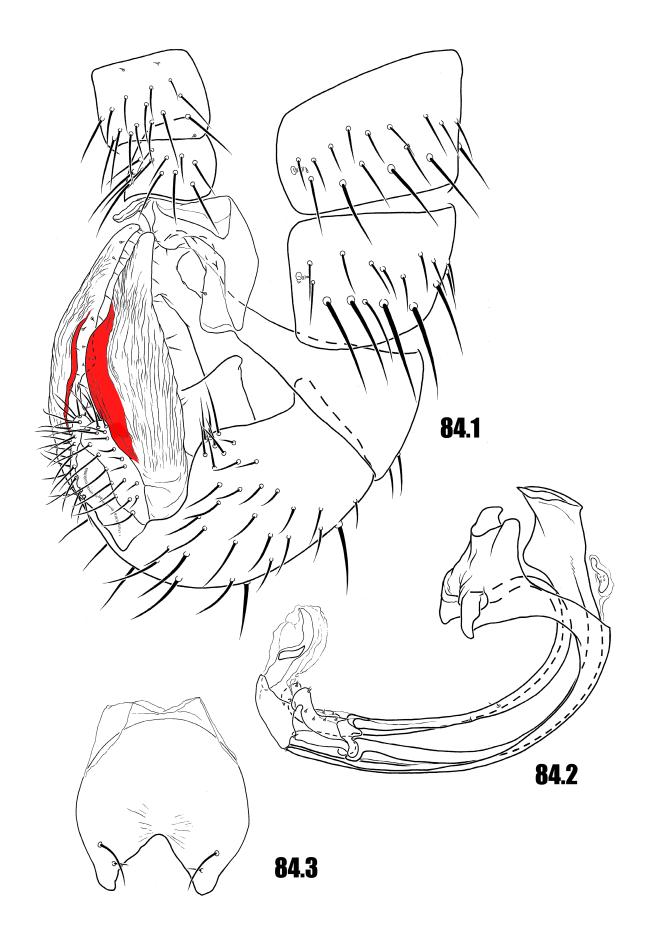
FIGURES 81.1–3: *Pseudopomyza* (*Pseudopomyza*) *inflexa* **sp. nov.**, male terminalia (Costa Rica). 81.1, terminalia left ventrolateral (inner lamella of surstylus marked red); 81.2, phallus and associated structures left lateral; 81.3, subepandrial sclerite anterior surface.



FIGURES 82.1–4: *Pseudopomyza (Pseudopomyza) inflexa* **sp. nov.**, female terminalia (Costa Rica). 82.1, terminalia dorsal; 82.2, terminalia ventral; 82.3, terminalia left lateral; 82.4, spermathecae and associated structures ventral.



FIGURES 83.1–4: *Pseudopomyza (Pseudopomyza) machaera* **sp. nov.**, male habitus (Guatemala). 83.1, left lateral; 83.2, dorsal; 83.3, head; 83.4, terminalia, ventrolateral.



FIGURES 84.1–3: *Pseudopomyza* (*Pseudopomyza*) *machaera* **sp. nov.**, male terminalia (Guatemala). 84.1, terminalia left ventrolateral (inner lamella of surstylus marked red); 84.2, phallus and associated structures left lateral; 84.3, subepandrial sclerite anterior surface.

Body length 2.1 mm.

Head: Frons black or dark brown, fronto-orbital plates and ocellar triangle slightly paler. Head macrochaetae lost, chaetotaxy not observed. Face mostly yellow, each side with dark brown marking on outer face, dorsal inner margin of facial ridge and inner face tannish-yellow. Gena brown, except yellow to tan anterior margin; anterodorsally glossy, remainder pruinose through to postgena and occiput; genal height $0.35 \times$ eye height.

Thorax: Scutum dark brown; shallowly corrugated; pruinose anterior to prescutellar dorsocentral seta, posterior part glossy. Most of macrochaetae lost, but according to sockets presutural and postsutural acrostichal setae present; prescutellar pair distinct; anterior intra-alar, supra-alar (1+1) and 1 postalar setae present. Anepisternum and katepisternum glossy.

Legs: Fore femur dark brown except for yellow base; fore tibia dark brown; tarsomere 1 dark brown, remaining segments white or creamy white. Mid femur brown except for yellow base; mid tibia and tarsus yellow. Hind femur dark brown except yellow base; hind tibia and tarsus yellow.

Male terminalia (Figs. 84.1–3): Anterolateral arms of S6 distally dilated and rounded with an anterior point; mid-section of sternite anteriorly curved. Ventrolateral corners of S7+8 prominent and triangular, ventral bridge prominently arched anteriorly. Epandrium with pruinose anterior and posterior margins, remainder glossy; epandrium of uniform width, width $0.7 \times$ length. Cercus with slightly spatulate apex. Surstylus glaive-shaped, long and broadest at mid-width, distally tapered to a point; inner lamella long and wide, outwardly bent from surface of surstylus. Subepandrial sclerite rounded, surface relatively flat; anterior seta distinctly longer than posterior seta and placed more laterally.

Phallapodeme laterally compressed towards apex; length beyond phallic plate 0.44× sheathed length; phallic guide width 3.3× height. Postgonite spatulate with posteroapical edge excavated to form hook-like point. Basal distiphallus slightly curved, distal opening strongly oblique, length 2× width; distal distiphallus membranous, containing small sclerite not articulated to basal distiphallus, length of distal distiphallus 1.25× length of basal distiphallus.

Etymology: The name refers to the glaive-like surstylus in males (Latin 'machaera': sword, glaive).

Type specimen: Holotype: ♂: **GUATEMALA**: **El Progreso:** Cerro Pinalón, 15°5'1"N 89°56'42"W, 2575 m, treefall gap edge in cloud forest, MT, 29.iv–5.v.2009, debu00347880 (UVGC).

Pseudopomyza (Pseudopomyza) nigrimana (Hennig) (Figs. 49a-c, 50a, b, 51a, c, 85.1-4, 86.1-4, 87, 88.1-3, 89.1-4)

Rhinopomyzella nigrimana Hennig, 1969: 598. Pseudopomyza (Rhinopomyzella) nigrimana (Hennig)—McAlpine,

Diagnosis

Frons dark brown to black; widespread form more often with yellow at anterior margin of frons; Puerto Rican form with thicker yellow band at anterior margin of frons. Face of typical and widespread forms mostly yellow, with dark brown marking on inner face; Puerto Rican form with entirely yellow face. Typical and widespread forms with dark brown spot below lower eye margin, posterior half of gena dark brown; Puerto Rican form with gena mostly yellow dark brown restricted to postocular area. Fore tarsus dark brown; mid femur of typical form yellow; mid femur of widespread and Puerto Rican yellowish-brown except base and apex. Anterolateral arms of male S6 distolaterally expanded. Surstylus paddle-shaped; inner lamella wide; C-shaped indentation near base of surstylus trunk visible through inner lamella. Subepandrial sclerite with protuberance medial to anterior seta. Postgonite ovoid with small preapical medial hook. Basal distiphallus curved ventrally at mid-length, dorsal-ventrally flattened. Female S7 with pair of circular desclerotized depressions. Spermathecae bulbous, transversely grooved with dimples.

Description

Body length 1.5–2.0 mm (males), 2.0–2.3 mm (females). As Hennig noted, *P. nigrimana* includes different colour forms. Here, three forms are described from specimens available to us: Typical form (Figs. 85.1, 85.2), described by Hennig, found in southern Brazil and northern Argentina; Puerto Rican form (Figs. 85.3, 85.4), found on main island of Puerto Rico; widespread form (Figs. 86.1–4), found across Central and South America except above-mentioned areas.

Head: Frons dark brown to black, sometimes yellow at anterior margin, fronto-orbital plates (rarely ocellar triangle) paler. Widespread form more often with yellow at anterior margin of frons, Puerto Rican form with thicker yellow band at anterior margin of frons. Length of first fronto-orbital seta $0.8 \times 2^{\text{nd}}$, 2^{nd} subequal to 3^{rd} . Face of typical and widespread forms mostly yellow, with dark brown marking on inner face; Puerto Rican form with entirely yellow face. Typical and widespread forms with dark brown spot below lower eye margin, posterior half of gena dark brown; Puerto Rican form with gena mostly yellow, dark brown restricted to postocular area; gena glossy on anterior half, pruinose on posterior half and through to postgena; genal height $0.4 \times$ eye height.

Thorax: Scutum dark brown; uniformly pruinose except for glossy band posterior to prescutellar acrostichal setae, band no wider than scutellum. Presutural acrostichal setae small but differentiated, half as long as postsutural acrostichal setae; prescutellar pair present. Anterior intraalar and supra-alar (1+1) setae subequal, half as long as postalar seta. Anepisternum and katepisternum glossy.

Legs of typical form: Fore femur yellow on basal half, distal half dark brown; tibia and tarsus dark brown.



FIGURES 85.1–4: *Pseudopomyza (Pseudopomyza) nigrimana* (Hennig), male habitus 85.1, left lateral (Brazil); 85.2, head (Brazil); 85.3, left lateral (Puerto Rico); 85.4, head (Puerto Rico).



FIGURES 86.1–4: *Pseudopomyza* (*Pseudopomyza*) *nigrimana* (Hennig), male habitus. (Costa Rica). 86.1, left lateral; 86.2, dorsal; 86.3, head; 86.4, terminalia, ventral.



FIGURE 87. Pseudopomyza (Pseudopomyza) nigrimana (Hennig). Wing interference pattern.

Mid leg yellow but last tarsal segment brownish. Hind leg with basal half or more yellow, distal half dark brown; tibia and tarsus yellow, last tarsal segment brownish.

Legs of widespread and Puerto Rican form: Foreleg dark brown except yellow base of femur. Base and apex of mid femur yellow, mid-section yellowish-brown; tibia and tarsus yellow. Hind femur dark brown except base; hind tibia and tarsus yellow.

Male terminalia (Figs. 88.1–3): Anterolateral arms of S6 distolaterally expanded, apex with 1–2 long and 0–1 short setae; connecting sclerite present between arms at distal 1/3; mid-section of sternite with slight anterior curvature. Ventrolateral corners of S7+8 without apparent protuberance. Epandrium mostly glossy, except pruinose area on posterolateral surfaces; subequal in length and width, slightly widened distally. Cercus somewhat tapered. Surstylus paddle-shaped; inner lamella wide; C-shaped indentation near base of surstylus trunk visible through inner lamella. Subepandrial sclerite rounded, with ovoid protuberance or rise medial to anterior seta; anterior seta only slightly longer than posterior seta and slightly displaced laterally.

Phallapodeme unusually long and slender, apex slightly expanded; length beyond phallic plate 1.5× sheathed length; phallic guide absent. Postgonite ovoid with tapered base and small preapical medial hook. Basal distiphallus curved ventrally at mid-length, dorsal-ventrally flattened, length at least 5× width; distal distiphallus membranous, apically spiculate, almost as long as basal distiphallus.

Female terminalia: S6 weakly sclerotized, with a pair of setae. S7 with basal, well sclerotized strip, distally followed

by pair of circular desclerotized depressions. Spermathecae bulbous, transversely grooved with dimples.

Type specimens: Holotype (not examined): ♂: "Nova Teutônia, 27°11'S., 52°23'W., Brazil, 300–500 m, VIII.1961, F. Plaumann. Type number 9926" (CNC)².

Paratypes: "Nova Teutônia, 27°11'S., 52°23'W., Brazil, 300–500 m, XI.1962, F. Plaumann. Type number 9926" (2\(\times\), CNC) \(^3\); "Nova Teutônia, 27°11'S., 52°23'W., Brazil, 300–500 m, IX.1965, F. Plaumann. Type number 9926" (1\(^2\), CNC) \(^4\); "Hardwar Gap, Jamaica, 4000ft, 6.VII.1966, Howden and Becker. Type number 9926" (5\(^3\), CNC) \(^5\); "Hardwar Gap, Jamaica, 4000ft, 10.VII.1966, Howden and Becker. Type number 9926" (3\(^3\), 2\(^2\), CNC, USNM) \(^6\); "Hardwar Gap, Jamaica, 4000ft, 13.VII.1966, Howden and Becker. Type number 9926" (1\(^3\), 2\(^2\), CNC) \(^7\); "Hardwar Gap, Jamaica, 4000ft, 29.VII.1966, Howden and Becker. Type number 9926" (2\(^2\), CNC).\(^8\)

We have not seen the holotype, but images were reviewed online https://cnc.agr.gc.ca/taxonomy/Specimen.php?id=419979.

³ Disparity in date between labels (Nov 1962) and Hennig's description (Aug 1961).

⁴ Disparity in date between label (Sep 1965) and Hennig's description (Aug 1961).

⁵ Disparity in date between labels (6.vii.1966) and Hennig's description (29.vii.1966).

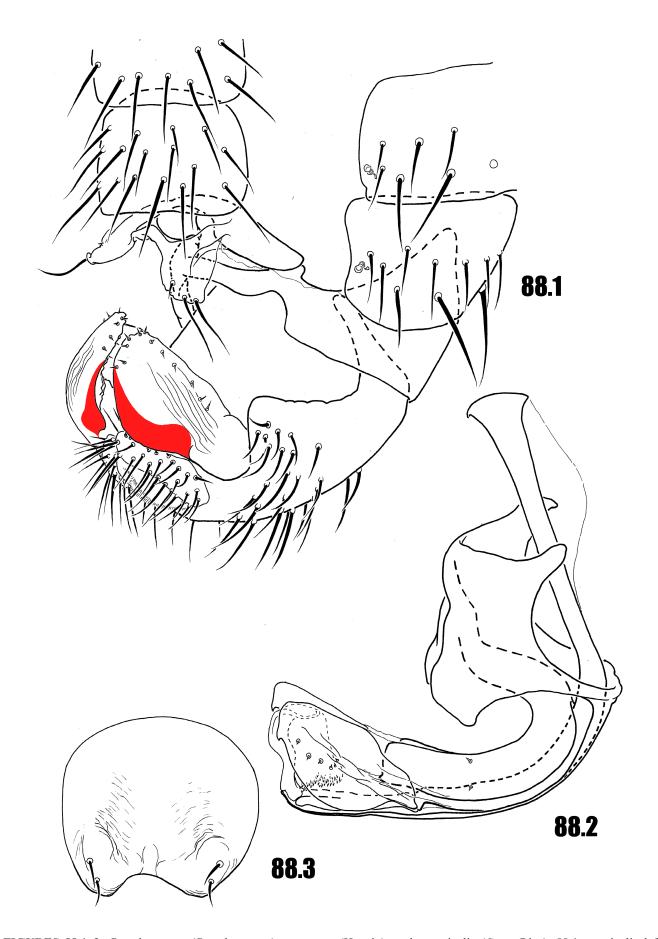
⁶ Disparity in date between labels (10.vii.1966) and Hennig's description (29.vii.1966).

⁷ Disparity in date between labels (13.vii.1966) and Hennig's description (29.vii.1966).

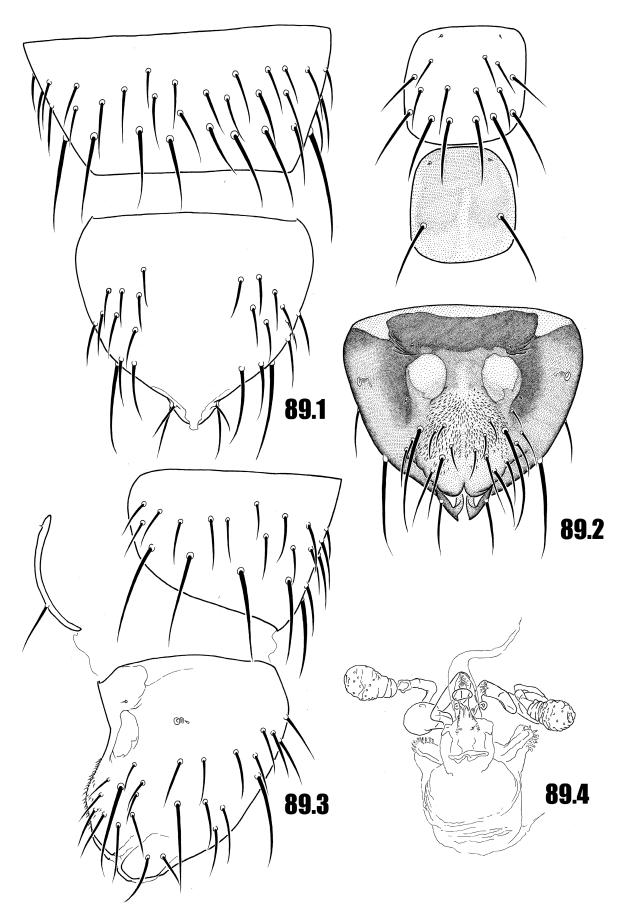
⁸ Only 80, 89 out of the 110, 119 from Hardwar Gap, Jamaica were borrowed from the CNC.

Other material examined: ARGENTINA: Jujuy: Calilegua National Park, Mirador, forest, 600 m, MT FIT, 18–28.xii.1987, S. & J. Peck (1♀, DEBU); Misiones: 5km E Puerto Iguazo, by small stream, sweep, 3.ii.1992, SAM (16, DEBU); Salta: La Caldera, forest, 1500 m, sweep roadside, 27.ii.1992, SAM (1\delta, DEBU). BELIZE: Cayo: Mountain Pine Ridge, falls, 1000', full sweep, 14.i.1991, SAM (2\$\int\$, DEBU). BOLIVIA: Beni, S. Inicua Riv. Alto Beni, 1100 m, 15-18.i.1976, L.E. Peña (13, CNC); La Paz: Arroyo Tuhiri W Mapiri, 15°17'27"S 68°15'29"W, 10.iv.2001, SAM (20, 19, DEBU); Chulumani, Apa Apa Reserve, 16°21'15"S 67°30'21"W, 2000 m, sweep, 1. iv.2001, SAM (16, DEBU); Coroico, 36km NE on Caranavi Rd, pan traps, 7–15.iv.2001, SAM (3 \circlearrowleft , 5 \updownarrow , DEBU); Coroico, Cerro Uchumachi, 16°12'43"S 67°42 49"W, 2550 m, 6.iv.2001, SAM (1[♀], DEBU); Cumbre Alto Beni, vicinity of Caranavi, 15°40'19"S 67°29'35"W, 1685 m, MT, 15-21.iv.2004, S.D. Gaimari & M. Hauser (2♂, 2♀, CSCA); San Antonio, ca. 8km S Mapiri, 15°20'56"S 68°13'31"W, 2° forest, dung pans, 11.iv.2001, SAM (1\$\int_{\infty}\$, DEBU); Zongo, 16\infty6'32"N 68\infty4'30"W, roadside cut foliage, sweep, 18.iv.2001, SAM (23, DEBU); Zongo Valley, 16°16'36"S 68°7'9"W, cushion plants, approx. 4000 m, dung traps, 18.iv.2001, SAM (12, DEBU); Santa Cruz: loc. Siringalito nr. Pampa Grande, 2.x.1996, Bettella & Rossi (16, DEBU). BRAZIL: Minas Gerais: Congonhas, foot of serra, along stream, sweep, 22.ii.1990, SAM (3♂, 3♀, MZUSP); Paraná: Curitiba, under fallen epiphyte in mata nr. National History Museum, 5.ii.1990, SAM (3\delta, MZUSP); Curitiba, University campus, wet area, FIT/pans, 2-5.ii.1990, SAM (1\(\frac{1}{3}\), MZUSP); East of Curitiba, nr. Creek debris, sweep, 8.ii.1990, SAM (4 \circlearrowleft , 2 \updownarrow , MZUSP); Rio de Janeiro: Nova Friburgo, 10km S Sitio Edelweiss, 27.i.1990, SAM (13, MZUSP); ditto, MT, 26.i.1990 (2♂, 1♀, MNRJ); ditto, Muri, 1-23.ii.1990 (18, MNRJ); ditto, Muri, MT head, 1–28.ii.1990 (1♀, MNRJ); Teresópolis, trail to Pedra do Sino, 1300–1700m, 25.i.1990, SAM (12 \circlearrowleft , 6 \updownarrow , MNRJ); ditto, sweep (76, MNRJ); Teresópolis, trail to Pedra do Sino, 1500–2000m, 14.i.1990, SAM (13, MNRJ); Teresópolis, near river, 1200m, sweep, 13.iii.1990, SAM (1♀, MNRJ); Santa Catarina: Nova Teutônia, ix.1949, F. Plaumann ($2 \circlearrowleft$, $6 \hookrightarrow$, USNM); São Paulo: São Carlos, Canchin Farm, MT, 4–6.i.1996, M.J. Sharkey (1♀, MZUSP); São José do Barreiro, 1650m, MT, i.1969, M. Alvarenga (1♂, 2♀, MZUSP). COLOMBIA: Antioquia: La Unión, Solanum andigenum, Alt. 2500 m, 16.xi.1955, L. Posada (1♀, USNM); Bogotá: Bogotá vicinity, W. B. Heed (16, USNM); Cauca: 30 km N Popayán, iii.1958, M.R. Wheeler (2♂, 1♀, USNM); Valle del Cauca: Tablones Valle Finca La Florida, 7.i.1959, J.F.G. Clarke (1♀, USNM). COSTA RICA: Alajuela: Volcán Tenorio, N slope nr. Bijagua Biological Station, tree fall, 700 m, pans, 18.vi.2000, M. Buck & SAM (13, 22, DEBU); Volcán Tenorio, Bijagua Biological Station, decayed vegetation, 700 m, sweep, 16.vi.2000, M. Buck (20, 14), DEBU); Volcán Tenorio, N slope nr. Bijagua Biological Station, rainforest (trail), 700 m, sweep, 17.vi.2000, SAM (26, DEBU); Volcán Tenorio, N slope, trail to laguna, ~1000 m, sweep, 18.vi.2000, SAM (4\frac{1}{1000}, DEBU); Cartago:

La Suiza, 1924, P. Schild, A.L. Melander Collection 1961 (13, USNM); ditto, 6.v.1926 (39, USNM); Hwy 2, 67km, roadside, 6.viii.1995, SAM (12, DEBU); Paraíso, Tapantí National Park, 1600 m, MT, 14–21.iv.2013 (1♀, MNCR); ditto, 17–24.ii.2013 (12, MNCR); ditto, 21–29.ix.2013 $(2 \circlearrowleft, MNCR)$; ditto, 3–9.iii.2013 $(2 \circlearrowleft, 1 \circlearrowleft, MNCR)$; ditto, 9–17.iii.2013 (2♀, MNCR); ditto, 25.viii.–1.ix.2013 (1♀, MNCR); ditto, 25.ii.–3.iii.2013 (26, MNCR); Tapantí National Park, outside nr. W entrance, trail, 1150 m, sweep, 8-9.x.1999, SAM & M. Buck (1 \updownarrow , DEBU); Guanacaste: Cacao, 1100–1200 m, 15.ii.1996, SAM (13), MNCR); Guanacaste National Park, Biological Station Cacao, screen sweeps, 13.ii.1995, LM (13, DEBU); Heredia: 16km SSE La Virgen, 10°16'N 84°5'W, 1050-1150 m, transect, 21.iii.2001 (1 \circlearrowleft , 1 \circlearrowleft , DEBU); ditto, 9. iv.2001 (12, DEBU); Moravia, nr. Border of Braulio Carrillo National Park, creek bed, yellow pans, 3-4. iii.1996, LM (23, DEBU); Vara Blanca, 6km ENE, 10°11'N 84°7'W, 2000 m, 21.ii.2002 (13, DEBU); Puntarenas: Coto Brus. Zona Protectora Las Tablas. Est. Biol. Las Alturas, 1500–1600 m, MT, 26.xi.-3.xii.2012 (23, MNCR); Las Alturas, Grand Eciton raid, 1600 m, 15.viii.1995, SAM (1&, DEBU); Monteverde Biological Reserve, tree fall, 1500 m, sweep and pans, 14.vi.2000, M. Buck (18 \circlearrowleft , 4 \circlearrowleft , DEBU); Monteverde Biological Reserve, cloud forest, 1500 m, 11–13.vi.2000, SAM (13), 2♀, DEBU); Monteverde Biological Reserve, kitchen compost, 1500 m, white pans, 12.vi.2000, M. Buck (13, DEBU); Monteverde Biological Station, 10.32°N 84.31°W, along stream, 1500 m, 12.vi.2000, J.M. Cumming (1\delta, CNC); Monteverde Biological Reserve, along creek, 1550 m, yellow pans, 18.iii.1996, LM (13), DEBU); Monteverde Biological Reserve, tree fall and trail, 1500 m, sweep, 14.vi.2000, M. Buck (1♀, DEBU); Monteverde Reserve, cloud forest, 1500m, ii.1980, W. Mason (16, CNC); Monteverde Reserve, 1500 m, 15-20.viii.1986, LM ($4 \circlearrowleft$, $5 \circlearrowleft$, DEBU); Monteverde Reserve, cloud forest, 1500 m, MT, 15–20.viii.1986, LM (2♂, 3♀, CNC); Monteverde, San Luis Ecolodge Espajito trail, 1–24.iii.2007, P.D. Careless (1♂, DEBU); Monteverde, Summit Cerro Chomogo, 1800 m, MT, 1-10.iii.1992, D.M. Wood (1♀, CNC); Monteverde, FIT, 27.ii.1991, H. & A. Howden (30, 49, DEBU); Monteverde, cloud forest, 1500 m, FIT, 23.ii.1983, H.F. Howden (32, DEBU); Monteverde, Finca Canada, 1500 m, 5.vi.1988, B.V. Brown (12, CNC); San Vito de Coto, Las Alturas Biological Station, 1500 m (1♀, CNC); San José: behind Hotel Bougainvillea, compost pile, 6.viii.1995, SAM (13), DEBU); Sto. Domingo, INBio Park, 25.viii.2001 (13), CNC); Moravia, Zurquí de Moravia, 1600 m, hand collected, 23.ix.2012 (12, MNCR); Moravia, Zurquí de Moravia, 1600 m, MT, 29.viii.−8.ix.2012 (1♀, MNCR); ditto, 6–12.ix.2012 (1\(\frac{1}{2}\), MNCR); ditto, 12.ix.2012 (1\(\frac{1}{2}\), 2° , MNCR); ditto, 12–18.ix.2012 (1 $^{\circ}$, 3 $^{\circ}$, MNCR); ditto, 9–19.x.2012 (16, MNCR); ditto, 22.x.-1.xi.2012 $(1 \circ, MNCR)$; ditto, 13-20.ix.2013 (5 \circlearrowleft , $3 \circ$, MNCR); Moravia, Zurquí de Moravia, creek, 1600 m, MT, 10-17.xi.2012 (1♂, 1♀, MNCR); Moravia, Zurquí de Moravia creek river, 1600 m, bucket light trap, 22.ix.2012 (13, MNCR); Moravia, Zurquí de Moravia, tower path, 1600



FIGURES 88.1–3: *Pseudopomyza (Pseudopomyza) nigrimana* (Hennig), male terminalia (Costa Rica). 88.1, terminalia left ventrolateral (inner lamella of surstylus marked red); 88.2, phallus and associated structures left lateral; 88.3, subepandrial sclerite anterior surface.



FIGURES 89.1–4: *Pseudopomyza (Pseudopomyza) nigrimana* (Hennig), female terminalia (Costa Rica). 89.1, terminalia dorsal; 89.2, terminalia ventral; 89.3, terminalia left lateral; 89.4, spermathecae and associated structures ventral.

m, FIT, 18–25.i.2013 (4 \circlearrowleft , 5 \updownarrow , MNCR); ditto, 30.iii.–6. iv.2013 (2, MNCR) Moravia, Zurquí de Moravia, tower path, 1600 m, MT, 21.xii.2012 (4\,\times, MNCR); ditto, 29. xii.2012–3.i.2013 (40, 49, MNCR); ditto, 11–18.i.2013 (30, 69, MNCR); ditto, 18–25.i.2013 (10, 39, MNCR); ditto, 25.i.–1.ii.2013 (1\delta, MNCR); ditto, 1–8.ii.2013 (3\delta, 7° , MNCR); ditto, 8–15.ii.2013 (1 $^{\circ}$, 3 $^{\circ}$, MNCR); ditto, 15–22.ii.2013 (2♂, 1♀, MNCR); ditto, 28.ii.– 8.iii.2013 (23, MNCR); ditto, 30.iii.-6.iv.2013 (593, 292, MNCR); ditto, 5–12.iv.2013 (12, MNCR); ditto, 12–19.iv.2013 (13, 29, MNCR); ditto, 26.iv.-3.v.2013 (13, 29,MNCR); ditto, 17–24.v.2013 (2 \circlearrowleft , MNCR); ditto, 1–7. vi.2013 (2 \circlearrowleft , 1 \circlearrowleft , MNCR); ditto, 5–12.vii.2013 (3 \circlearrowleft , MNCR); ditto, 12–19.vii.2013 (20♂, 23♀, MNCR); ditto, 26.vii.-2.viii.2013 (13 $^{\circ}$, 6 $^{\circ}$, MNCR); ditto, 2-9.viii.2013 $(13^{\circ}, 12^{\circ}, MNCR)$; ditto, 3–10.viii.2013 (4 $^{\circ}, 7^{\circ}$, MNCR); ditto, 9–16.viii.2013(5° , MNCR); ditto, 16–23. viii.2013 (3 \circlearrowleft , 3 \circlearrowleft , MNCR); ditto, 30.viii.-6.ix.2013 (1 \circlearrowleft , MNCR); ditto, 6–13.ix.2013 (9 \circlearrowleft , 13 \updownarrow , MNCR); ditto, 11–18.x.2013 (1 \bigcirc , MNCR); ditto, 21–29.ix.2013 (2 \bigcirc , MNCR); Moravia, Zurquí de Moravia, tower path, 1600 m, mercury light trap, 23.ii.2013 (26, MNCR); Zurquí, 10°2.8′N 84°0.4′W, 19.ii.2003, W.N. Mathis (1♂, USNM); Zurquí De Moravia, 1600m, iii.1981, P. Hanson (23, 12, 12)DEBU); Zurquí De Moravia, 1600m, iv.1991, P. Hanson (2 $^{\circ}$, DEBU); San Antonio de Escazú, 9 $^{\circ}$ 54'15"N 84°7'41"W, creek bed, 1300 m, yellow pans, 4–5.iii.1996, LM (2 \circlearrowleft , DEBU); San Carlos, La Virgen, 9°54'50"N 84°7'51"W, 2° forest, 821 m, sweep, 25.ii.2006, SAM (16, DEBU); 1km S de P. N. Braulio Carrillo, valle ripario, 1500–1600 m, manual, 15.ii.2003, O. Lonsdale (1 δ , MNCR). CUBA: Santiago: Gran Piedra, Met. Radar, DEBU); Pico Turquino, 6000', 16-21.vi.1936, Darlington (13, USNM). DOMINICA: Saint George: Freshwater Lake, 22.ii.1964, D.F. Bray (13, 12, USNM); DOMINICAN REPUBLIC: Independencia, 32km NW La Descubierta, Sabana Real, cloud forest, 1800 m, trail sweep, 26.xi.1991, Masner & Peck (2° , DEBU); Pedernales: Cabo Rojo, Alcoa Road km26, FIT, 17-20. i.1989, SAM & J. Swann (1\(\frac{1}{2}\), DEBU); Cabo Rojo, Alcoa Road km26, pan traps, 17-20.i.1989, SAM & J. Swann (13, 19, DEBU); nr. Cabo Rojo, Las Abejas, cloud forest, sweep, 17.i.1989, SAM (26, DEBU); Las Abejas, cloud forest, 1300 m, sweep, 17.i.1989, J.E. Swann (2♀, DEBU). ECUADOR: Azuay: Tarqui, 2800 m, 7-8.iii.1965, L.E. Peña (1♀, CNC); Chimborazo: Chimborazo Bugna, L. Castillo (1 \circlearrowleft , USNM); ditto, 1400 m (2 \circlearrowleft , 1 \updownarrow , USNM); Manabí: La Palma, viii.1955, L. Castillo (16, USNM); Napo: Baeza, wet montane rainforest, 1500 m, MT, 16-19.v.1987, Coote & Brown (3 \circlearrowleft , 1 \updownarrow , DEBU); Baeza, wet montane rainforest/pasture, 1550 m, MT off stone trail, 15-19.v.1987, L.D. Coote & B.V. Brown, ROM 870010 (1♀, DEBU); 7km S Baeza, 2000 m, carrion trap, 21. ii.1979, H. & A. Howden (12, DEBU); El Chaco, 2000 m, MT, 15–23.ii.1983, LM & M. Sharkey (16, DEBU); 5km N El Chaco, MT and wet net, 15.ii.1983, M.J. Sharkey (2♂, 2♀, DEBU); 10km SW Pto. Napo. Limon Chicta, 1° rainforest, 500 m, MT head, 23–27.v.1987, B. V. Brown & L.D. Coote (1♂, DEBU); SierrAzul Reserve,

14km W Cosanga, 0°40'55"S 77°56' 9"W, tree fall, 2200 m, yellow pans, 10-11.v.2002, SAM & S. Paiero (1 \updownarrow , DEBU); Pichincha: Maquipucuna Biological Reserve, main trail, ca. 1300 m, 27.x.1999, SAM (13, DEBU); Maquipucuna Biological Reserve, 'mirador', tree fall, sweep, 29.x.1999, SAM (16, DEBU); Maquipucuna Biological Reserve, river trail, 1200 m, sweep, 29.x.1999, SAM (1\(\frac{1}{2}\), DEBU); Nanegalito, 7km SE, trout farm 'San José', riverine forest, tree fall, 1500 m, sweep, 27–30. x.1999, SAM (13, DEBU). GUATEMALA: Baja Verapaz: 4.8km E Purulha, 1680 m, exterior FIT, 29.vi.–3.vii.1993, J.S. Ashe & R.W. Brooks (13° , 19° , DEBU); 2 km SPurulha, FIT, 25.v.1991, H. Howden (13, CNC); 7.4km S Purulha, 1650 m, FIT, 2.vii.1993, J.S. Ashe & R.W. Brooks (36, DEBU); 8km S Purulha, FIT, 25.v.1991, H. Howden $(40^\circ, 19^\circ, CNC)$; 8km S Purulha, FIT, 23–25. v.1991, H. Howden (2 %, DEBU); 17km N Salama, Hwy5, 1700 m, FIT, 29.vi.-3.vii.1993, J.S. Ashe & R.W. Brooks (16, DEBU); 17km N Salama, Hwy5, 1700 m, FIT, 25. vi.-3.vii.1993, J.S. Ashe & R.W. Brooks (20, 32, DEBU); El Progreso: Cerro Pinalón, 15°5'1"N 89°56'42"W, tree fall gap edge in cloud forest, 2575 m, MT, 29.iv.-5.v.2009 (1♀, DEBU); Quetzaltenango: 8km SE Zunil, 2500 m, exterior FIT, 19-21.vi.1993, J.S. Ashe & R.W. Brooks (16, DEBU); San Marcos: San Lorenzo 5 mi. N, FIT, 4 18.vii.1986, J.M. Campbell (13, DEBU); Zacapa: 3.5 km SE La Unión, 1500 m, FIT, 23-25.vi.1993, J.S. Ashe & R.W. Brooks (2♀, DEBU); San Lorenzo, pans and FIT traps, 12–17.xi.1986, M.J. Sharkey (1♀, DEBU) San Lorenzo, pine forest, MT, 7–18.vii.1986, L. LeSage (1♀, CNC). GUYANA: Mazaruni-Potaro: Takutu Mountains, 6°15'N 58°55'W, montane rainforest near logging area, window trap, 8-10.xii.1983, Earthwatch Research Expedition, P.D. Perkins & W.E. Steiner (12, USNM). HONDURAS: El Paraíso: Cerro Montserrat, 1800 m, MT, 24.v.1994, H. Howden (1♀, DEBU); Olancho: La Muralla National Park, 15°5'49"N 86°44'17"W, 150 m, FIT, 4-7.vii.2002, Smith & Ocampo (3 \circlearrowleft , 3 \circlearrowleft , DEBU); La Muralla, FIT, 12.i.1995, R. Cordiro (1♂, DEBU). JAMAICA: Portland: Hollywell, 18°5.5'N 76°43.6'W, 1170 m, 27.iv.2000, W.N.Mathis (1♂, 1♀, USNM); Saint Andrews: Hardwar Gap, 4000', 10.vii.1966, Howden & Becker $(10^\circ, 10^\circ, CNC)$; ditto, 13.vii.1966 $(10^\circ, CNC)$; Hardwar Gap, 10.iii.1970, Wirth & Farr $(1 \circlearrowleft, 1 \updownarrow, USNM)$; ditto, stream margin (13, USNM); Saint Thomas: below Port Gap Co. Surrey, 4500', dung trap, 1–5.viii.1974, S. Peck (1♀, DEBU). MEXICO: Chiapas: Custepac, 2 km SE, 15°43'15"N, 92°57'2"W, 1510 m, mesophil forest, MT, 17.v.2008 (16, DEBU); Lagos de Montebello, Lago Pojoj, 1500 m, FIT, 2-12.vi.1990, B. Gill & H. Howden (1♂, 3♀, DEBU). NICARAGUA: Jinotega: Reserva Natural Cerro Datanlí, El Diablo, 13°6'14"N, 85°52'7"W, cloud forest, 1400 m, ex. sifted leaf litter, 18.v.2011 (13), DEBU). PANAMA: Chiriquí: Hartmann's Finca, 1700 m, 28.vi.–3.vii.1981, B. Gill (1♀, DEBU). PARAGUAY: Caazapá: Hermosa, San Rafael Res., prop. Lopez family, 26°18'29"S 55°45'3"W, 80m, FIT, 1–3.xii.2000, Z.H. Falin (1♀). PERU: Cusco: Cock-of-the-Rock Lodge, NE Paucartambo, 13°3'18"S, 71°32'42"W, 1120 m, FIT, 4–9. xi.2007, D. Brzoska (21 $\stackrel{?}{\circ}$, 32 $\stackrel{?}{\circ}$, DEBU); Cock-of-theRock Lodge, 13°3'21"S 71°32'46"W, 1380 m, MT, 18-20.x.2006, J. Skevington ($1 \circlearrowleft$, $2 \updownarrow$, DEBU); Paucartambo, Puente San Pedro (ca. 50 km NW Pilocopata), 1600 m, 3.ix.1988, Mathis (12 \circlearrowleft , 1 \circlearrowleft , USNM); Junín: Pampa Hermosa lodge, 22km N San Ramón, 10°59'18"S, 71°25'30"W, 1220 m, FIT, 24–27.xi.2007, D. Brzoska (10♂, 4♀, DEBU); Leoncio Prado: Tingo María, ix.1955, Th. Dobzhansky & C. Pavan (1♂, 1♀, USNM); ditto, ii.1956, M. Breuer (2♀, USNM). PUERTO RICO: Ciales: Toro Negro, PVF. Rd.143, km19.9, human dung, 3-4. vii.1977, J.Micheli & R.E. Woodruff ($1 \circlearrowleft$, $2 \circlearrowleft$, DEBU); ditto, km14.3, dung, Woodruff (2♀, DEBU); Río Grande: El Verde, 550m, FIT, Bamboo, 1-3.ii.1989, SAM (4\$\frac{1}{2}\$, 3\,\times, DEBU); El Verde, dung traps, 1–6.ii.1989, SAM (1\,\times, DEBU); El Yunque Trail, sweep along road, 4.ii.1989, SAM (3♀, DEBU); . TRINIDAD AND TOBAGO: Eastern Tobago: Charlotteville, Man-o-war Bay cottages, littoral rainforest, UV light, 26–31.vi.1993, S. & J. Peck (1♀, DEBU); 93-50, 10km NE Roxborough, Gilpin Trail, montane rainforest, 400-500 m, FIT, 26-31.vi.1993, S. & J. Peck (10, DEBU). VENEZUELA: Amazonas: Cerro Yutaje Station, 5°45'35"N 66°08'63"W, 750 m, yellow pans, 19.ii.1995, J. Clavijo (2Å, DEBU); Aragua: Colonia Tovar, bamboo forest, 2400 m, sweep, 10.iii.1995, SAM (5♂, 1♀, DEBU); Colonia Tovar, steep forest trail, 2300 m, sweep, 10.iii.1995, SAM (12, DEBU); Parque Nac. Henri Pittier Hwy. Maracay-Choroní, km19, creek, 1330 m, s.s, 15.iv.1994, LM (2♂, 2♀, DEBU); Henri Pitter National Park, 12km W Maracay on Choroní Rd, 1290 m, 7.iii.1995, SAM (2♂, 2♀, DEBU); Henri Pitter National Park, 9km N Maracay, Choroní Rd, along creek, 1000 m, sweep, 7.iii.1995, SAM (12, DEBU); Henri Pitter National Park La Toma Trail, 1100 m, 17.iv.1994, LM (23, DEBU); Henri Pitter National Park, Rancho Grande, MT/intercept, 12–30.xii.1987, M. Sanborne (2 \Diamond , 3 \Diamond , DEBU); Maracay, Rancho Grande Biological Station, wet area, 1200 m, pan traps, 25–28.ii.1995, SAM (1♂, 1♀, DEBU); Maracay, Rancho Grande Biological Station, Portachuelo Pass, 1400 m, 27.ii.1995, SAM ($1 \stackrel{?}{\circ}$, $1 \stackrel{?}{\circ}$, DEBU); Henri Pitter National Park, trails at Rancho Grande, ca. 2000 m, MT, 20–21.i.1996, J. & A. Skevington (1♂, 1♀, DEBU); Henri Pitter National Park, Rancho Grande, 1500 m, 3.ix.1992, LM (16, DEBU); Rancho Grande Biological Station, 10°21'N 67°41'W, 1200 m, FIT, 14.v.1998, Ashe, Brooks & Hanley (3^{\(\sigma\)}, DEBU); Bolivar: Auyán Tepuy, 5°46'7"N 62°31'56"W, 2075 m, MT, 19-25.iv.1994, LM, J. García (1♀, CNC); Mérida: Tabay, La Mucuy, Truchicola trail, cloud forest, 2300 m, FIT, 17.vi.-3.vii.1989, S. & J. Peck (26, DEBU); Táchira: Pregonero, Presa Las Cuevas, rainforest, 650 m, MT, 9-31.vii.1989, S. & J. Peck (13, 1♀, DEBU); Trujillo: 10km E Boconó, "Laguna de Lucerdo" [= Laguna de los Cedros], slash/compost, 1760 m, 3.iii.1995, SAM (5 \circlearrowleft , 2 \updownarrow , DEBU); Guaramacal NP, 14km NE Boconó, 2000 m, 25.viii.−1.ix.1992, LM (6♂, 4♀, DEBU); Guaramacal NP, 2000-3000 m, car net, 26.viii.–1.ix.1992, LM (3♀, DEBU).

Comments: Pseudopomyza nigrimana is externally variable in head and leg colouration, but the uniform genitalic structures support the treatment of all colour forms as one species. Since we do not have complete

transects across the entire range, it is hard to assess the intergrading of colour forms. However, if we compare the Jamaican, Cuban and Dominican Republic specimens to the mainland and Puerto Rican specimens, we see smaller face markings on Jamaican specimens and paler gena markings on Cuban and Dominican Republic specimens, suggesting intermediate states between the widespread form and the Puerto Rican colour form. We have not seen northern Brazil specimens, but we expect them to exhibit the typical form, which was described from southern Brazil and northern Argentina (Misiones). Venezuelan specimens are sometimes paler brown on the second basal quarter of the fore femur, suggesting some intergrading of colour forms.

Pseudopomyza (Pseudopomyza) parabinaevia Yau and Marshall sp. nov.

(Figs. 49p, 50n, 51v, 90.1–4, 91.1–3, 92.1–4)

Diagnosis

Frons yellow at anterior margin and with medial yellow stripe. Face mostly yellow, with brown marking on outer face and most of inner face, dorsal half of sub-antennal depression with dark brown marking. Anterior ½ to 3/4 of gena yellow, remainder dark brown. Anepisternum pruinose. Fore tarsus brown; mid femur yellow. Anterolateral arms of male S6 long, apices dilated. Surstylus long with 2–3 prominent teeth on apical inner margin; inner lamella not particularly narrow, width 0.5× width of surstylus. Subepandrial sclerite with slight protuberance medial to anterior seta. Postgonite spatulate. Basal distiphallus straight, tapered towards apex. Female S7 with weak pair of pouch-like protuberances. Spermathecae elongated, striate on distal 2/3 of length.

Description

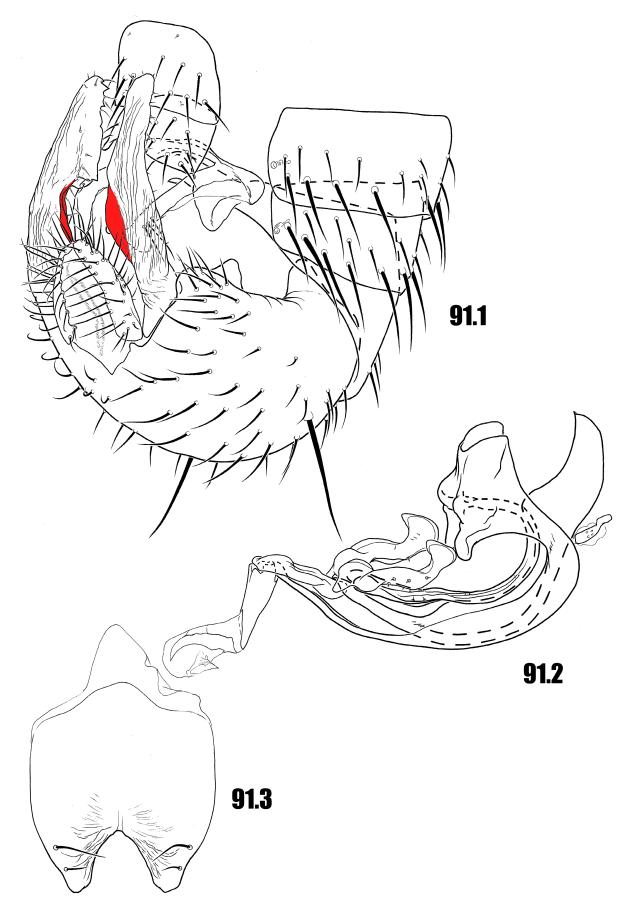
Body length 1.9 mm (male), 2.3–2.5 mm (females). External characters similar to *P. binaevia* except scutum uniformly pruinose, anepisternum pruinose, katepisternum posteroventrally pruinose.

Male terminalia (Figs. 91.1–3): Anterolateral arms of S6 long, apices dilated, with 3 preapical lateral setae; midsection of sternite with minimal curvature. Ventrolateral corners of S7+8 prominent and triangular. Epandrium uniformly pruinose except circular patch around long dorsal setae; wider at posterior half, width $0.85 \times 10.85 \times 10.8$

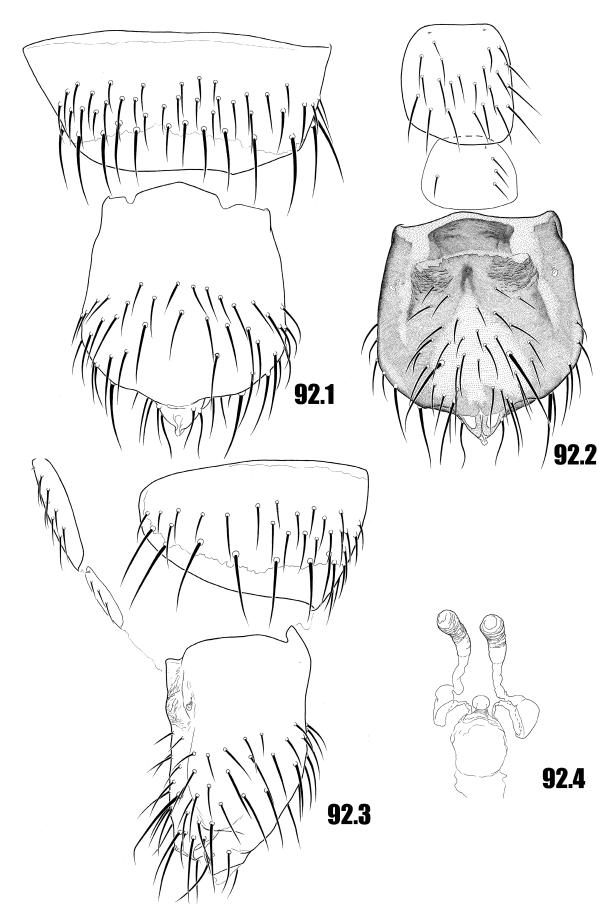
Phallapodeme laterally compressed towards apex; length beyond phallic plate 0.5× sheathed length; phallic guide width 3.2× height. Postgonite spatulate. Basal



FIGURES 90.1–4: *Pseudopomyza (Pseudopomyza) parabinaevia* **sp. nov.**, male habitus (Venezuela). 90.1, left lateral; 90.2, dorsal; 90.3, head; 90.4, terminalia, ventral.



FIGURES 91.1–3: *Pseudopomyza (Pseudopomyza) parabinaevia* **sp. nov.**, male terminalia (Venezuela). 91.1, terminalia left ventrolateral (inner lamella of surstylus marked red); 91.2, phallus and associated structures left lateral; 91.3, subepandrial sclerite anterior surface.



FIGURES 92.1–4: *Pseudopomyza (Pseudopomyza) parabinaevia* **sp. nov.**, female terminalia (Venezuela). 92.1, terminalia dorsal; 92.2, terminalia ventral; 92.3, terminalia left lateral; 92.4, spermathecae and associated structures ventral.

distiphallus straight, tapered towards apex, length 2.9× width; distal distiphallus with V-shaped sclerite lining surface of membranous portion, arms of V-shape joined by weaker sheet of sclerite, length 0.8× length of basal distiphallus.

Female terminalia: S6 weakly sclerotized, three left and one right setae on dissected specimen. S7 with weak pair of pouch-like protuberances. Spermathecae elongated, striate on distal 2/3 of length.

Etymology: The name refers to the similarity between this species and *P. binaevia*.

Type specimens: Holotype: \circ : VENEZUELA: Aragua: Maracay, Rancho Grande Biological Station, Portachuelo Pass, 1400 m, 27.ii.1996, SAM (MIZA).

Paratypes: **BOLIVIA:** La Paz: Cumbre Alto Beni, vicinity of Caranavi, 15°40'19"S 67°29'35"W, 1685 m, MT, 15–21.iv.2004, S.D. Gaimari & M. Hauser (1♀, CSCA). **PERU:** Cusco: Cock-of-the-Rock Lodge, NE Paucartambo, 13°3'18"S 71°32'42"W, 1120 m, FIT, 4–9.xi.2007, D. Brzoska (1♀, MUSM). **VENEZUELA:** Aragua: Henri Pittier National Park, La Toma Trail, Rancho Grande, yellow pan traps, 9–10.iv.1994, LM (1♀, DEBU).

Pseudopomyza (Pseudopomyza) proboscis Yau and Marshall sp. nov.

(Figs. 49d, 50c, 51b, 93.1-4, 94.1-3, 95.1-4)

Diagnosis

Frons dark brown. Face and gena brown. Fore tarsus dark brown; mid femur brown except yellow apex. Male S6 with long, stout and slightly curved ventromedial lobe instead of lateral arms. Surstylus hatchet-shaped; inner lamella of surstylus sickle-shaped. Subepandrial sclerite with slight rise medial to anterior seta. Postgonite rod-like with gently tapered apex, and base drawn out into spike. Basal distiphallus ring-like. Female S7 flat ventrally. Spermathecae cylindrical to bulbous, smooth without striation.

Description

Body length 1.6-1.8 mm (males), 1.6 mm (female).

Head: Frons dark brown, fronto-orbital plates and ocellar triangle paler. Three subequal fronto-orbital setae. Face generally brown, inner face darkest, dorsal half of sub-antennal depression and facial ridge sometimes yellowish-brown. Gena entirely brown; glossy on anterior half or less, pruinose on posterior half through to occiput and postgena; genal height $0.4 \times$ eye height.

Thorax: Scutum dark brown, uniformly pruinose except for glossy band posterior to prescutellar acrostichal setae, band no wider than scutellum. Presutural acrostichal setae small but differentiated, less than half as long as postsutural and prescutellar acrostichal setae. Presutural supra-alar, anterior intra-alar and postsutural supra-alar setae consecutively shorter, anterior intra-alar half as long as postalar seta. Anepisternum glossy. Katepisternum ventrally pruinose.

Legs: Fore femur dark brown, at most with some yellow at base; tibia and tarsus dark brown. Basal 3/4 of mid femur brown, distal ½ yellow; tibia and tarsus yellow. Hind femur dark brown; hind tibia with basal ½ yellow or yellowish-brown, distal half brown; hind tarsus yellow.

Male terminalia (Figs. 94.1–3): S6 lacking lateral arms but instead with long, stout and slightly curved ventromedial lobe. Epandrium pruinose on anteromedial edge and posterior half, remainder glossy; slightly shorter than wide, slightly widened distally. Cercus broad, relatively short. Surstylus hatchet-shaped; inner lamella of surstylus sickle-shaped, inner margins broadly separated medially. Subepandrial sclerite subquadrate with ventral emargination, with slight rise medial to anterior seta; anterior seta only slightly longer than posterior one, both more or less aligned vertically.

Phallapodeme thin, laterally compressed towards apex; length beyond phallic plate $0.6\times$ sheathed length; phallic guide width $2.5\times$ height. Postgonite rod-like with gently tapered apex, and base drawn out into spike. Basal distiphallus ring-like, length at most $0.5\times$ width; distal distiphallus elongate and entirely membranous, length $7.6\times$ basal distiphallus.

Female terminalia: S6 weakly sclerotized, with two pairs of setae. S7 flat ventrally. Spermathecae cylindrical to bulbous, smooth without striation.

Etymology: The name refers to ventromedial lobe of male S6 which resembles an elephant trunk (Latin '*proboscis*': elephant trunk).

Type specimens: Holotype: ♂: **COSTA RICA**: **Limón**: Estrella Valley, Pandora, MT, 19.ii.1984, H. & A. Howden (MNCR).

Paratypes: **BOLIVIA:** La Paz: Cumbre Alto Beni, vicinity of Caranavi, 15°40'19"S 67°29'35"W, 1685 m, MT, 15–21.iv.2004, S.D. Gaimari & M. Hauser (1♀, CSCA). **COSTA RICA:** Alajuela: Volcán Tenorio, N slope nr. Bijagua Biological Station, tree fall, 700 m, pan trap, 19.vi.2000, M. Buck & SAM (1♂, DEBU). **GUATEMALA:** Izabal: Las Escobas, 300 m, at light, 16.xi.1986, M.J. Sharkey (1♀, DEBU).

Comments: *Pseudopomyza proboscis* has relatively short setae on the scutum (10–20% shorter than in other species with the exception of *P. albimana*). This species is one of the few species of the *P. nigrimana*-group that is only known from elevations below 1000 m.

Pseudopomyza (Pseudopomyza) prolata Yau and Marshall sp. nov.

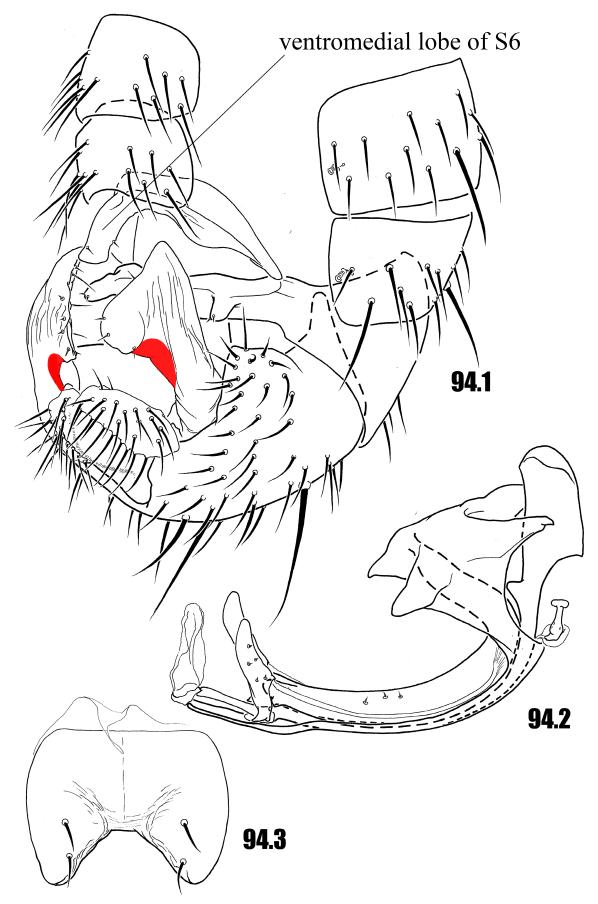
(Figs. 49e, 50d, 51c, 96.1–4, 97.1–3, 98.1–4)

Diagnosis

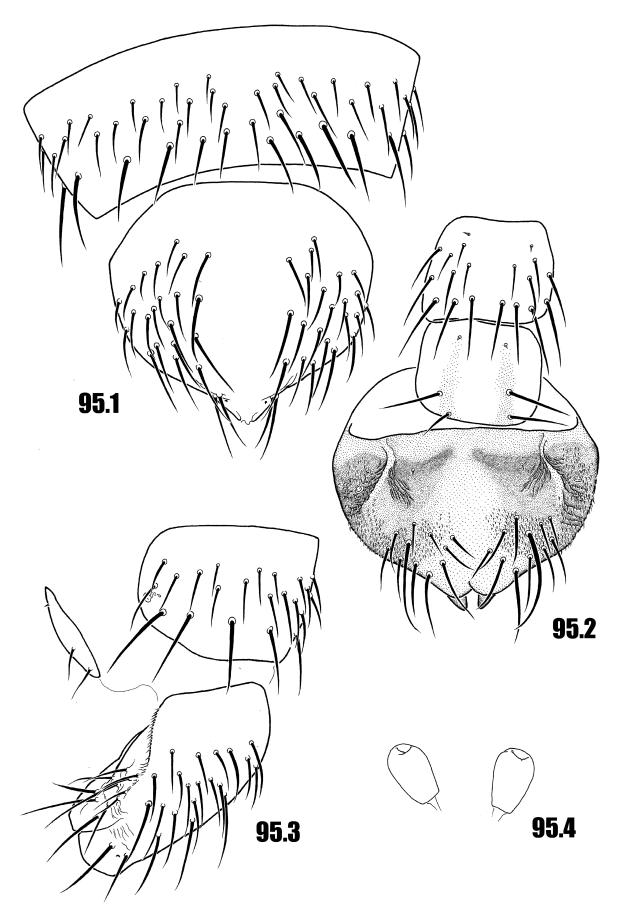
Frons black or dark brown. Face mostly yellow, with dark brown marking on inner face. Gena dark brown, except anterior margin yellow to tan. Fore tarsus dark brown; mid femur yellow. Anterolateral arms of male S6 twisted medially, apical margin parallel to posterior margin of S5; outer corner of each arm expanded. Cerci fused into slender shaft in apical half. Surstylus hatchet-



FIGURES 93.1–4: *Pseudopomyza (Pseudopomyza) proboscis* **sp. nov.**, male habitus (Costa Rica). 93.1, left lateral; 93.2, dorsal; 93.3, head; 93.4, terminalia, ventral.



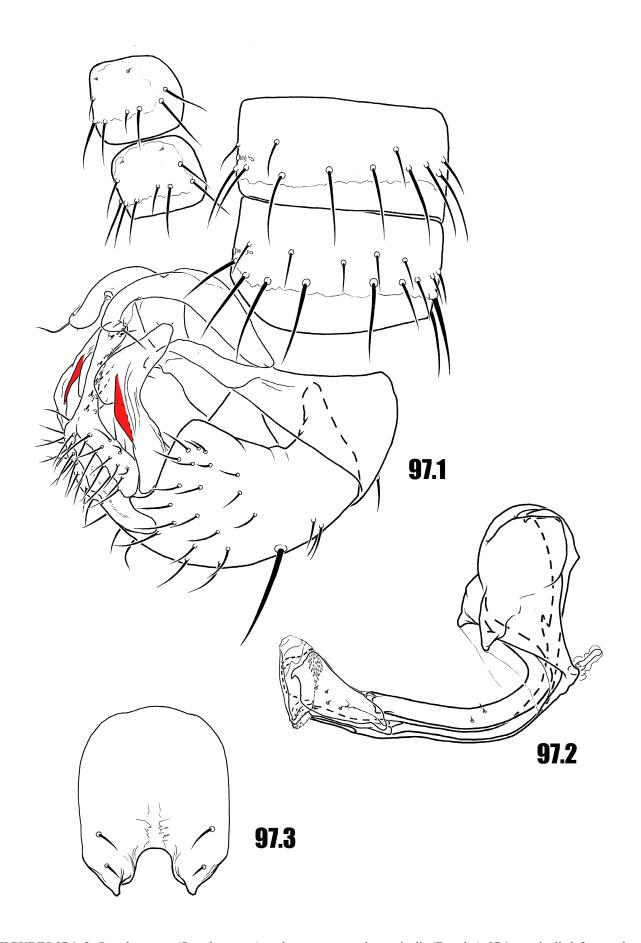
FIGURES 94.1–3: *Pseudopomyza* (*Pseudopomyza*) *proboscis* **sp. nov.**, male terminalia (Costa Rica). 94.1, terminalia left ventrolateral (inner lamella of surstylus marked red); 94.2, phallus and associated structures left lateral; 94.3, subepandrial sclerite anterior surface.



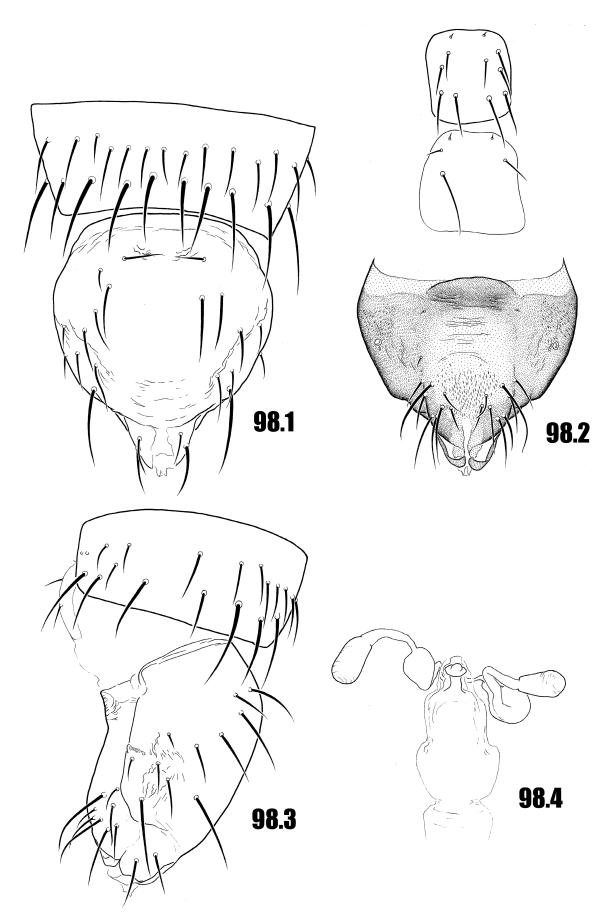
FIGURES 95.1–4: *Pseudopomyza (Pseudopomyza) proboscis* **sp. nov.**, female terminalia (Guatemala). 95.1, terminalia dorsal; 95.2, terminalia ventral; 95.3, terminalia left lateral; 95.4, spermathecae ventral.



FIGURES 96.1–4: *Pseudopomyza (Pseudopomyza) prolata* **sp. nov.**, male habitus (Ecuador). 96.1, left lateral; 96.2, dorsal; 96.3, head; 96.4, terminalia, ventral.



FIGURES 97.1–3: *Pseudopomyza (Pseudopomyza) prolata* **sp. nov.**, male terminalia (Ecuador). 97.1, terminalia left ventrolateral (inner lamella of surstylus marked red); 97.2, phallus and associated structures left lateral; 97.3, subepandrial sclerite anterior surface.



FIGURES 98.1–4: *Pseudopomyza (Pseudopomyza) prolata* **sp. nov.**, female terminalia (Ecuador). 98.1, terminalia dorsal; 98.2, terminalia ventral; 98.3, terminalia left lateral; 98.4, spermathecae and associated structures ventral.

shaped; inner lamella overlapping expanded distal half of surstylus at base. Subepandrial sclerite relatively flat. Postgonite wedge-shaped with preapical medially directed hook. Basal distiphallus ring-like. Female S7 with basal, well sclerotized strip. Spermathecae bulbous, generally smooth.

Description

Body length 1.8–2.1 mm (males), 1.9–2.5 mm (females).

Head: Frons black or dark brown, fronto-orbital plates and ocellar triangle paler. Three subequal fronto-orbital setae. Face mostly yellow, each side with dark brown marking on inner face. Gena generally dark brown, except anterior margin yellow to tan, yellow or tan colour sometimes extend further to posterior half of gena; gena glossy, pruinose at junction of gena, postgena and lower occiput; genal height $0.3 \times$ eye height.

Thorax: Scutum dark brown, glossy and corrugated except for triangular pruinose area anterior to prescutellar pair of acrostichal setae. Presutural acrostichal setae short but differentiated, $0.3\times$ postsutural acrostichal setae and subequal to prescutellar acrostichals. Presutural supraalar seta $1.25\times$ postsutural supra-alar and anterior intraalar setae, and $0.67\times$ postalar seta. Anepisternum and katepisternum glossy.

Legs: Fore femur yellow on basal half, distal half dark brown; tibia and tarsus dark brown. Mid leg yellow but tarsomere 5 brownish. Hind leg with basal half or more yellow, distal half dark brown; tibia and tarsus yellow, tarsomere 5 brownish.

Male terminalia (Figs. 97.1–3): Anterolateral arms of S6 twisted medially, apical margin parallel to posterior margin of S5; outer corner of each arm expanded and tipped with seta; weak connecting sclerite present between arms at distal 1/3; mid-section of sternite curved anteriorly. Ventrolateral corners of S7+8 protruding and connected by ledge. Epandrium entirely glossy; slightly wider at mid-length, width 0.56× length. Cerci almost as long as surstyli, fused into slender shaft in apical half, shaft with 2 rows of setulae along length of ventral surface. Surstylus hatchet-shaped; inner lamella overlapping expanded distal half of surstylus at base. Subepandrial sclerite quadrate to rounded anteriorly, surface relatively flat; anterior seta only slightly longer than posterior seta and slightly displaced laterally.

Phallapodeme laterally compressed towards apex; length beyond phallic plate 0.47× sheathed length, and almost entirely shielded by hypandrium; phallic guide width 1.5×height. Postgonite wedge-shaped with preapical medially directed hook. Basal distiphallus ring-like, length at most 0.3× width; distal distiphallus membranous, with long slender sclerite on posterior edge and weakly sclerotized undulate preapical ring; membranous portion spiculate in front of ring-shaped sclerite; length of distal distiphallus 11× length of basal distiphallus.

Female terminalia: S6 weakly sclerotized, with at least one pair of setae. S7 with basal, well sclerotized strip. Spermathecae bulbous, generally smooth.

Etymology: The name refers to the fused and elongated male cerci (Latin '*prolatus*': extended, elongated).

Type specimens: Holotype: ♂: **ECUADOR**: **Napo:** SierrAzul Reserve, 14km W Cosanga, 0°40'55"S 77°56' 9"W, tree fall, 2200 m, yellow pans, 10–11.v.2002, SAM & S. Paiero, debu00194772 (QCAZ).

Paratypes: **ECUADOR**: **Napo**: 5km N El Chaco, MT and wet net, 15.ii.1983, M.J. Sharkey ($1 \circlearrowleft$, DEBU); Same collection data as holotype ($4 \circlearrowleft$, DEBU, QCAZ).

Comments: *Pseudopomyza prolata* can be easily identified by its cerci, which are fused into a slender shaft in the apical half. The coloration of *P. prolata* resembles the typical colours of *P. nigrimana*.

Pseudopomyza (Pseudopomyza) simulatrix Yau and Marshall sp. nov.

(Figs. 49f, 50h, 99.1–3, 100.1–3)

Diagnosis

Frons, face and gena brown. Fore tarsus bicoloured; mid femur yellow. Apex of anterolateral arms of male S6 posteriorly curved. Surstylus paddle-shaped, inner lamella narrow. Subepandrial sclerite relatively flat. Postgonite spatulate. Distal opening of basal distiphallus wide, distoventral area weakly sclerotized.

Description (male only)

Body length 1.9 mm. External characters similar to *P. albimana* (postsutural acrostichals, most intra-alar and supra-alar setae; forelegs absent on specimen).

Male terminalia (Figs. 100.1–3): Apex of anterolateral arms of S6 posteriorly curved; mid-section of sternite anteriorly curved. Ventrolateral corners of S7+8 nublike. Epandrium almost entirely glossy except pruinose at extreme posterolateral corners adjacent to lateral margin; widest at mid-length, width 0.8× length. Cerci slightly wider at mid-length and tapering toward apex. Surstylus paddle-shaped, of uniform width; inner lamella narrow, outwardly bent from surface of surstylus. Subepandrial sclerite trapezoidal with anterior margin shallowly arcuate, surface relatively flat; anterior seta distinctly longer than posterior seta and placed more laterally.

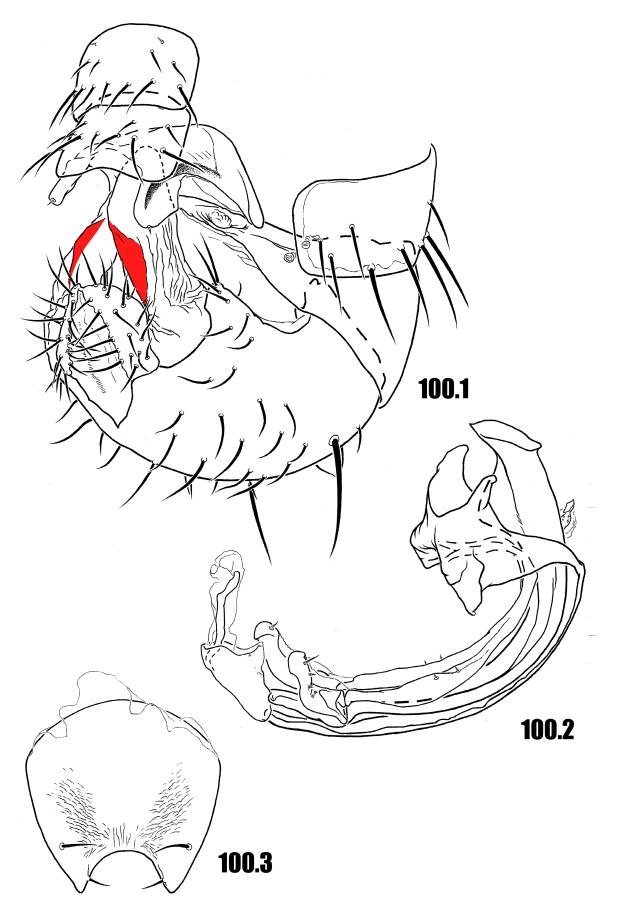
Phallapodeme laterally compressed towards apex; length beyond phallic plate $0.5\times$ sheathed length; phallic guide width $2.5\times$ height. Postgonite spatulate. Basal distiphallus length $1.5\times$ width, distal opening wide, distoventral area weakly sclerotized; distal distiphallus membranous, with thin, undulate medial sclerite, length subequal to basal distiphallus.

Etymology: The name refers to its external similarity to *P. albimana* (Latin '*simulatrix*': imitator).

Type specimen: Holotype: ♂: **BOLIVIA**: **La Paz:** near Mapiri Arroyo Tuhiri, 15.2805, 68.25°W, 500 m, MT (upper), 9–12.iv.2004, B. Brown (CSCA).



FIGURES 99.1–3: *Pseudopomyza (Pseudopomyza) simulatrix* **sp. nov.**, male habitus (Ecuador). 99.1, left lateral; 99.2, dorsal; 99.3, head.



FIGURES 100.1–3: *Pseudopomyza (Pseudopomyza) simulatrix* **sp. nov.**, male terminalia (Ecuador). 100.1, terminalia left ventrolateral (inner lamella of surstylus marked red); 100.2, phallus and associated structures left lateral; 100.3, subepandrial sclerite anterior surface.

Genus Pseudopomyzella Hennig

(Figs. 101.1–4, 102.1–6, 103.1–3)

Pseudopomyzella Hennig, 1969: 594 (Figs. 5–6, 9, 11, 20, 22). Type species Pseudopomyzella flava Hennig, 1969 (Monotypy).
Hennig, 1969: 590 (keyed), 594 (diagnosis); Krivosheina, 1979: 186 (phylogenetic notes), 187 (keyed); Prado, 1984: 1 (Neotropical catalog); Buck & McAlpine, 2010: 824 (keyed).

Diagnosis

With 4 fronto-orbital setae. Carina with 2 rows of minute setulae. Subvibrissa absent. Arista pubescent. With 6–7 dorsocentral setae, intra-alar position with irregularly positioned small setae, 1+2 supra-alar setae, 3 scapular setae. Scutellum with discal setae and 3 marginal setae, apical pair laterally flattened in males but not females. Katepisternum with 1 long seta at posterior margin of plate. Subcosta distally merged with R₁. Crossvein bmm absent. S6 with inverted V-shaped sclerotization. S7+8 asymmetrical but clos-ringed, with 2 pairs of outstanding setae. Epandrium ventrally with a small infolded tab. Surstylus and cercus fused, cercus weakly differentiated. Subepandrial sclerite with 7 setae. Hypandrium without ventral bridge. Pregonites arising from sides of hypandrium. Female with 1+2 spermathecae.

Monotypic

Pseudopomyzella flava Hennig

Description

Length 2.5–3.2 mm (males), 2.5–3.5 mm (females). Small, compact flies. General colour yellow to orange with darker brown markings.

Head: Fronto-orbital plate yellow, frontal vitta orange with a pair of brown stripes at the bases of interfrontal setae and continuing through to the otherwise yellow vertex, ocellar triangle dark brown. With 4 reclinate to lateroclinate fronto-orbital setae, posterior 3 setae gradually increase in length but do not differ too much in length, 1st setae more noticeably shorter and weaker. Areas of frontal vitta lateral and ventral to interfrontal setae with uniformly scattered medioclinate black setulae; interfrontal setae only slightly longer than black setulae on frontal vitta; area medial to interfronals pruinose. Ocellar, inner vertical and outer vertical setae well developed. Postocellar setae cruciate; paravertical seta small, slightly longer than ventral postocular setae. Occiput flat to slightly concave, with some small, weakly sclerotized setulae, 3 longer setae lateral to occipital foramen; supracervical setae cannot be seen. Antennae porrect; arista pubescent, inserted dorsally and subapically, as long as head width. Gena posterior half pruinose, height 0.33× eye height; vibrissa very well developed, subvibrissa absent, with scattered small setulae and a longer seta at posteroventral corner (possibly homologous to setae on postgena of other pseudopomyzid taxa). Face membranous ventromedially,

but sub-antennal plate and outer face plate intact, inner face plate small and weak; carina extends to ventral points of sub-antennal depression, with 2 rows of minute setulae.

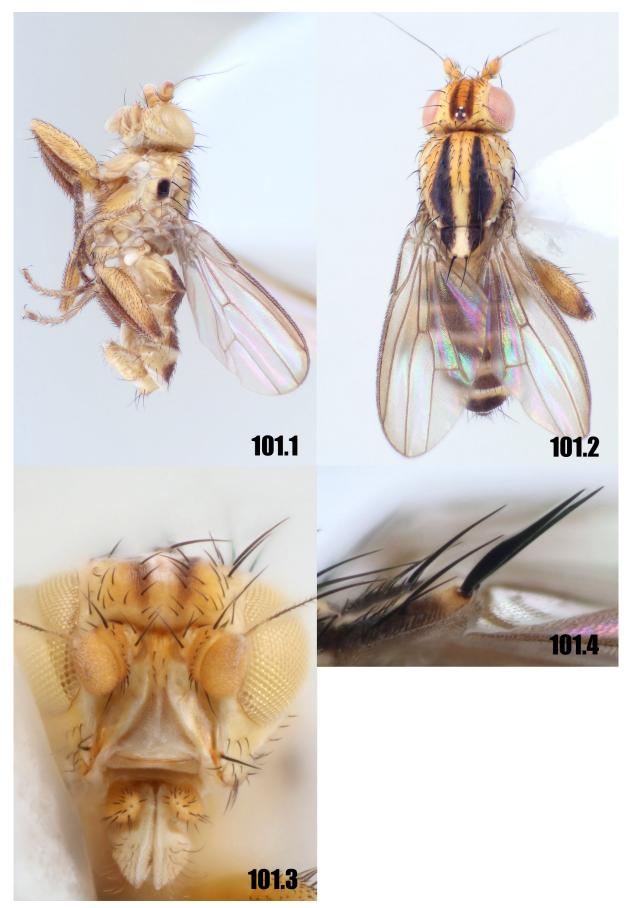
Thorax: Mesonotum orange anteromedially and ivory white laterally and posteriorly towards scutellum, 2 dark brown stripes starting from anterior margin of scutum and extending posteriorly on the course of the dorsocentral setae to sides of scutellum, widening gradually. Pleuron yellow with rectangular dark brown spot on dorsal margin of anepisternum. Four postsutural dorsocentral setae, only posterior-most seta long and strong, 2-3 presutural setae only slightly longer than background setae. Three rows of somewhat irregular setae between dorsocentrals, middle row slightly longer and ends where orange turns to yellow, lateral rows gradually converge and extend till prescutellar pair of setae. Intra-alar position and remaining ventral surface of scutum with irregular rows of small setae, some slightly larger than others; supraalar setae (1+2) as strong as dorsocentrals; intrapostalar seta small; postalar as large as posterior supra-alar seta. Three scapular setae; 1 strong postpronotal seta and multiple small, scattered setae; 2 strong notopleural setae. Scutellum with several scattered small discal setae and 3 pairs of strong marginal setae, apical pair laterally flatten in males but not females. One proepisternal seta. Anepisternum with 1 long posterior seta and a few small setae scattered on posterodorsal surface. Katepisternum with 1 longer seta at posterior margin of plate and smaller setae on anterior surface.

Legs: Mainly yellow, except brown fore tibia (except base) and tarsus, dorsoapical spot of hind femur and distal two thirds of hind tibia. Fore and hind femur more swollen. Fore femur with 1 row of slightly stronger setae on posterodorsal surface; posteroventrally with a row of slightly longer setae of increasing length towards apex, except second last seta non-sequentially longer. Fore tibia with a pair of ventral preapical setae. Base of first tarsomere with 2 stronger setae on posterior edge of dense ventral comb of setae. Male mid femur with a row of anterior setae slightly longer than background setae, absent in female. Mid tibia with a ventroapical seta. Hind femur with a row of stronger anterodorsal setae on distal half. Hind tibia with a pair of slightly stronger dorsal setae and 1 strong ventral seta.

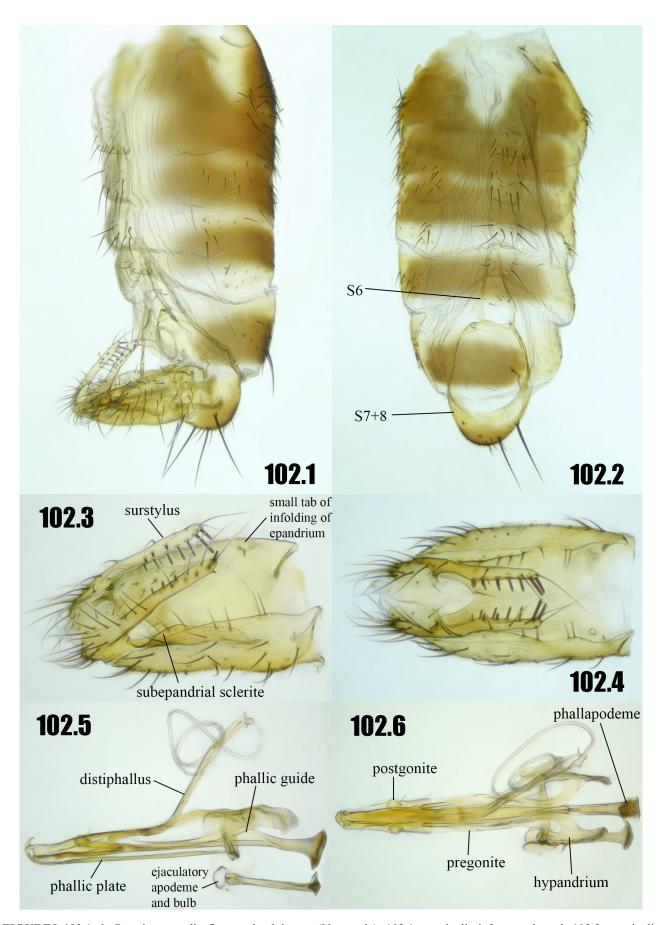
Wing: Costa surpassing $R_{_{4+5}}$ and reaching $M_{_{1}}$. Subcosta incomplete, distally merged with $R_{_{1}}$. Crossvein bm-m absent. Crossvein CuA absent and cell cua open.

Abdominal tergites well developed and sclerotized; with numerous black setae; dorsally brown, except sides of tergites, most of T1, dorsal triangle of T2, anterior margin of T5, 6 (somewhat of T4) yellow. Sclerites 1–5 small and subquadrate; with black setae.

Male terminalia (Figs. 102.1–6): S6 with inverted V-shaped sclerotization on outer margin, anterior half shielded behind S5, posterior half with few setae, arms of "V" widen on posterior half; articulation with S7+8 asymmetrical. S7+8 dorsally brown medially; strongly convex; with 2 pairs of outstanding setae, anterior pair only slightly shorter than posterior pair; ventral arm of S7 anteriorly sclerotized with weak lamella extending



FIGURES 101.1–4: *Pseudopomyzella flava* male habitus (Venezuela). 101.1, left lateral; 101.2, dorsal; 101.3, head; 101.4, scutellum left lateral.



FIGURES 102.1–6: *Pseudopomyzella flava* male abdomen (Venezuela). 102.1, terminalia left ventrolateral; 102.2, terminalia ventral; 102.3, epandrium ventral; 102.5, phallus and associated structures left lateral; 102.6, phallus and associated structures ventral.



FIGURES 103.1–3: *Pseudopomyzella flava* female abdomen (Venezuela). 103.1, terminalia dorsal; 103.2, terminalia ventral; 103.3, 103.4, spermathecae and associated structures.

posteriorly, and a small sclerotized lobe presumably from S8; ring asymmetrical but closed; left side of S7+8 with cleft indicating boundaries of S7 and S8. Epandrium yellow, with numerous black setae, and a pair of outstanding setae; uniform in width until rounding towards apex at distal quarter; ventrally with a small tab of infolding at anterior 1/3 bearing 3 setae. Surstylus and cercus fused, cercus almost indifferentiable, weakly sclerotized towards medial margin, with only a few relatively weak and widely spaced setae; surstylus hemispherical at base with long medioclinate setae, distally elongate with thick blunt setae on medial surface and long setae on ventral surface. Subepandrial sclerite broad and sheet-like, relatively flat, protruding further than ventral margins of epandrium, lateral margins with 7 setae. Hypandrium medially separated without ventral bridge, anterolateral corners flat and medially bending, posterolateral corners rounded; dorsal bridge short, phallic plate well sclerotized, straight and flat, apex surpassed articulating point. Pregonites arising from sides of hypandrium, gently bowed laterally and slightly arched ventrally, arched section flattened with 2 sensory setulae, entire length except apices widely separated from phallapodeme. Apex of postgonite rounded with serrate edge and 1 long setulae. Phallapodeme straight; length anterior to dorsal bridge of hypandrium 1/2 of remaining length; triangular remnant of phallic guide relatively large compared to other pseudopomyzid taxa. Distiphallus with slightly more sclerotized band before strong bend at mid-length; apical section forked, apex of right fork with short perpendicular lobe, left fork with dilated small bulb before continuing as a fine coiled duct. Ejaculatory apodeme long and straight with uniform width except flared apex, ejaculatory bulb simple.

Female terminalia: Sternites progressively smaller posteriorly, S6 slightly less sclerotized than S2–5, setose with longer marginal setae. T7 with medial brown stripe starting at anterior 1/6 and continue until posterior margin of T7; S7 uniformly yellow except posterior tip; S7 with anteromedial T-shaped sclerotization. Spermathecae (1+2) small and weakly sclerotized; paired spermathecae with one on significantly shorter fork of spermathecal duct, spermatheca frustoconical; remaining spermathecae bulbous.

Type specimens: Holotype (not examined): ♂: **PERU: Madre de Dios:** Avispas, 400 m, 10–20.ix.1962, L. Peña (CNC).

Paratype: Same collection data as holotype $(2 \circlearrowleft, 4 \updownarrow, CNC)$ (3 not examined); **ECUADOR: Orellana:** Coca on Río Napo, v.1965 ($1 \updownarrow, AMNH$) (not examined).

Other material examined: BOLIVIA: La Paz: Heath River Wildlife Centre, treefall, yellow pans, 5–9.v.2007, Paiero & Kits (1\$\,\text{p}\), DEBU); ditto, ~21 km SSW Puerto Heath, 12°40'S 68°42'W (1\$\,\text{d}\), 1\$\,\text{p}\, DEBU); ECUADOR: Napo: Jatun Sacha Res., 6 km E Misahuallí, 1°4'S 77°37'W, 450 m, compost, yellow pans, 1–2.v.2002, M. Buck (1\$\,\text{p}\), DEBU); GUYANA: Potaro-Siparuni: Mount Wokomung, 5°7'43"N 59°48'40"W, 736 m, 1° forest, MT, 21–26.x.2004, B. Hubley (1\$\,\text{d}\), DEBU); PERU: Loreto: Campamento San Jacinto, 175–215 m, FIT, 5.vii.1993, R. Leschen (1\$\,\text{d}\), DEBU); Madre de Dios: Amazonas Lodge, N of Atalaya, 12°52'12"N 71°22'36"W,

480 m, FIT, 10–13.xi.2007, D. Brzoska (2♀, DEBU); **VENEZUELA: Táchira:** Pregonero, Presa Las Cuevas, 650 m, rainforest, MT, 9–31.vii.1989, S. & J. Peck (3♂, 4♀, DEBU).

Genus Tenuia Malloch

Tenuia Malloch, 1926: 493, (in Geomyzidae, now Opomyzidae Fallén). Type species: *Tenuia nigripes* Malloch, 1926 (original designation).

Steyskal, 1970: 871 (diagnosis, classification), 873 (key to distinguish *Tenuia* from *Latheticomyia*); Vockeroth, 1977:
7 (Oriental catalog); Krivosheina, 1979: 186 (diagnosis, phylogenetic notes), 187 (keyed); Shatalkin, 1994: 143 (diagnosis, key to *Tenuia*, *Polypathomyia* and *Pseudopomyza atrimana*, illustr.); Krivosheina, 1999: 501 (keyed).

The genus includes two species, *T. nigripes* Malloch from the Oriental region (Philippines) (Type female in USNM) and *T. smirnovi* Shatalkin from the Palaearctic region (northern part of India and Russia) (Type male in ZMUM). Little is known about the biology of *Tenuia* species but Yatoo *et al.* (2022) collected specimens of *T. smirnovi* in India from willow tree trunks with sap exuding from cracks and from rotten fig fruits. Yatoo *et al.* (2022) reported male-male competition, male territoriality involving aggression against other insects, and courtship behaviour. Males were seen to approach females raising both wings, tapping, lunging and head-butting. Morphological characters suggest that *Tenuia* is closely related to the New World genus *Latheticomyia*.

Diagnosis

With 3 fronto-orbital setae. Carina with 2 rows of minute setulae. Subvibrissa absent. Arista weakly pubescent. With 1+4 dorsocentral setae, anterior intra-alar, 1+1 supra-alar, 3-4 scapular setae. Scutellum with discal setulae and 3 marginal setae. Katepisternum with 2 setae. Second costal sector of wing with spines. Subcosta distally merged with R₁. Crossvein bm-m present. S6 symmetrical, modified posteriorly, area anterior to arcuate sclerotization very weak. S7+8 asymmetrical but close-ringed. Base of cercus articulating only with surstylus. Subepandrial sclerite with multiple setae on apices of prominent lobe(s). Hypandrium medially separated, but each side with tusklike extension on inner surface. Pregonites arising from sides of hypandrium and short. Pregonite ending position and postgonite starting position within hypandrium hugging boundaries.

Description

This description relies on Malloch (1926), Shatalkin (1994), Steyakal (1970) and Yatoo *et al.* (2022).

Length 3.4–4.3mm. Slender flies with elongated body and relatively long legs. General colour greyish/slivery brown, with variegated ivory white to orange patterns on head, and thorax.

Head: Fronto-orbital plate ivory white to yellow, through to postocular plate and part of gena; frontal vitta colour variable but anterior margin often lighter and ocellar triangle dark; face ivory white to yellow, with or without dark brown patterning; antennae dorsally dark brown to black, ventrally orange to light brown; gena anteriorly ivory white to yellow, posteriorly with variegated white and brown patterning; postgena brown. Length of 3 reclinate fronto-orbital setae increasing consecutively; setulae scattered throughout frons. Frontal vitta longitudinally depressed, more so anteriorly. Ocellar, inner vertical and outer vertical setae well developed, inner vertical of greatest length. Postocellar setae well developed and cruciate; paravertical seta small or absent, if present, length similar to most ventral postocular setae. Postocular plate flat to slightly convex, median occipital sclerite flat to slightly concave, ventral half of occiput with uniformly scattered small setae, ones close to occipital foramen longest, supracervical setae cannot be seen/ absent. Antennae somewhat porrect; 1 large dorsal and ventromedial seta at margin of pedicel in addition to ring of setulae; arista 3/4 head width, weakly pubescent, inserted dorsally and subapically. Vibrissa well developed, no distinguishable subvibrissa from a row of setulae along length of gena. Gena 0.15× eye height. Postgena with 2 strong setae, and uniformly scattered setulae. Face membranous ventromedially and often sunken, subantennal plate and outer face plate present; carina almost indistinct, at most extends to ventral margin of antennal socket, with 2 rows of extremely minute setulae.

Thorax: Uniformly pruinose, brown except parts of notopleuron, upper margins of postpronotal lobe and anepisternum, postalar callus and apical half of scutellum. Mesonotum with 3 hardly discernible stipes along acrostichal and dorsocentral lengths. Five (1+4) pairs of dorsocentral setae, all well developed, posterior most seta longest. Prescutellar acrostichal setae small but differentiable. Anterior intra-alar, supra-alar (1+1) and postalar setae large, intrapostalar seta small. Scutum with 3–4 scapular setae. Postpronotal seta and 2 notopleural setae large. Scutellum with 3 pairs of marginal setae progressively longer basal to distally, several discal setulae medial to basal most setae. One proepisternal seta. Katepisternum with a pair of equal length setae and setulae scattered at base, ventral corner with several setae.

Legs: Uniformly brown, except coxae yellow to brown. Mid and hind tibia with 1 strong ventroapical seta and several weaker apical and preapical setae along distal margin.

Wings: Costa slightly surpassing R_{4+5} and weakening before reaching M_1 ; second costal sector with spines. Subcosta incomplete, distally merged with R_1 . Crossvein bm-m present; CuA present and cell cua closed.

Abdominal tergites uniformly brown except anterior margin of T1 ivory white to yellow, well developed and sclerotized, with numerous setae. Sclerites 1–5 elongate, with well-developed setae.

Male terminalia: S6 symmetrical, modified posteriorly, area anterior to arcuate sclerotization very weak (marked by sensory setulae) making sclerotization appear to be on

outer margin of sclerite. S7+8 asymmetrical but closeringed; left side of S7+8 with cleft indicating boundaries of S7 and S8. Epandrium with a pair of outstanding setae. Surstylus elongate, posteriorly directed. Cerci posteriorly directed, multi-lobed, fused at ventral end of anal opening; only articulating with surstyli. Subepandrial sclerite, sheet-like, subquadrate, with prominent lobe(s) and multiple (4 in T. smirnovi) setae at apices of lobes. Hypandrium medially separated but with posteriorly directed tusk-like extensions overlapping each other; dorsal bridge short; phallic plate straight and relatively flat. Pregonites arising from sides of hypandrium, short, not flanking phallapodeme, with 2 long setae. Postgonite larger than pregonite, with one long seta. Phallapodeme relatively straight or with some curvature. Distiphallus apically skewed to the right.

Female terminalia: Sternites progressively shorter from sternite to sternite, S6 well sclerotized, setose with setae at posterolateral corners slightly thicker. S7 uniformly brown and uniformly sclerotized.

Key to species of Tenuia Malloch

Paravertical setae absent, fore coxae yellowish in front.....

 T. nigripes Malloch (Oriental)

Paraverticals present, fore coxae entirely black

T. smirnovi Shatalkin (Palaearctic)

Phylogeny

Phylogeny of Cypselosomatidae s.l.—Morphological data

Analysis

Mesquite version 3.04 (Maddison and Maddison, 2015) was used for constructing the character matrix (Tables 4.1, 4.2, 4.3). For parsimony analysis, the matrix was analyzed using TNT version 1.5 (Goloboff & Catalano, 2016). The dataset was analyzed using New Technology search (using ratchet, tree-drifting, tree-fusing, and sectorial search, random seed = 1, 1000 random addition sequences). Trees were optimized in Winclada (Nixon, 2002) and visually enhanced in Adobe Illustrator CS6 (Adobe, California USA).

Phylogeny of the family Cypselosomatidae s.l. and the families of Nerioidea

List of characters

Multistate characters are treated as unordered.

Head

- 1. Vibrissa: (0) absent; (1) present
- 2. Subvibrissa: (0) absent; (1) present

- 3. Setulae on carina: (0) indistinct or absent; (1) present (Figs. 12.1, 101.3)
- 4. Desclerotization of face: (0) absent; (1) present
- 5. Ptilinal fissure position: (0) not highly arched but close to antennal socket; (1) highly arched and widely separated from antennal sockets
- 6. Interfrontal seta: (0) absent; (1) present
- 7. Fronto-orbital setae: (0) 3 or less; (1) 4
- 8. Ocellar setae: (0) well developed; (1) reduced
- 9. Postocellar seta: (0) divergent or parallel; (1) convergent and or cruciate; (2) absent
- 10. Paravertical seta: (0) absent or undifferentiated; (1) differentiated

Thorax

- 11. Scapular setae: (0) absent; (1) 1 seta; (2) 2 setae; (3) 3 setae (Figs. 9.2, 101.2)
- 12. Postsutural dorsocentral setae: (0) 1–3; (1) 4 or more
- 13. Scutellum chaetotaxy (marginal pairs): (0) 2; (1) 3; (2) 1
- 14. Scutellum chaetotaxy (discal setulae): (0) absent; (1) present
- 15. Prosternum: (0) laterally separated from proepisternum by membrane; (1) laterally fused to proepisternum to form a precoxal bridge
- 16. Katepisternum: (0) without ridge forming shelf on dorsal surface; (1) with ridge forming shelf on dorsal surface (Figs. 2.1, 5.1, 8.1)
- 17. Outstanding katepisternal setae: (0) 1; (1) 2; (2) 3 or more; (3) absent
- 18. Humeral break: (0) absent; (1) present or costa with weakening at h
- 19. Subcostal break: (0) absent; (1) present or costa with weakening at sc
- 20. Subcosta: (0) complete and reaching costa; (1) incomplete but not fused with R₁; (2) incomplete and fused with R₁
- 21. Costal spines: (0) absent; (1) present (Fig. 9.1)
- 22. Length of M_1 between r-m and dm-m compared to length of dm-m: $(0) \ge 2 \times$; $(1) \le 1.7 \times$
- 23. M₄ after crossvein dm-m: (0) present; (1) extend only slightly past dm-m or absent
- 24. CuA+CuP: (0) reach or nearly reach wing margin; (1) not reaching wing margin
- 25. Cells bm and dm: (0) separated by crossvein bm-m;(1) confluent, crossvein bm-m weak, incomplete or absent
- 26. Cell dm posterodistal corners: (0) angulate; (1) rounded (Figs. 2.2, 5.2)
- 27. Ventrobasal seta on femur: (0) absent; (1) present (Figs. 12.4, 101.1)
- 28. Posteroventral row of setae or spines on fore femur: (0) absent; (1) present
- 29. Preapical dorsal setae on tibiae: (0) present; (1) absent

Abdomen

- 30. Male S6: (0) reduced and fused to S7 on the left, often as a sclerotized ventral arm; (1) independent, a curved sclerotization running though middle of sclerite, area posterior to sclerotization may be desclerotized, anterior area may extend ventrally but always with sensory setulae (Figs. 3.1, 10.2, 13.2); (2) independent but highly reduced, atrophied or absent
- 31. Sternite 7 and 8: (0) present; (1) atrophied or absent
- 32. Spiracle 7: (0) present; (1) absent
- 33. Outstanding setae on S7+8: (0) absent; (1) 1 pair; (2) 2 pairs
- 34. Postspiracular sclerites enclosed within S7+8: (0) absent; (1) present
- 35. Outstanding setae on epandrium: (0) absent; (1) 1 pair; (2) 2 pairs
- 36. Surstyli: (0) present; (1) absent or fused with epandrium
- 37. Cerci: (0) enclosing at least half of anal opening; (1) not enclosing anal opening, often present at posterior margin of anal opening
- 38. Subepandrial sclerite: (0) undivided; (1) paired
- 39. Subepandrial sclerite form: (0) variable, mostly sheet-like without protuberance; (1) with protuberance
- 40. Subepandrial sclerite chaetotaxy: (0) absent; (1) 5 or more; (2) 3; (3) 2; (4) 1 seta
- 41. Hypandrium: (0) dorsally not fused; (1) dorsally fused
- 42. Setae on ventral surface of hypandrium-pregonite transition: (0) more than 1 seta; (1) at least 1 strong seta; (2) absent
- 43. Hypandrium ventral bridge: (0) absent (Fig. 102.6); (1) present (Fig. 10.5)
- 44. Hypandrium anterior bridge: (0) independent from transitional surface of phallic guide; (1) fused with transitional surface of phallic guide; (2) reduced to sclerotization on anterolateral corners
- 45. Phallic plate: (0) absent; (1) possible homologous structure that may also be interpreted as the epiphallus;(2) present and attached to base of basiphallus but far from phallus; (3) present, attached to base of basiphallus and close to phallus
- 46. Phallic guide connection with hypandrium: (0) firmly bridging between phallapodeme and hypandrium, smooth transition into hypandrium; (1) articulating or loosely connecting to hypandrium; (2) not connecting to hypandrium
- 47. Phallic guide form: (0) whole, broad, almost forming a funnel like surface; (1) bifurcate; (2) reduced to only a triangular remnant; (4) absent
- 48. Pregonite arising position: (0) side of hypandrium; (1) mid-width of hypandrium
- 49. Pregonite form: (0) variable but usually stout and compact; (1) narrow and elongate; (2) shortened and representing a transitional sclerite becoming the postgonite
- 50. Number of setulae on pregonite: (0) more than 2; (1)
- 51. Position of setulae on pregonite: (0) always on apex,

TABLE 4.1. Character state matrix for genera of Cypselosomatidae, families of Nerioidea and selected outgroup families (Taxa of former Pseudopomyzidae marked with "*").

				Characters			
		1	2	3	4	5	6
Taxon	123456789	0123456789	0123456789	0123456789	0123456789	0123456789	012
Agromyzidae	110010100	0000000101	2000100001	2100001100	300001??00	0120000030	111
Japanagromyza sp.	110010100	0000000101	2000100001	2100001100	300001::00	0120000030	111
Cypselosomatidae	100101000	0110101101	1001111011	1001010000	4121222211	1110101110	11?
Clisa australis	100101000	0110101101	1001111011	1001010000	7121222211	1110101110	11.
Cypselosomatidae	100101000	0110101101	1001111111	1001010000	3121222211	1110101110	111
Cypselosoma sp.	100101000	0110101101	1001111111	1001010000	U1-111	1110101110	
Cypselosomatidae	101100101	1311100111	2110110111	1000?200??	?????????	?????????	?1?
Eopseudopomyza szadziewskii *	101100101	1011100111		1000.200			
Cypselosomatidae	110100001	1301100111	2100110111	1000120000	2121232211	1110111111	111
Heloclusia imperfecta *	110100001	1001100111	2100110111	1000120000		1110111111	
Cypselosomatidae	101100001	1211100111	2000110111	1000100001	2121232202	1111101111	110
Latheticomyia tricolor *	101100001	1211100111	2000110111	1000100001	2121232202	1111101111	110
Cypselosomatidae	101100001	$1\frac{2}{5}01100111$	1100100111	1000110001	2121232211	1110101111	11?
Polypathomyia stackelbergi *		-3					
Cypselosomatidae	110100001	$1201000\frac{0}{1}$ 11	2010110111	1000110000	3121232211	1120111111	111
Pseudopomyza collessi *		1201000111					
Cypselosomatidae	101100101	1311100011	2010110111	$1002\frac{0}{1}10000$	1120232201	0120101111	110
Pseudopomyzella flava *				1002110000			
Cypselosomatidae	101100001	1311100111	2100100111	1000100001	$112\frac{0}{1}232202$	1111001111	11?
Tenuia smirnovi *					1		
Diopsidae							
Sphyracephala subbifasciata	00?000012	0002110300	0000010111	2000000010	0000000000	000002???0	000
Fitch							
Fergusoninidae	110110000	0000000210	2010110111	2100010100	1020100001	012000112?	101
Fergusonina sp.							
Heleomyzidae	100100001	1000000101	$010000\frac{0}{1}10$	0000000100	1000000100	0120000000	000
Anorostoma jersei Garrett			1				
Megamerinidae	000100012	0002100300	0000000001	0000000000	0100110000	0000000031	121
Texara sp.							
Micropezidae	000100012	0002100300	0000100001	1000100000	$0120020\frac{0}{1}01$	0110101120	110
Cnodacophora stylifera (Loew)					1		
Micropezidae	000100012	0002100300	0000100001	1000100000	1120021101	1110101120	110
Paracalobata univitta (Walker)							
Neriidae	$1\frac{0}{1}0100011$	0002000301	0000100111	1000100000	3120232301	0120101121	110
Nerius plurivittatus Bigot	1						
Neriidae	$0\frac{0}{1}0100011$	0002000301	0000100111	1000100000	3120232301	0120101121	110
Telostylus maccus Osten Sacken	1						
Piophilidae	100100000	0000000101	0000100111	0000000110	0100000000	0100000021	001
Prochyliza brevicornis Melander							
Sciomyzidae	000000000	0000000300	$00000000\frac{0}{1}10$	0000000010	0120001100	$000\frac{0}{1}00030$	001
Pherbellia albocostata (Fallén)			1			1	
Strongylophthalmyiidae	00010000	0002010201	2000100001	0010001000	0010011101	000000001	001
Strongylophthalmyia pengellyi	000100000	0002010201	2000100001	0010001000	0010011101	$0\frac{1}{1}2002???1$	001
Barber							
Tanypezidae	000100012	0000010301	0000100001	0010001010	0010011101	$0\frac{0}{1}2002???0$	001
Neotanypeza grandis (Enderlein)							

- sometimes on body; (1) lined along the body, none on apex
- 52. Length of setulae on pregonite: (0) strong like regular setae; (1) not as strong as regular setae but longer than the normally known sensory setulae; (2) like regular sensory setulae
- 53. Pregonite ending position and postgonite starting position: (0) outside of hypandrium hugging boundaries; (1) within hypandrium hugging boundaries (Fig. 13.5)
- 54. General shape of postgonite: (0) variable, but not as below; (1) with stalk-like base and dilated apices

- 55. Postgonite shape: (0) variable, not forked; (1) forked; (2) absent
- 56. Postgonite arising position: (0) not at or near apex of pregonite; (1) at or near apex of pregonite
- 57. Postgonite sitting position: (0) sandwiched between phallapodeme and pregonite; (1) not sandwiched between phallapodeme and pregonite
- 58. Postgonite chaetotaxy: (0) with multiple strong setae; (1) with 1 outstanding seta/setulae and some "sensory setulae" or remaining pits; (2) with only "sensory setulae" or remaining pits; (3) absent
- 59. Basiphallus: (0) independent of distiphallus; (1) fused with distiphallus
- 60. Female S7: (0) separated sclerites; (1) fused to from oviscape
- 61. Spiracle in female segment 7: (0) at membrane; (1) enclosed in sclerite; (2) absent
- 62. Number of spermathecae: (0) more than 2; (1) 2

Taxon selection

Families/superfamilies were selected for consideration with reference to the Schizophora phylogeny of Bayless (2021). Dissections of a selection of taxa within each major clade were examined and compared. Possible groundplan states were considered with reference to Cumming *et al.* (1995) and Sinclair *et al.* (2013). Exemplars showing more plesiomorphic states, and thus thought to be most representative of the ground-plans of the taxa considered, were selected for the analysis.

Many genera of the former Pseudopomyzidae are monotypic and character states used for higher classification are generally stable within genera with multiple species, therefore, only one exemplar species was chosen from each genus. Strongylophthalmyiidae, Tanypezidae and Fergusoninidae are included because they were treated with the nerioids by Lonsdale (2020).

Results and discussion of the phylogenetic analysis of the former Pseudopomyzidae and related Nerioidea

Two most parsimonious trees were obtained, differing only with regard to the monophyly of Neriidae. The strict consensus tree is presented that is 214 steps in length, with a consistency index of 0.41 and retention index of 0.68 (Fig. 104) The relationships shown for genera of the former Pseudopomyzidae roughly agree with McAlpine (1996), who arranged them into three probable monophyletic groups, Latheticomyia + Tenuia, Heloclusia + Polypathomyia + Pseudopomyza, Pseudopomyzella + Eopseudopomyza. Based on the descriptions of the amber fossils of the extinct genus Eopseudopomyza made by Hoffeins and Woźnica (2013), it shares external characters with Pseudopomyzella and Tenuia. Our results agree with McAlpine's (1996) placement of Eopseudopomyza as the sister taxon to Pseudopomyzella and with Hennig's (1971) treatment of these genera as the sister group to the

remaining genera. *Latheticomyia* and *Tenuia* form a clade here supported by synapomorphies including the shortened postgonite (Character 49) and the tucked-in pregonite-postgonite junction (Character 53). Instead of forming a clade with *Heloclusia* and *Polypathomyia* as predicted by McAlpine (1996), *Pseudopomyza* is recovered as the sister group to a clade including Cypselosomatidae, *Heloclusia*, *Polypathomyia*, *Latheticomyia* and *Tenuia*.

Pseudopomyzidae is shown as paraphyletic, with part of the group more closely related to Cypselosomatidae s.s. than to other genera traditionally treated as pseudopomyzids. The Cypselosomatidae s.l. (former Pseudopomyzidae + Cypselosomatidae s.s.) are also consistently shown as the sister group to the family Neriidae (or part of the Neriidae in the case of one of the parsimonious trees). The most significant characters supporting the monophyly of Cypselosomatidae s.l. (former Pseudopomyzidae + Cypselosomatidae s.s.) include the differentiated paravertical setae (Character 10) (here interpreted as the setae on the median occipital sclerite behind the postocellar setae and between the inner vertical setae), the scapular seta(e) (Character 11), the 3 pairs of marginal scutellar setae (reversed to 2 in most Pseudopomyza species) (Character 13), the incomplete subcosta (Character 20) (also found in the Agromyzidae-Fergusoninidae group), the confluent cell bm and dm (Character 25) (also found in Fergusoninidae), the outstanding setae on the epandrium (Character 35) (absent in Latheticomyia and Tenuia), and the one outstanding seta/setula and some sensory setulae or remaining pits on the postgonite (Character 58).

The Micropezidae + (Neriidae + Cypselosomatidae s.l.) clade is characterized by an independent male S6 that is more or less symmetrical, with a curved sclerotization running through the middle of the sternite. The area posterior to the curved sclerotization may be desclerotized and the area anterior to it may be reduced or extended ventrally but always bears the paired sensory setulae that typically mark the sternite (Character 30) (Neriidae males have S6 with a wider, less obvious sclerotization that is often at an angle to the anterior portion of S6). The clade is also supported by the presence of the postspiracular sclerite(s) (Character 34) and the phallic plate (Character 45). The postspiracular sclerite(s) are enclosed within segment 7+8 and posterior to spiracle 7, they vary widely and are absent in some subgroups but are most often distinct sclerites in the middle or right lateral of segment 7 (many Micropezidae), elongated and in a y-formation next to S8 (Neriidae), reduced to an elongated sclerite extending from S8 (in some former Pseudopomyzidae) or absent as S7 and 8 are completely fused (in some former Pseudopomyzidae and all Cypselosomatidae s.s.). The phallic plate extends posteriorly from the inner surface of the dorsal hypandrial bridge and articulates with the anterodorsal corners of the basiphallus. It is often a simple, flat, unbroken sheet-like sclerite. The families of this clade also share a distinct general shape of the postgonites (Character 54). The absence of setae on the ventral surface of the hypandrium-pregonite transition area (Character 42) was consistent for the putatively basal

Micropezidae taxa included in this analysis (two species of Calobatinae), however, some *Micropeza* have setulae present and positioned in a way that maybe homologous to the ancestral state of this character (on the pregonites but very close to the hypandrial-pregonite transition area). Therefore, character 42 may be a homoplastic character.

Postulated character state transitions in hypandrial and associated structures provide important support for the systematic placement of species formerly treated as part of the Pseudopomyzidae, and for their inclusion in the Cypselosomatidae (Fig. 105). The characters involved include the anterior bridge of the hypandrium, the ventral bridge of the hypandrium, the pregonites and the phallic guide.

The ground-plan of Nerioidea is here interpreted to have an anterior bridge but no ventral bridge of the hypandrium, pregonites arising from the sides of the hypandrium, and a well-developed phallic guide connecting the phallapodeme with the hypandrium. The hypandrium generally resembles a round shield when viewed ventrally. These character states are found in families such as the Diopsidae, Megamerinidae, Piophilidae, Strongylophthalmyiidae and Tanypezidae. In the Nerioidea, only the basal lineages of Micropezidae, including Calobatinae (*Cnodacophora* and *Compsobata*) and Micropezinae (*Micropeza*), exhibit all the ground-plan character states.

In Neriidae and *Pseudopomyzella flava* (former Pseudopomyzidae), the anterior bridge of the hypandrium is absent/atrophied and the well sclerotized anterior corners of the hypandrium possibly represent vestiges of the anterior bridge (Fig. 102.5). The hypandrium no longer retains the round shield shape but is often more compact and straight-edged. The phallic guide is also reduced or absent.

The ventral bridge of the hypandrium starts to appear in some taxa, weak in some (*Latheticomyia*), but well developed in most Cypselosomatidae *s.l.* genera (*Tenuia* does not have a "regular" ventral bridge as found in other Cypselosomatidae *s.l.*, the unique tusk-like extensions in place of the ventral bridge may be an autapomorphy or a unique modification of the character). Taxa with a well-developed ventral hypandrial bridge also have the bases of the pregonites moved to the middle of the hypandrium, so they often appear to originate from the ventral bridge (*Heloclusia*, *Polypathomyia*, *Pseudopomyza* and Cypselosomatidae *s.s.*).

If the suggested evolutionary sequence of hypandrial and related structures in Nerioidea is correct, Micropezidae is the basal group of Nerioidea; Neriidae is the sister taxon to the Cypselosomatidae *s.l.* and the latter forms a monophyletic group. It is very unlikely that Cypselosomatidae *s.s.* developed the ventral bridge (Character 43) and the medially shifted position of the pregonite (Character 48) independently from, yet with such similarity to, most members of the former Pseudopomyzidae. Considering that both are strong structural genitalic characters (Characters

43, 48) that are unlikely to be replicated identically by convergence, the most parsimonious interpretation is that Cypselosomatidae s.s. is the sister taxon to most members of the former Pseudopomyzidae except Pseudopomyzella (and possibly Eopseudopomyza). Pseudopomyzella (probably in addition to Eopseudopomyza) is the sister group to Cypselosomatidae s.s. + former Pseudopomyzidae in part, as it exhibits plesiomorphic states of the above two characters (Characters 43, 48) but shares a number of derived characters with the remainder of the family (Characters 8, 10, 11, 13, 17, 18, 20, 25, 35, 58, 62). Without Cypselosomatidae s.s., the former Pseudopomyzidae is paraphyletic. This refutes the linear phylogeny (Pseudopomyzidae (Cypselosomatidae (Neriidae, Micropezidae))) proposed by D.K. McAlpine (1966) or the phylogeny ((Cypselosomatidae, Pseudopomyzidae) (Micropezidae, Neriidae)) proposed by Hennig (1971) and Griffiths (1972), but most resembles the phylogeny (Micropezidae (Neriidae (Pseudopomyzidae, Cypselosomatidae))) proposed by J.F. McAlpine (1989). McAlpine, however, treated Pseudopomyzidae as a monophyletic group separate from Cypselosomatidae.

Lonsdale (2020) included Strongylophthalmyiidae and Tanypezidae in the Nerioidea and considered the twopiece sclerite attached to the basiphallus, generally treated as the epiphallus, to be homologous to the phallic plate. Although his illustrations suggest the structure may have a hypandrial origin, there is insufficient evidence that the phallic plate of Nerioidea is homologous to the epiphallus of Strongylophthalmyiidae and Tanypezidae, which means that a Nerioidea including Strongylophthalmyiidae and Tanypezidae lacks putative synapomorphies other than the narrow and elongated pregonites (Character 49), which are also recovered here as a homoplastic character in Fergusoninidae. Although the current tree (Fig. 104) shows Strongylophthalmyiidae + Tanypezidae next to the clade including the four families traditionally treated as Nerioidea, without better supporting characters, it may be premature to include Strongylophthalmyiidae and Tanypezidae in the Nerioidea.

Lonsdale (2020) also included Fergusoninidae in Nerioidea and considered it to be closely related to the former Pseudopomyzidae + Cypselosomatidae s.s., however the character states he cited as evidence for a close relationship between Fergusoninidae and the Nerioidea families are here shown to be convergent. The current morphological analysis does not recover Fergusoninidae in the superfamily but instead groups it with Agromyzidae, where it is traditionally placed. Although both Fergusoninidae and former Pseudopomyzidae + Cypselosomatidae s.s. are characterized by an outstanding pair of setae on the epandrium and a superficially similar elongated tubular phallus, Fergusoninidae lack crucial synapomorphies of the Nerioidea such as the phallic plate, the fused dorsal bridge of the hypandrium and the characteristic ventral form of the hypandrium, S6 and S7+8.

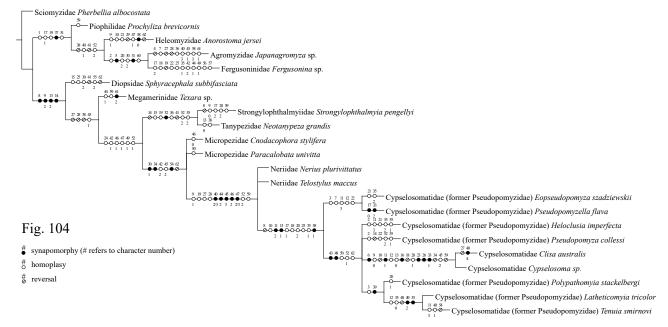


FIGURE 104. The strict consensus of four most parsimonous morphological phylogenetic trees of Cypselosomatidae *s.l.* (L= 218, Ci=40, Ri=67).

Phylogeny of Pseudopomyza

List of characters

Multistate characters are treated as unordered. *Heloclusia imperfecta* was treated as the outgroup in order to assign character polarity.

Head

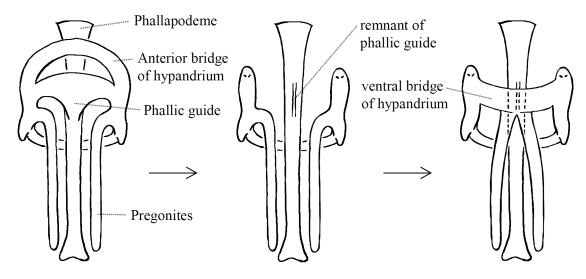
- 1. Number of fronto-orbital setae: (0) 3; (1) 2
- 2. Subvibrissa: (0) present; (1) absent
- 3. Subvibrissa length: (0) strong, ≥ 0.5× length of vibrissae and distinguished from background setulae (Figs. 15.3, 18.3, 23.1, 65.3); (1) weak, ≤ 0.3× length of vibrissae or only 2× length of background setulae (Figs. 35.3, 38.3, 85.3)
- 4. Subvibrissa position: (0) on vibrissal angle (Figs. 35.1, 38.3, 85.1); (1) posterior to vibrissal angle (Figs. 15.1, 18.1, 21.1, 23.1)
- 5. Eye and genal height ratio: (0) eyes large, height \geq 2.5× genal height (Figs. 18.3, 35.1. 38.3); (1) eyes small, height \leq 2× genal height (Fig. 44.3)
- 6. Outstanding ventral seta(e) on pedicel: (0) 1 (Fig. 27.3); (1) 2 (Fig. 35.3)
- 7. Colour of pedicel: (0) light cream to yellow; (1) brown to black
- 8. Colour of first flagellomere: (0) bicoloured (Figs. 18.3, 21.1, 85.3); (1) uniformly brown (Figs. 15.3, 23.3, 90.3)
- 9. Desclerotization of face: (0) dorsal to ventral point of sub-antennal depression (Figs. 16.3, 18.3, 21.3); (1) ventral to ventral point of sub-antennal depression (Figs. 35.3, 44.3, 27.3)

Thorax

- 10. Scapular seta(e): (0) 2 or more setae (Fig. 27.2); (1) 1 seta (Figs. 21.2, 38.2, 85.1)
- 11. Anterior intra-alar seta: (0) present (Figs. 35.2, 38.2, 44.2, 85.2); (1) absent (Figs. 15.2, 21.2, 23.2, 27.2)
- 12. Presutral acrostichal setae: (0) well developed, at least 2× background setulae; (1) reduced or absent (Figs. 21.2, 27.2)
- 13. Prescutellar acrostichal setae: (0) absent, bare; (1) with a prominent pair; (2) only with scattered setulae
- 14. Scutellar chaetotaxy (basal setulae): (0) without a cluster of 3 setulae at base of basal seta; (1) a cluster of 3 minute setulae at basal of basal seta, setulae immediate anterior to basal seta often slightly more distinct (Figs. 38.2, 44.2)
- 15. Scutellar chaetotaxy (marginal setae): (0) 3 pairs; (1) 2 pairs
- 16. Scutellar chaetotaxy (discal setulae): (0) present; (1) absent
- 17. Leg colour patterns: (0) showing light base colour with various dark patterns; (1) uniformly dark, no light base colour showing
- 18. Length of M_1 between r-m and dm-m compared to length of dm-m: (0) $2\times$; (1) $1.4\times$
- 19. Length of M₄ after dm-m compared to length of dm-m: (0) shorter; (1) equal or longer

Abdomen

20. S6: (0) with arcuate sclerotization through sclerite (Figs. 16.1, 19.1, 22.1, 24.1, 28.1); (1) H-shaped (Figs. 36.1, 39.1, 88.1)



- Micropezidae Calobatinae, Micropezinae
- Neriidae
- former Pseudopomyzidae Pseudopomyzella flava
- former Pseudopomyzidae Pseudopomyza, Heloclusia, Polypathomyia
- Cypselosomatidae *s.s.*



Paracalobata univitta



Nerius Pseudopomyzella plurivittatus flava



Heloclusia imperfecta

Cypselosoma sp. debu00153246

105

FIGURE 105. Proposed transformation series for the hypandrium and related structures.

- 21. Extension from sclerotization of S6: (0) longest anteriorly; (1) uniformly distributed
- 22. S7+8: (0) sclerotization often not continued over to ventral right, or ventral right weaker than left, not forming a closed ring (Figs. 16.1, 19.1, 24.1, 28.1,
- 31.2, 34.2, 36.1); (1) sclerotization continued over to ventral right, ventral left and right equally sclerotized, forming a closed ring (Figs. 22.1, 34.1, 45.1)
- 23. Postspiracular sclerite: (0) present (Figs. 16.1, 24.1, 28.1, 31.2, 34.2); (1) absent

TABLE 4.2. Character state matrix for *Pseudopomyza* species with *Heloclusia imperfecta* as the outgroup. Abbreviations: ASG, subgenus *Apops*; DSG, subgenus *Dete*; HSG, subgenus *Heluscolia*; NSG, *P. nigrimana* species group; PSG, subgenus *Pseudopomyza*.

	Characters			
		1	2	3
Taxon	123456789	0123456789	0123456789	012345
Heloclusia imperfecta Malloch	000000000	0000000000	0000000000	000000
P. antipoda (Harrison) (HSG)	$000\frac{0}{1}01000$	1000011011	0000110101	000000
P. aristata (Harrison) (PSG)	001001111	1011011011	1101100000	000000
P. atrimana (Meigen) (PSG)	001001001	1002111011	1111001010	000100
P. brevicaudatus (Harrison) (PSG)	001011110	1001011111	0100000???	0?0000
P. brevifacies (Papp) (PSG)	11??11011	1002111011	$\frac{0}{1}$ 111100000	000100
P. brevis (Harrison) (HSG)	000101000	00000110??	0000010101	0000??
P. chilensis Yau and Marshall (ASG)	000101010	1100011011	0100000000	000011
P. collessi McAlpine (DSG)	11??00001	0110001011	0000100000	000000
P. flavitarsis (Harrison) (ASG)	100101010	1100011011	0101000000	000011
P. medianentis Yau and Marshall (ASG)	100101000	1110011011	0111000000	00000?
P. nigrimana (Hennig) (NSG)	001001001	1001111011	1111001010	111?00
P. nigritarsis Yau and Marshall (ASG)	$\frac{0}{1}$ 00101010	1100011011	0100000000	000001
Sp.n. 1 CNC729345 (PSG)	001011110	0001001111	?????????	????00
Sp.n. 2 CNC729327 (ASG)	000101000	1110011011	?????????	????01

- 24. Epandrium posteroventral corner: (0) not extending posteriorly; (1) extending posteriorly (Figs. 28.3, 36.2, 45.3)
- 25. Posteroventral corner of epandrium: (0) rounded; (1) sharp perpendicularly angulated
- 26. Surstylar lamella: (0) absent; (1) present (Fig. 39.3, and marked as red in left ventrolateral view of the terminalia of the *P. nigrimana* species group)
- 27. Subepandrial sclerite seta(e) base: (0) unmodified; (1) elongated
- 28. Length of hypandrium ventral bridge: (0) short, 1–2× width of pregonite (Figs. 16.6, 19.5, 22.5, 36.5, 45.6); (1) long, 4x width of pregonite (Fig. 39.5)
- 29. Shape of phallic plate: (0) straight or slightly arched ventrally; (1) anterior half with prominent dorsomedial ridge (Figs. 31.5, 34.4)
- 30. Pregonites: (0) often separate at origin, if fused at base, less than one third of length fused, not strongly arched dorsally (Figs. 16.6, 22.5, 24.5, 28.6, 36.5, 39.5); (1) more than two thirds of length fused, strongly arched dorsally (Fig. 88.2)
- 31. Postgonite: (0) forked, often shaped like chameleon foot (Figs. 39.5, 19.5, 22.5); (1) shape variable but not forked (Fig. 88.2)
- 32. Distiphallus: (0) asymmetrical (Figs. 16.6, 19.5, 28.6, 36.5, 39.5); (1) symmetrical (Fig. 88.2)
- 33. Phallus length: (0) base of distiphallus surpassing anterior margin of anal opening (Figs. 16.3, 19.2, 28.3, 36.2); (1) base of distiphallus not reaching anterior margin of anal opening

- 34. Oviscape sclerotized structure: (0) without spot-like sclerotization; (1) with spot-like sclerotization (Figs. 17.2, 20.1)
- 35. Oviscape desclerotization pattern: (0) variable but not spectacle or bow-tie-shaped; (1) spectacle or bow-tie-shaped (Figs. 17.2, 20.1, 25.1)

Pseudopomyza was previously divided into five subgenera, Apops, Dete, Macalpinella, Pseudopomyza s.s. and Rhinopomyzella (Buck & McAlpine, 2010). The monophyly of Rhinopomyzella is clearly indicated by the fused and strongly arched pregonites, the equally arched phallapodeme and symmetrical distiphallus (Hennig, 1971; Buck & McAlpine, 2010). McAlpine (1994) considered Apops to be structurally intermediate between Pseudopomyza s.s. and Dete. Both Apops and Dete have two fronto-orbital setae and no anterior intra-alar seta but, like *Pseudopomyza s.s.*, *Apops* have more than one long ventral setae on the pedicel and a pruinose scutum. According to McAlpine, all three subgenera have different facial desclerotization. Macalpinella, a monotypic taxon described by Papp (2005) as a separate genus, was included as a subgenus of Pseudopomyza by Buck and McAlpine (2010) because it clearly shares apomorphies with Pseudopomyza s.s. and Rhinopomyzella. The discovery of new taxa and new characters, along with the reconsideration of character state distribution and homology for previously studied characters, makes it necessary to synonymize these subgenera with Pseudopomyza s.s..

Taxon selection

Pseudopomyza nigrimana is included as the sole exemplar of the P. nigrimana-group because all other species in this group are coded uniformly for all characters included in this analysis. All other *Pseudopomyza* species except P. arenae and P. neozelandica are included in the analysis, along with the two undescribed species known from females only. Pseudopomyza arenae seems to be externally identical to P. chilensis (only differing in male S6 chaetotaxy) and P. neozelandica resembles P. aristata in having an unusual pruinose/ pollinose pleuron. Pseudopomyza arenae and P. neozelandica are not included in the matrix because specimens were not examined, and the available descriptions and habitus photos were inadequate to code the taxa. Heloclusia imperfecta is treated as the outgroup as it is the probable sister group to the genus Pseudopomyza.

Results and discussion of the phylogenetic analysis of *Pseudopomyza*

Three most parsimonious trees (Figs. 106.1–3) were obtained (L=59, Ci=61, Ri=69) and used to generate a strict consensus tree (L=62, Ci=58, Ri=65) (Fig. 107).

Buck and McAlpine (2010) considered Apops, Dete and some of the Australasian species with asymmetrical, open-ringed S7+8 to be more primitive members of the genus Pseudopomyza, but they were unsure of the placement of each group. The morphological data considered here suggests that Dete is the sister group to the rest of the genus and that other Australasian species fall into other, more widely distributed subgenera. Characters used to define McAlpine's clade of Dete + Apops, namely the number of fronto-orbital setae (Character 1) and the absence of the anterior intra-alar seta (Character 11), are shown here to be homoplastic, occurring independently in Dete and Apops. Pseudopomyza species have different degrees of facial desclerotization, however Dete and the clade including P. aristata, P. brevifacies, P. atrimana and the P. nigrimana species group are all characterized by a relatively well sclerotized face (Character 9).

The three equally parsimonious trees show consistent grouping of the major clades but Heluscolia was recovered as either the sister group to the remaining Pseudopomyza except Dete or as the sister group to Apops. Characters contributing to the conflict include the position of the subvibrissa (Character 4), the colour of the pedicel (Character 8) and the extension widths from the arcuate sclerotization of S6 (Character 21). Pseudopomyza antipoda can be confidently grouped with the brachypterous P. brevis based on the sharp perpendicularly angulated ventroposterior corner of the epandrium (Character 25), elongated base(s) of subepandrial sclerite seta(e) (Character 27) and the prominent dorsomedial ridge on the anterior half of the phallic plate (Character 29)—strong characters not seen in other Pseudopomyza species.

The morphological data strongly suggest that the

subgenus *Pseudopomyza* as defined by previous authors is not monophyletic because of the sister-group relationship between *P. atrimana* (the type species of *Pseudopomyza*) and the former subgenus *Rhinopomyzella* (a new synonym of *Pseudopomyza*). This relationship is strongly supported by synapomorphies including the inner lamella of the surstylus (Character 26) and the long ventral bridge of the hypandrium (Character 28). Its constituent species are shown to belong to a larger clade, here treated as the subgenus *Pseudopomyza*, that also includes *P. brevifacies*, (the only species of the former subgenus *Macalpinella*), *P. aristata*, *P. brevicaudata* and Sp.n. 1 CNC729345 (an undescribed species from New Zealand). *Pseudopomyza antipoda* and *P. brevis*, formerly in *Pseudopomyza s.s.*, belong in the subgenus *Heluscolia*.

The subgenus *Apops* is characterized by the absence of the anterior intra-alar seta (Character 11) and the presence of a spectacle- or bow-tie-shaped desclerotization on the ventral surface of the oviscape (Character 35). *Apops* is now expanded to include newly described species with three fronto-orbital setae (anterior seta often small) instead of only two as in the original members of the subgenus. It now includes *P. chilensis*, *P. flavitarsis*, *P. medianentis*, *P. nigritarsis*, *P. arenae* and Sp.n. 2 CNC729327.

Phylogeny of the *Pseudopomyza nigrimana* species group

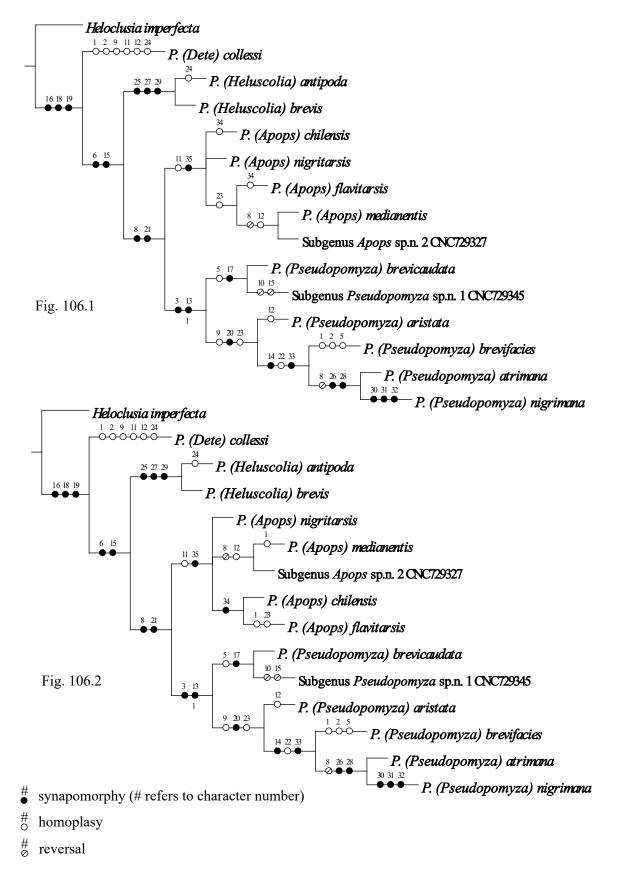
Buck & McAlpine (2010) recognized the *P. nigrimana* species group (formerly subgenus *Rhinopomyzella*) as a monophyletic group based on one unique synapomorphic character: fused and strongly dorsally arched pregonites. Further synapomorphies recognized here include the strongly dorsally arched phallapodeme and symmetrical distiphallus.

List of characters

Multistate characters are treated as unordered. *Pseudopomyza atrimana* was treated as the outgroup in order to assign character polarity.

Head

- Fronto-orbital setae: (0) $1^{\text{st}} < 2^{\text{nd}}$, $2^{\text{nd}} = 3^{\text{rd}}$; (1) $1^{\text{st}} = 2^{\text{nd}} = 3^{\text{rd}}$; (2) $1^{\text{st}} < 3^{\text{rd}} < 2^{\text{nd}}$
- 2. Frons: (0) without medial longitudinal yellow stripe; (1) with medial longitudinal yellow stripe (Figs. 49l, n, p, 63.3, 71.3, 80.3)
- 3. Face markings: (0) markings absent or only inner face of darkest brown (Figs. 49a, b, d, e, 85.3, 93.3, 96.3); (1) outer face of darkest brown (Figs. 49f, g, i, 1, n, 54.3, 57.3, 65.3, 71.3, 80.3)
- 4. Markings on upper half of sub-antennal depression: (0) absent; (1) present (Figs. 49p, 63.3, 90.3)
- 5. Genal markings: (0) uniformly brown, or mainly yellow, or of different pattern; (1) anterior margin of gena yellow or tan, remaining dark brown (Figs. 50f,



FIGURES 106.1–3: The three most parsimonous morphological phylogenetic trees for the genus *Pseudopomyza* (L=59, Ci=61, Ri=69).

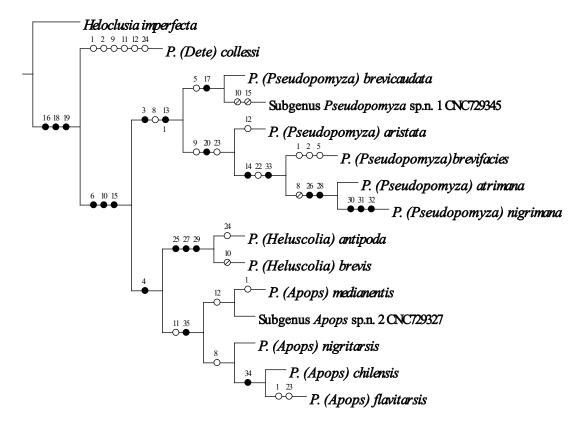


Fig. 106.3

- # synapomorphy (# refers to character number)
- # homoplasy
- # reversal

FIGURES 106. (Continued)

- i, 57.3, 65.3, 74.3); (2) dark brown below lower eye margin continuous with dark brown posterior half (Figs. 50j, k, l, 52.3, 77.3, 81.3); (3) anterior half of gena yellow, posterior dark brown (Figs. 50n, 63.3, 90.3)
- 6. Genal texture posterior to eye: (0) pruinose; (1) glossy
- 7. Genal texture at ventral margin: (0) glossy; (1) largely pruinose

Thorax

- 8. Fore femur colouration: (0) all or mainly brown except basal ¼ (Figs. 51a, b, d, e, f, q, r); (1) basal half or more yellow, remainder dark brown (Figs. 51c, g, i, k, o); (2) more than basal ¼ but less than half yellow, remainder dark brown (Figs. 51t, u, v)
- 9. Male fore tarsus colouration: (0) uniformly brown (Figs. 51a, b, c, d, u, v); (1) tarsal segment 1 brown, segment 2 white (Figs. 51e, t); (2) tarsal segment 1 brown, segment 2 bicoloured (Figs. 51g, i, k)

- 10. Mid femur colouration: (0) mainly brown except base and/or apex (Figs. 51a, b, d, e, f, r); (1) uniformly vellow
- 11. Hind tibia colouration: (0) with light tan band (Figs. 51a, b, c, d, v); (1) without light tan band

Male genitalia

- 12. Subepandrial sclerite, setae length: (0) anterior seta distinctly longer than posterior seta (Figs. 53.3, 55.3, 58.3); (1) anterior seta only slightly longer than posterior seta (Figs. 88.3, 94.3)
- 13. Structure of subepandrial sclerite: (0) flat or with protuberance medial to setae (Figs. 66.3, 81.3); (1) protuberance above dorsal seta (Figs. 53.3, 72.3)
- 14. Pregonites: (0) separate, not strongly arched dorsally; (1) fused and strongly arched dorsally
- 15. Shape of phallapodeme: (0) relatively straight; (1) strongly arched dorsally
- 16. Phallic guide: (0) small (Figs. 94.2, 97.2); (1) absent (Fig. 88.2); (2) large (Fig. 53.2)

TABLE 4.3. Character state matrix for the *Pseudopomyza nigrimana* species group (= *Rhinopomyzella*) with *P. atrimana* as the outgroup.

	Characters		
_		1	2
Taxon	123456789	0123456789	01
P. atrimana (Meigen)	000000000	0000000000	00
P. adunca Yau and Marshall	001020002	1101112101	01
P. albimana (Hennig)	001011012	1100112101	01
P. ampliata Yau and Marshall	?01010101	0100112101	??
P. angustifrons Yau and Marshall	201011012	1100112001	00
P. binaevia Yau and Marshall	011130020	11???????	11
P. brunneicacumen Yau and Marshall	001011012	1100112101	01
P. cordata Yau and Marshall	201000000	0100112001	11
P. cyathiformis Yau and Marshall	011020021	1101112101	01
P. flavicacumen Yau and Marshall	001011012	1100112101	01
P. gambiformis Yau and Marshall	001021012	1100112101	01
P. inflexa Yau and Marshall	011020001	0100112101	01
P. machaera Yau and Marshall	?01010102	0100112101	??
P. nigrimana (Hennig)	$0000000\frac{0}{1}0$	$\frac{0}{1}$ 010111011	00
P. parabinaevia Yau and Marshall	011130020	1000112101	11
P. proboscis Yau and Marshall	100000000	0010110002	00
P. prolata Yau and Marshall	100001010	1010110012	00
P. simulatrix Yau and Marshall	0010110??	1100112101	??

- 17. Postgonite shape: (0) not spatulate (Figs. 61.2, 88.2, 94.2) (1) spatulate (Fig. 53.2)
- 18. Structure of postgonite: (0) without preapical hook (Figs. 53.2, 94.2); (1) with preapical hook (Fig. 88.2)
- 19. Basal distiphallus: (0) asymmetrical, shape variable; (1) symmetrical, tubular (Fig. 53.2); (2) symmetrical, ring-like (Figs. 94.2, 97.2)

Female genitalia

- 20. Spermathecal length relative to width: (0) less than $3\times$; (1) greater than or equal to $3\times$ (Fig. 70.4)
- 21. Spermathecae, texture: (0) without striation (Figs. 95.4, 98.4); (1) with striation (Fig. 92.4)

Results and discussion of the phylogenetic analysis of the *P. nigrimana* species group

Six most parsimonious trees (Figs. 108.1–6) were obtained (Fig. 108.1–3, 5, 6 L=47, Ci=59, Ri=75; Fig 108.4 L=46, Ci=60, Ri=76). A strict consensus tree was generated (L=51, Ci=54, Ri=70) (Figs. 109). Topology shown by the six parsimonious trees is consistent except for the unstable placement of *P. adunca*, which appears alternately with the clades that include *P. albimana* or *P. inflexa* or in a larger clade that includes both. Characters contributing to the conflict include the genal markings

(Character 5), male fore tarsus colouration (Character 9) and mid femur colouration (Character 10). Colour characters are usually more homoplastic than structural characters but are included in this analysis because they provide additional resolution.

Phylogeny of the Nerioidea with focus on the relationships of the former Pseudopomyzidae—Molecular data

DNA sequencing

Outgroup selection: It is commonly accepted that Nerioidea consists of Cypselosomatidae s.s., former Pseudopomyzidae, Neriidae and Micropezidae (Griffiths, 1972; Hennig, 1971, 1973; J.F. McAlpine, 1989; Marshall, 2012). However, Lonsdale (2020) argued that Fergusoninidae, Tanypezidae and Strongylophthalmyiidae also belong in the same superfamily. The concept of Tanypezidae plus Strongylophthalmyiidae as a monophyletic group has been well established since Hennig (1958), with Strongylophthalmyiidae even being included as a subfamily of Tanypezidae (Griffiths, 1972; McAlpine, 1997a), but their position in the Schizophora is still debated. J.F. McAlpine (1989) positioned them in the Diopsoidea, yet D.K. McAlpine (1997a) proposed a possible relationship with the Nerioidea. A close relationship between Diopsoidea and Nerioidea

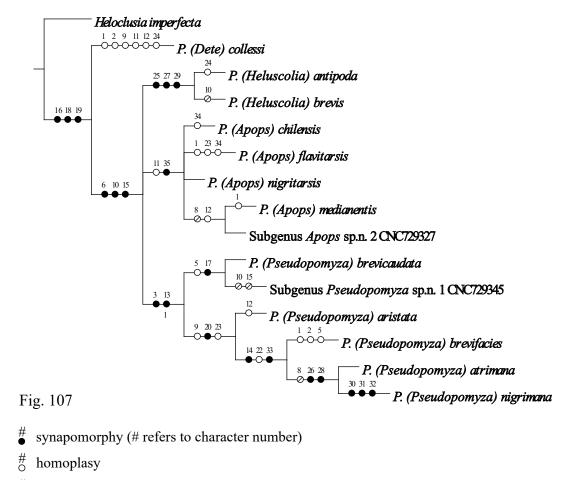


FIGURE 107. The strict consensus morphological phylogenetic tree for the genus *Pseudopomyza* (L=62, Ci=58, Ri=65)

has been postulated by several authors (Hennig, 1958; J.F. McAlpine, 1989; Rohdendorf, 1964, 1974, 1977) without compelling evidence, and D.K. McAlpine (1997a) questioned the relationship. Lonsdale's (2020) morphological study refuted a sister-group relationship between the two superfamilies, recovering Lonchaeidae as a sister taxon to the Nerioidea but then dismissing this relationship as an artifact of the analysis due to homoplastic characters. The molecular study of Wiegmann *et al.* (2011) also failed to support the Diopsoidea as closely related to the Nerioidea.

reversal

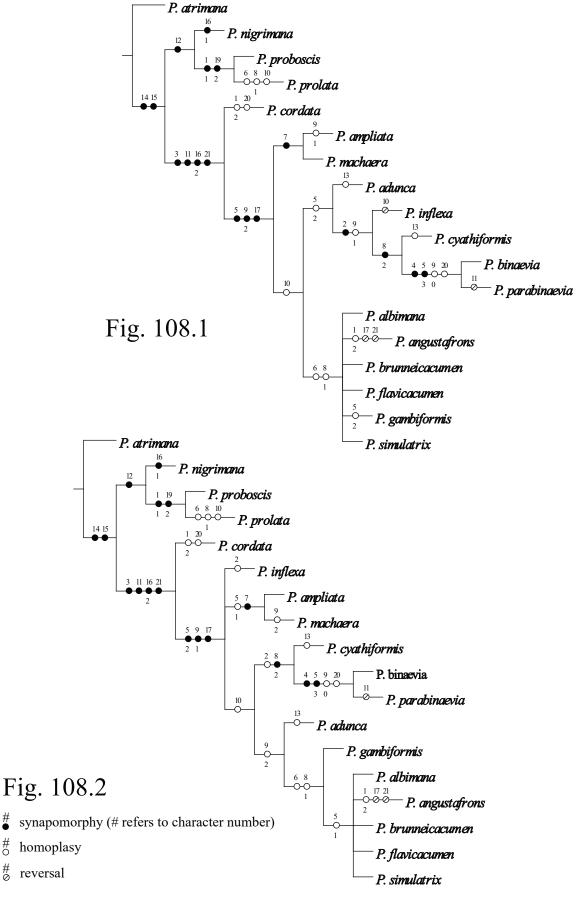
Fergusoninidae has been traditionally considered to be closely related to or part of the Agromyzidae (Malloch, 1924, 1925, 1932; Colless & D.K. McAlpine, 1970; J.F. McAlpine, 1989), although some authors were uncertain of this relationship and treated the family Fergusoninidae as unplaced in the Schizophora (Hennig, 1973; Griffiths, 1972). Lonsdale (2020) is the only author to suggest that Fergusoninidae belongs in the Nerioidea. Molecular studies of Wiegmann *et al.* (2011), Winkler *et al.* (2010) and Jackson (2019) did not recover Fergusoninidae as the sister taxon to, or part of, the Nerioidea.

Diopsidae, Fergusoninidae, Strongylophthalmyiidae, Tanypezidae, and Sphaeroceridae were included in the analysis as potential outgroups.

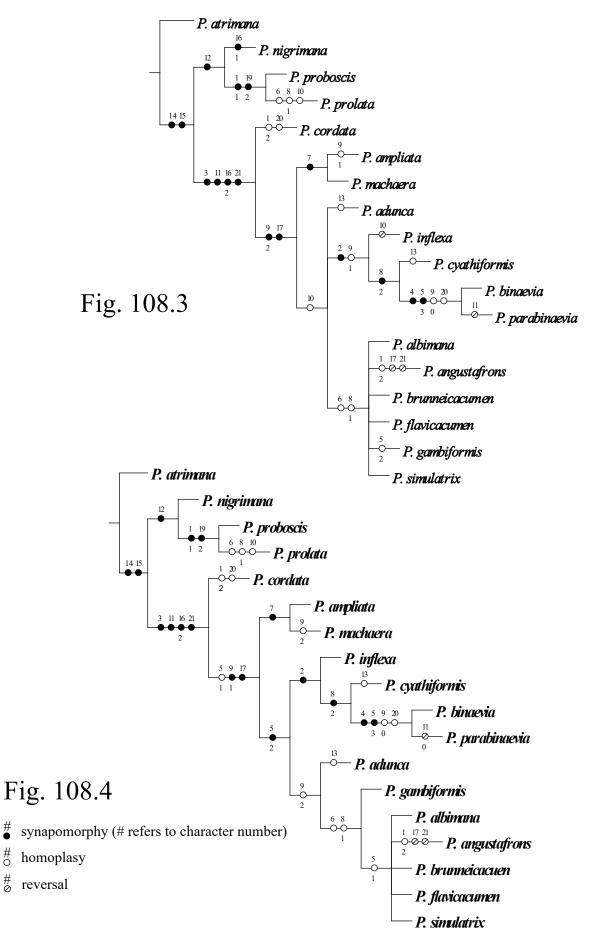
Taxon sampling: Twenty-two specimens of the former Pseudopomyzidae, six Cypselosomatidae s.s. and two Tanypezidae from the University of Guelph Insect Collection and the Canadian National Collection of Insects, Arachnids & Nematodes, were sent to the University of Guelph Biodiversity Institute of Ontario for sequencing of the 5' region of the cytochrome c oxidase I mitochondrial gene (COI-5'; the DNA barcode region). Following this, a plate of ninety-five DNA samples, including representatives of Cypselosomatidae s.s., Diopsidae, Fergusoninidae, Micropezidae, Neriidae, former Pseudopomyzidae, Strongylophthalmyiidae and Tanypezidae, was assembled for multi-gene sequencing. We included specimens that had been barcoded prior to this current project to resolve the phylogeny of Micropezidae at the University of Guelph Insect Collection (e.g., Jackson, 2019) and from the BOLD database (Barcode of Life Datasystems; www.boldsystems.org) made available by different projects worldwide. The full list of DNA samples and associated specimens is listed in Table 4.4. Access to the data on BOLD is available upon request.

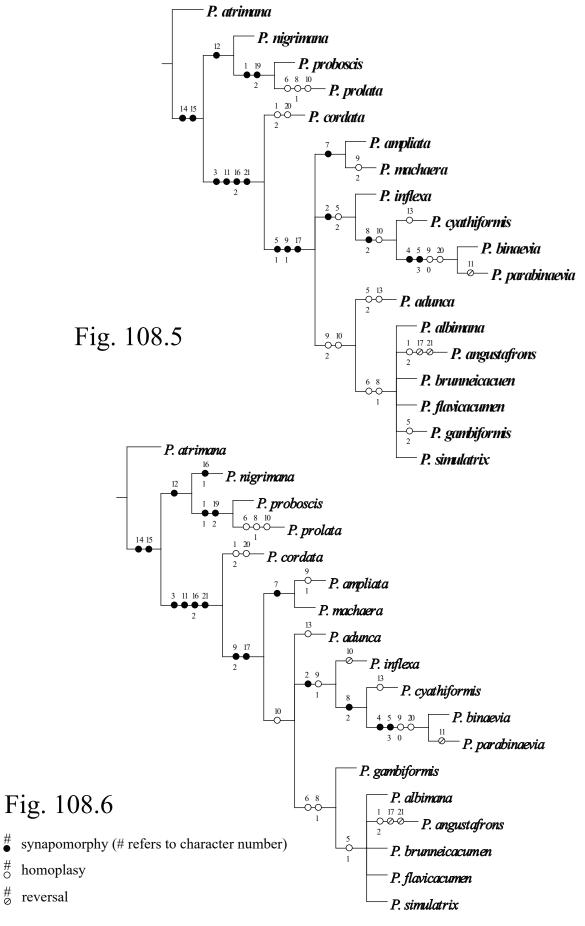
Two previously sequenced Sphaeroceridae specimens (Kits *et al.*, 2013) and *Pseudopomyzella flava* (Table 4.4) were added to the analyses afterwards.

Gene selection: The plate of 95 specimens of nerioid



FIGURES 108.1–6: The six most parsimonous phylogenetic trees for the *Pseudopomyza nigrimana* species group (Fig. 108.1–3, 5, 6 L=47, Ci=59, Ri=75; Fig 108.4 L=46, Ci=60, Ri=76).





FIGURES 108. (Continued)

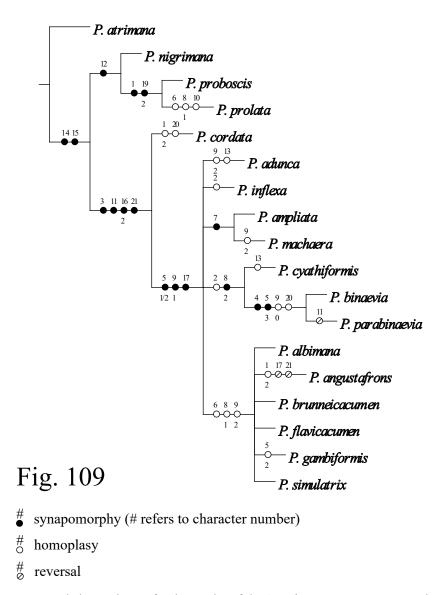


FIGURE 109. Strict consensus phylogenetic tree for the species of the *Pseudopomyza nigrimana* species group (L=51, Ci=54, Ri=70).

families and potential outgroups was sequenced for 12S ribosomal RNA, 28S ribosomal DNA (including 3 regions here named 28S, 28S-D2 and 28S-D3) and the 3' region of COI (COI-3P). The above genes were selected from a pool of markers that have been commonly used in Diptera phylogenetics (Gibson *et al.*, 2001) and which have been successfully used for phylogenetic analysis of some Micropezidae groups (Jackson, 2019; Ferro, 2019; Md Yusof, 2020; Lindsay, 2021).

The genes 12S and COI-5P of the two sequenced Sphaeroceridae were used in the analyses. Kits *et al.* (2013) sequenced a different gene region of 28S, these data were not comparable and were not included in the analyses.

Barcode data for *Pseudopomyzella flava* only became available after the completion of phylogenetic analysis, which was carried out as part of the first author's PhD thesis, and it was impractical to sequence the remaining

five genes from the single newly available specimen. Therefore, only the COI-5P gene of *Pseudopomyzella flava* is used in the updated molecular analysis.

Extraction, amplification and sequencing: Pinned specimens from the University of Guelph Insect Collection and the Canadian National Collection of Insects, Arachnids & Nematodes, had legs pulled for DNA extraction following the Center for Biodiversity Genomics (CBG) protocol outlined in Ivanova, deWaard & Hebert (2006). PCR amplification and sequencing followed protocols outlined in Hebert *et al.* (2013) and Prosser *et al.* (2016). The primers used for PCR and sequencing are listed in Table 4.5. All sequences were uploaded to BOLD and organized in the dataset DS-PSEU21.

Alignment: Sequence data were downloaded and aligned by MUSCLE (Edgar, 2004) on BOLD or CIPRES Science Gateway v3.3 computing cluster (Miller *et al.*, 2010). The sequences were then opened in AliView

TABLE 4.4. Taxa included in the molecular analysis, including specimens newly sequenced for this study and sequences contributed from other studies (Outgroup taxa marked with "*") (Taxa of former Pseudopomyzidae marked with "#"). Abbreviations: ASG, subgenus *Apops*; DSG, subgenus *Dete*; HSG, subgenus *Heluscolia*; NSG, *P. nigrimana* species group; PSG, subgenus *Pseudopomyza*.

Family	Subfamily	Taxon name	Sample ID	Country	State/Province
Cypselosomatidae		Cypselosoma gephyrae Hendel	CNC700641	Thailand	Kamphaeng Phet
Cypselosomatidae		<i>Cypselosoma</i> gephyrae Hendel	DEBU00153246	Nepal	
Cypselosomatidae		<i>Formicosepsis</i> de Meijere	BIOUG14876-E05	Malaysia	Selangor
Cypselosomatidae		<i>Formicosepsis</i> de Meijere	DEBU00320307	Philippines	Laguna
Cypselosomatidae		<i>Formicosepsis</i> de Meijere	DEBU00320310	Philippines	Laguna
Cypselosomatidae		<i>Formicosepsis</i> de Meijere	DEBU00320969	Philippines	Laguna
Cypselosomatidae		<i>Formicosepsis</i> de Meijere	DEBU00320980	Philippines	Laguna
Cypselosomatidae #		Heloclusia imperfecta	DEBU00372647	Chile	Los Ríos
Cypselosomatidae #		Heloclusia imperfecta	DEBU00373012	Chile	Araucanía
Cypselosomatidae #		Latheticomyia infumata	BIOUG31677-G07	Costa Rica	Guanacaste
Cypselosomatidae #		Latheticomyia infumata	BIOUG32773-A12	Costa Rica	Guanacaste
Cypselosomatidae #		Latheticomyia infumata	CCDB-33184-F07	Costa Rica	San José
Cypselosomatidae #		Latheticomyia tricolor	CCDB-33184-F06	United States	New Mexico
Cypselosomatidae #		Pseudopomyza flavitarsis (ASG)	BIOUG38389-G08	New Zealand	Waikato
Cypselosomatidae #		Pseudopomyza flavitarsis (ASG)	BIOUG39198-G07	New Zealand	Waikato
Cypselosomatidae #		Pseudopomyza flavitarsis (ASG)	BIOUG39232-B04	New Zealand	Waikato
Cypselosomatidae #		Pseudopomyza flavitarsis (ASG)	BIOUG39235-H03	New Zealand	Waikato
Cypselosomatidae #		Pseudopomyza flavitarsis (ASG)	BIOUG39383-G03	New Zealand	Waikato
Cypselosomatidae #		Pseudopomyza collessi (DSG)	BIOUG46308-D07	Australia	New South Wales
Cypselosomatidae #		Pseudopomyza collessi (DSG)	CNC729329	Australia	New South Wales
Cypselosomatidae #		Pseudopomyza collessi (DSG)	CNC729336	Australia	New South Wales
Cypselosomatidae #		Pseudopomyza brevifacies (PSG)	BIOUG16245-F05	Malaysia	Selangor
Cypselosomatidae #		P. nigrimana species group	BIOUG28781-G08	Costa Rica	Guanacaste

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TABLE 4.4. (Continued)

Family	Subfamily	Taxon name	Sample ID	Country	State/Province
Cypselosomatidae #		Pseudopomyza angustifrons (typical form) (NSG)	BIOUG25886-A04	Honduras	Cortés
Cypselosomatidae #		Pseudopomyza brunneicacumen (NSG)	BIOUG31499-E05	Costa Rica	Guanacaste
Cypselosomatidae #		Pseudopomyza flavicacumen (NSG)	BIOUG18853-E01	Honduras	Cortés
Cypselosomatidae #		Pseudopomyza nigrimana (NSG)	BIOUG29031-H02	Costa Rica	Guanacaste
Cypselosomatidae #		Pseudopomyza nigrimana (NSG)	debu00130643	Costa Rica	Alajuela
Cypselosomatidae #		Pseudopomyza nigrimana (NSG)	Sample-demo93	Costa Rica	San José
Cypselosomatidae #		Pseudopomyza antipoda (HSG)	BIOUG38739-A07	New Zealand	Waikato
Cypselosomatidae #		Pseudopomyza antipoda (HSG)	BIOUG38752-B11	New Zealand	Waikato
Cypselosomatidae #		Pseudopomyza antipoda (HSG)	BIOUG38951-D08	New Zealand	Waikato
Cypselosomatidae #		Pseudopomyza antipoda (HSG)	BIOUG38954-H02	New Zealand	Waikato
Cypselosomatidae #		Pseudopomyza antipoda (HSG)	BIOUG39547-H07	New Zealand	Waikato
Cypselosomatidae #		Pseudopomyza aristata (PSG)	CNC729339	New Zealand	West Coast
Cypselosomatidae #		Pseudopomyza atrimana (PSG)	BIOUG05391-C02	Germany	Bavaria
Cypselosomatidae #		Pseudopomyza atrimana (PSG)	BIOUG05392-A07	Germany	Bavaria
Cypselosomatidae #		Pseudopomyza atrimana (PSG)	BIOUG15648-F01	Norway	Sør-Trøndelag
Cypselosomatidae #		Pseudopomyza atrimana (PSG)	BIOUG15794-B01	Norway	Sør-Trøndelag
Cypselosomatidae #		Pseudopomyza atrimana (PSG)	BIOUG15794-C12	Norway	Sør-Trøndelag
Cypselosomatidae #		Pseudopomyza atrimana (PSG)	BIOUG15954-E10	Norway	Sør-Trøndelag
Cypselosomatidae #		Pseudopomyza atrimana (PSG)	BIOUG15965-B02	Norway	Sør-Trøndelag
Cypselosomatidae #		Pseudopomyza atrimana (PSG)	DEBU01089691	Russia	Altai Krai
Cypselosomatidae#		Pseudopomyza atrimana (PSG)	KWi-105	Finland	Tavastia boreali
Cypselosomatidae #		Pseudopomyzella flava	BIOUG84428-H04	Costa Rica	Limon
Diopsidae*	Diopsinae	Diopsis Linnaeus	BIOUG35719-C09	Gabon	Moyen-Ogoou
Diopsidae*	Diopsinae	Diopsis Linnaeus	BIOUG36082-D01	Gabon	Moyen-Ogoou

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TABLE 4.4. (Continued)

Family	Subfamily	Taxon name	Sample ID	Country	State/Province
Diopsidae*	Diopsinae	Sphyracephala subbifasciata Fitch	08TTML-2175	Canada	Ontario
Diopsidae*	Diopsinae	Sphyracephala subbifasciata Fitch	BIOUG09358-H11	Canada	Ontario
Diopsidae*	Diopsinae	Sphyracephala Say	BIOUG02140-C09	Pakistan	Islamabad
Diopsidae*	Diopsinae	Sphyracephala Say	BIOUG21741-E12	Pakistan	Punjab
Fergusoninidae		Fergusonina Malloch	BIOUG01078-F07	Australia	Australian Capital Territory
Fergusoninidae		Fergusonina Malloch	BIOUG02178-C03	Australia	Australian Capital Territory
Fergusoninidae		Fergusonina Malloch	BIOUG37515-G02	Australia	New South Wales
Fergusoninidae		Fergusonina Malloch	BIOUG41195-F01	Australia	Queensland
Fergusoninidae		Fergusonina Malloch	BIOUG45874-D06	Australia	New South Wales
Fergusoninidae		Fergusonina Malloch	gvc17788-1L	Australia	Queensland
Fergusoninidae		Fergusonina Malloch	BIOUG46112-F01	Australia	New South Wales
Micropezidae	Taeniapterinae	Calosphen sp.	UGIC146-15	Ecuador	Pichincha
Micropezidae	Taeniapterinae	Calosphen sp.	UGIC145-15	Peru	Cusco
Micropezidae	Calobatinae	Cnodacophora immaculata Merrit & Peterson	CCDB-33291-A05	United States	Alaska
Micropezidae	Calobatinae	Cnodacophora stylifera (Loew)	CCDB-33291-A01	Canada	Yukon Territory
Micropezidae	Calobatinae	Paracalobata columbiana (Merritt & Peterson)	CCDB-33291-A06	United States	Alaska
Micropezidae	Calobatinae	Paracalobata kennicotti (Banks)	CCDB-33291-A08	United States	Alaska
Micropezidae	Eurybatinae	Cothornobata paieroi Marshall & Yang	UGIC248-15	Vietnam	Ninh Binh
Micropezidae	Eurybatinae	Crepidochetus debilis (Walker)	Sample-demo68	Papua New Guinea	Mt. Wilhelm
Micropezidae	Eurybatinae	Crosa petasibarba (Enderlein)	Sample-demo42	Papua New Guinea	Madang
Micropezidae	Taeniapterinae	Grallipeza nigrinotata group	debu01089012	Peru	Cusco
Micropezidae	Taeniapterinae	Grallipeza nigrinotata Hennig	debu00388291	Bolivia	Santa Cruz
Micropezidae	Taeniapterinae	<i>Grallipeza</i> <i>unimaculata</i> (Macquart)	DEBU00402487	Brazil	Amazonas
Micropezidae	Metopochetinae	Metopochetus impar McAlpine	BIOUG43919-E08	Australia	Queensland

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TABLE 4.4. (Continued)

Family	Subfamily	Taxon name	Sample ID	Country	State/Province
Micropezidae	Micropezinae	Micropeza albiseta (Czerny)	BIOUG19591-G09	Costa Rica	Guanacaste
Micropezidae	Micropezinae	Micropeza albiseta (Czerny)	BIOUG28056-B11	Costa Rica	Guanacaste
Micropezidae	Eurybatinae	Papeza szentivanyi McApline	Sample-demo61	Papua New Guinea	Mt. Wilhelm
Neriidae	Neriinae	Glyphidops durus (Cresson)	BIOUG27990-D12	Costa Rica	Guanacaste
Neriidae	Neriinae	<i>Glyphidops</i> Enderlein	BIOUG08901-D02	Costa Rica	Guanacaste
Neriidae	Telostylinae	<i>Telostylinus</i> <i>lineolatus</i> (Wiedemann)	gvc9544-1L	Australia	Queensland
Neriidae	Telostylinae	<i>Telostylinus</i> <i>lineolatus</i> (Wiedemann)	gvc9593-1L	Australia	Queensland
Neriidae			BIOUG04585-F10	Costa Rica	Guanacaste
Neriidae			BIOUG08901-C08	Costa Rica	Guanacaste
Neriidae			BIOUG28180-C08	Costa Rica	Guanacaste
Neriidae			BIOUG43544-C09	Australia	Queensland
Neriidae			BIOUG43960-E04	Australia	Queensland
Sphaeroceridae*	Archiborborinae	Antrops yungas Kits & Marshall	DEBU0572	Peru	Cusco
Sphaeroceridae*	Copromyzinae	Copromyza equina Fallén	DEBU0591	United States	California
Strongylophthalmyiidae		Strongylophthalmyia angustipennis Melander	10BBCDIP-1437	Canada	Saskatchewan
Strongylophthalmyiidae		Strongylophthalmyia angustipennis Melander	10BBCDIP-3437	Canada	Alberta
Strongylophthalmyiidae		Strongylophthalmyia pengellyi Barber	BIOUG04612-H06	Canada	Saskatchewan
Strongylophthalmyiidae		Strongylophthalmyia pengellyi Barber	BIOUG07330-G01	Canada	Saskatchewan
Strongylophthalmyiidae			BIOUG14981-D03	Malaysia	Selangor
Strongylophthalmyiidae			BIOUG15985-B01	Malaysia	Selangor
Strongylophthalmyiidae			BIOUG16573-B01	Malaysia	Selangor
Tanypezidae		Neotanypeza claripennis (Schiner)	DEBU00177864	Ecuador	Pichincha
Tanypezidae		Neotanypeza claripennis (Schiner)	DEBU00177866	Ecuador	Pichincha
Tanypezidae		Neotanypeza Hendel	BIOUG27746-G02	Costa Rica	Guanacaste
Tanypezidae		Neotanypeza Hendel	BIOUG28379-D10	Costa Rica	Guanacaste
Tanypezidae		Tanypeza longimana Fallén	10BBCDIP-1373	Canada	Ontario
Tanypezidae		Tanypeza longimana Fallén	10BBCDIP-3091	Canada	Saskatchewan

v.1.26 (Larsson, 2014) and further aligned or modified by manually excluding non-informative base pairs to maintain the reading frame if deemed necessary.

Single gene trees: Maximum-likelihood analysis (ML) was conducted using IQ-Tree (2.1.2) (Nguyen *et al.*, 2015) run on XSEDE on the CIPRES cluster. The dataset was partitioned by gene. Best-fit evolution models were determined by ModelFinder (Kalyaanamoorthy *et al.*, 2017) for each gene locus as listed in Table 4.6, and branch supports were obtained with the ultrafast bootstrap algorithm (Hoang *et al.*, 2018).

Concatenated multi-gene trees: Representatives from each genus (with preference given to species that maximized global coverage) from each family were selected for the analysis. Sequences were concatenated and partitioned using the AMAS program as a Python module (Borowiec, 2016). The ML analysis was performed as described above, with partition type set to allow for different evolutionary rates (-p). Evolutionary models (6) determined by ModelFinder are listed in Table 4.7.

Bayesian analysis (BI) was conducted using MrBayes (3.2.7a) (Ronquist and Huelsenbeck, 2003) run on XSEDE on CIPRES, using a partition block produced by the AMAS program. Settings for the Markov Chain Monte Carlo (MCMC) simulation include four chains running simultaneously for 2,000,000 generations twice, sampling trees every thousand generations with a burn-in of 25%.

Both single gene trees and concatenated trees were rooted on the Diopsidae clade, bootstrap support values and posterior probability estimations for each node were visualized, and the output trees were exported as PDF files in FigTree (Rambaut, 2009). Trees were visually enhanced in Adobe Illustrator CC.

Results

All Cypselosomatidae *s.s.* and Tanypezidae returned sequences, compared to the six out of twenty-two samples of the former Pseudopomyzidae. The low success rate in sequencing specimens of the former Pseudopomyzidae is most likely due to the age and sub-ideal preservation methods after collection; only three of the six specimens that did return sequences yielded barcodes of 450 basepair (bp) length or greater.

Sequence lengths after editing and alignment were 509 bp for 12S, 545 bp for 28S, 493 bp for 28S-D2, 584 bp for 28S-D3, 816 bp for COI-3P and 579 bp for COI-5P, resulting in a total of 3526 bp for the final concatenated dataset.

Single-gene trees: Independent analysis of all six gene regions did not consistently show families of Nerioidea as monophyletic. None of the single gene trees showed Micropezidae and Neriidae as monophyletic, and only one showed Cypselosomatidae *s.l.* as monophyletic (Figs. 110.1–6). The 28S tree showed Cypselosomatidae *s.s.*

TABLE 4.5. Primers used for PCR amplification.

Gene	Primer name	Sequences 5'-3'	References
locus			
12S	12Sbi	AAGAGCGACGGCGATGTGT	Simon et al. 1994
	12Sh	GACAAAATTCGTGCCAGCAGT	Simon et al. 1994
28S-2	28S-Dipt-4534F	CCTATTCTCAAACTTTAAATGGG	Gibson et al. 2011
(28S)	28S 2073-R	GGAACCGTATTCCCTTTCG	Scott Kelso - unpublished
28S-3	28S-Dipt-4997F	GGAGGACTGAAGTGGAGAAGG	Gibson et al. 2011
(28S-D2)	28S 2456-R	CTCAATCTTCAGAGCCAATCC	Scott Kelso - unpublished
28S-5	28S 3631-F	CTCGGCCTATCGATCCTTTTGG	Gibson et al. 2011
(28S-D3)	28S-Dipt-7176R	CCACTTACAACACCTTGCC	Scott Kelso - unpublished
COI-3'	Jerry	CAACATTTATTTTGATTTTTTGG	Simon et al. 1994
(COI-3P)	Pat	TCCATTGCACTAATCTGCCATATTA	Gibson et al. 2011; modified
			from Simon et al. 1994
COI-5'	C_LepFolF	LepF1:LCO1490	
(COI-5P)	C_LepFolR	LepR1:HCO2198	
	LepF1	ATTCAACCAATCATAAAGATATTGG	Hebert et al. 2004
	LepR1	TAAACTTCTGGATGTCCAAAAAATCA	Hebert et al. 2004
	MLepF1	GCTTTCCCACGAATAAATAATA	Hajibabaei et al. 2006
	MLepF2	GCWTTCCCMCGWATAAATAATATAAG	Hebert et al. 2013
	MLepR2	GTTCAWCCWGTWCCWGCYCCATTTTC	Hebert et al. 2013
	LCO1490	GGTCAACAAATCATAAAGATATTGG	Folmer et al. 2011
	HCO2198	TAAACTTCAGGGTGACCAAAAAATCA	Folmer et al. 2011
	LCO1490_t1	TGTAAAACGACGGCCAGTGGTCAACAAATCATAAAGA	Foottit et al. 2009
	HCO2198_t1	TATTGGCAGGAAACAGCTATGACTAAACTTCAGGGTGA	Foottit et al. 2009
	PcoF	CCAAAAAATCACCTTCAACTAATCATAAAAAATATYAG	Park et al. 2010

TABLE 4.6 Evolutionary model used for each single gene maximum-likelihood analysis. Abbreviations: F, equal/unequal frequencies; G, Gamma rate variation; GTR, generalized time-reversible model; I, proportion of invariable sites; R, substitution rate variation; TVM, transversion model.

Gene locus	Number of sequences	Number of parsimony informative sites	Evolutionary model
12S	69	242	GTR+F+R3
28S	77	87	GTR+F+I+G4
28S-D2	75	65	TVM+F+I+G4
28S-D3	84	138	GTR+F+I+G4
COI-3P	88	251	GTR+F+I+G4
COI-5P	78	358	GTR+F+I+G4

TABLE 4.7 Evolutionary model used for each partition in a maximum-likelihood analysis with one representative from each taxon. Abbreviations see Table 4.6.

Gene locus	Number of sequences	Number of parsimony informative sites	Evolutionary model
12S	28	194	GTR+F+I+G4
28S	31	57	TVM+F+R2
28S-D2	30	55	TVM+F+I+G4
28S-D3	34	113	GTR+F+I+G4
COI-3P	30	311	GTR+F+I+G4
COI-5P	32	219	GTR+F+I+G4

as the sister group to the former Pseudopomyzidae (Fig. 110.2). The 28S-D2 tree showed part of Neriidae as the sister group to the former Pseudopomyzidae (Fig. 110.3). All remaining trees showed the former Pseudopomyzidae as paraphyletic with regard to Neriidae (Figs. 110.1, 4–6) (disregarding the position of *Pseudopomyzella flava* on the COI-5P tree).

Concatenated multi-gene trees: The trees produced by ML and BI analyses were mostly congruent and the major clades have good node support (ML bootstrap support ≥95%, BI posterior probability ≥0.95) (Figs. 111.1-2). Both analyses showed all families to be monophyletic, except for the former Pseudopomyzidae with Pseudopomyzella flava placed outside of the superfamily Nerioidea (Cypselosomatidae Micropezidae + Neriidae). Latheticomyia is recovered as a sister taxon to Neriidae in the BI tree, thus rendering the former Pseudopomyzidae paraphyletic even when disregarding the unexpected position of Pseudopomyzella flava. Although Latheticomyia is shown to be basal to the remaining former Pseudopomyzidae (except Pseudopomyzella) in the ML tree, node support for the former Pseudopomyzidae clade is weak. The BI tree also shows a polytomy for the basal *Pseudopomyza* species. Node support for the entire *Pseudopomyza* genus is weak for the ML tree.

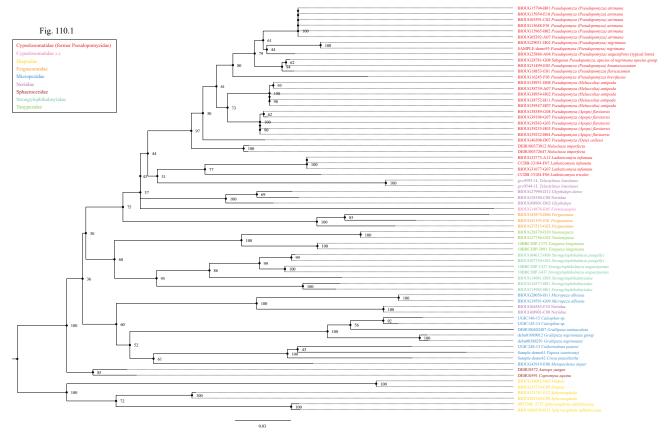
Summary discussion

The molecular analysis (Figs. 111.1–2) showed a sister-group relationship between *Pseudopomyza* (*Pseudopomyza*) atrimana and *P.* (*Pseudopomyza*) nigrimana (from the *P. nigrimana* species group), with *P.*

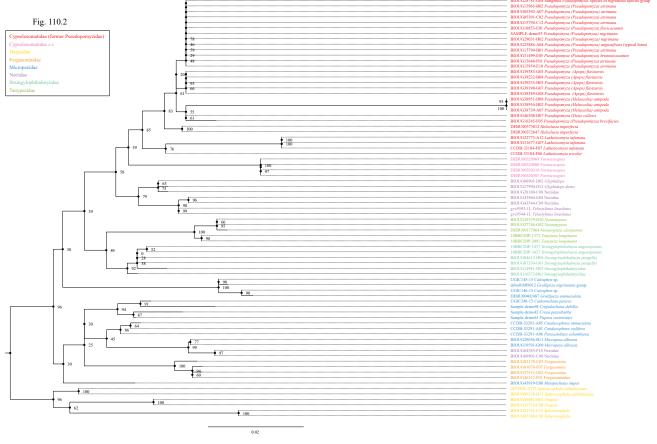
nigrimana + P. atrimana forming the sister group to the remaining members of the P. nigrimana species group. This contradicts the monophyly of the P. nigrimana species group otherwise indicated by unique morphological synapomorphies including the fused and strongly dorsally arched pregonites, the similarly arched phallapodeme and symmetrical distiphallus.

The morphological and molecular analyses differ regarding the placement of P. (Pseudopomyza) brevifacies and P. (Dete) collessi; the ML tree (Fig. 111.1) places P. (Pseudopomyza) brevifacies as a sister taxon to the remaining Pseudopomyza species and P. (Dete) collessi as a sister taxon to P. (Apops) flavitarsis + P. (Heluscolia) antipoda; the BI tree (Fig. 111.2) shows P. (Pseudopomyza) brevifacies, P. (Dete) collessi, Apops and Pseudopomyza s.s. as a polytomy. Pseudopomyza (Dete) collessi is shown as the sister group to the rest of the Pseudopomyza on the morphological analysis (Fig. 106.1-4) but several characters interpreted as homoplasies could be synapomorphies indicating alternative interpretations of relationship to other subgenera, especially Apops. Pseudopomyza (Pseudopomyza) brevifacies shares a number of synapomorphies confirming its placement in the subgenus *Pseudopomyza* (Characters 3, 9, 14, 22, 23, 33), and therefore is unlikely to be a basal lineage of Pseudopomyza as shown in the molecular trees.

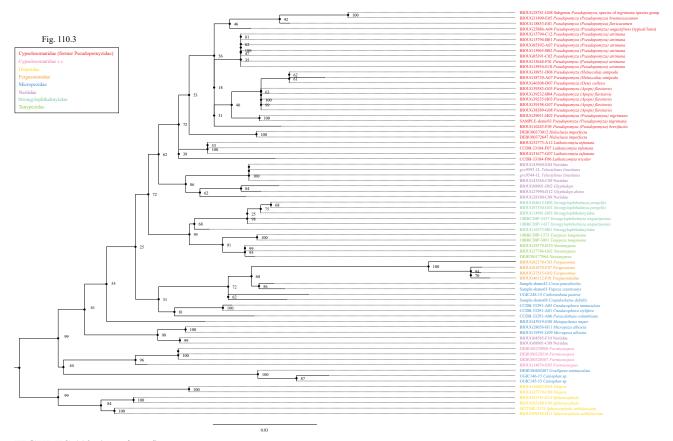
The addition of *Pseudopomyzella* COI-5P data to the analysis did not provide better resolution and instead resulted in unexpected tree topologies. All resulting molecular trees placed *Pseudopomyzella* outside of Nerioidea, as sister group to all taxa except Diopsidae (single gene tree and ML tree) (Figs. 110.6, 111.1) or sister to *Sphyracephala* (BI tree) (Fig. 111.2) (with weak support). *Latheticomyia* is shown to be basal to the former



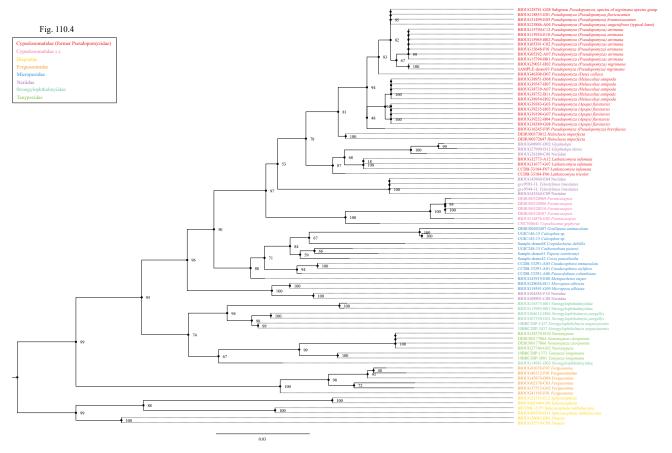
FIGURES 110.1–6: Single-gene trees of Nerioidea. 110.1, 12S; 110.2, 28S; 110.3, 28S-D2; 110.4, 28S-D3; 110.5, COI–3P'; 110.6, COI–5P'.



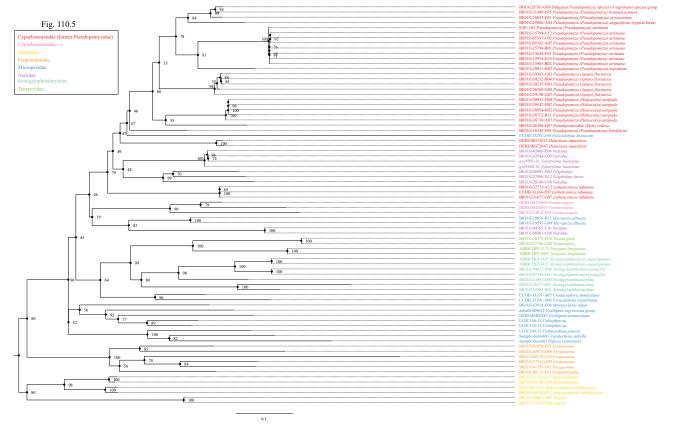
FIGURES 110. (Continued)



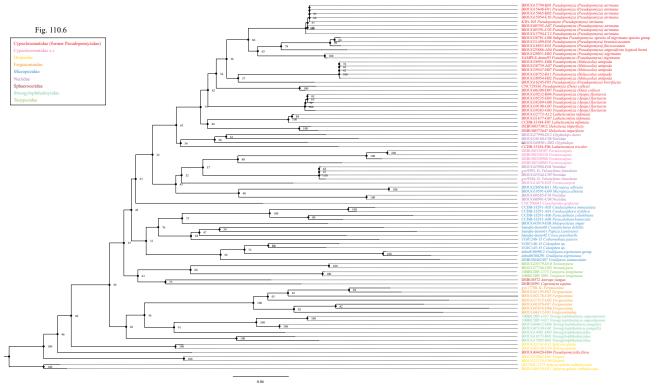
FIGURES 110. (Continued)



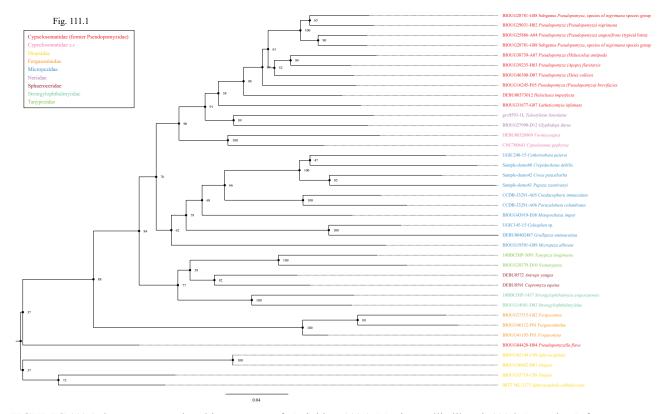
FIGURES 110. (Continued)



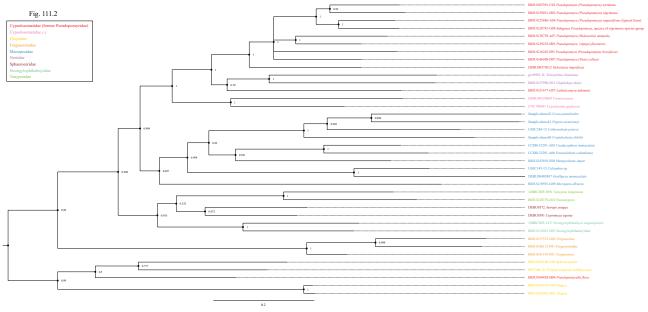
FIGURES 110. (Continued)



FIGURES 110. (Continued)



FIGURES 111.1–2: Concatenated multi-gene trees of Nerioidea. 111.1, Maximum likelihood; 111.2, Bayesian Inference.



FIGURES 111. (Continued)

Pseudopomyzidae group (except Pseudopomyzella) in the ML tree (Fig. 111.1) but as a sister taxon to Neriidae in the BI tree (Fig. 111.2), conflicting with the morphological analysis (Fig. 104) where Latheticomyia (and Tenuia) is shown to be closer to Cypselosomatidae s.s. than to Pseudopomyza (however with relatively weak support). The unusual placement of *Pseudopomyzella* shown by the molecular analyses (Figs. 110.6, 111.1-2) in contrast to the morphological analysis (Fig. 104), which recovered it (with Eopseudopomyza) as the sister group to the rest of the Cypselosomatidae s.l., is most likely due to the lack of sufficient sequence data (only COI-5P available). Both ML and BI trees (Figs. 111.1-2) showed Heloclusia to be the sister group to Pseudopomyza, rather than a part of a larger clade next to Dete as in the morphological tree (Fig. 104).

The molecular phylogeny presented here (concatenated multi-gene ML and BI trees; Figs. 111.1-2) differs from the phylogenetic hypotheses of D.K. McAlpine (1966), J.F. McAlpine (1989), Hennig (1971) or Griffiths (1972). Instead of Cypselosomatidae s.s. appearing as the sister group to the former Pseudopomyzidae or any of its constituents, in four of the single-gene trees (disregarding the position of a Micropezidae on the COI-3P tree) and in the BI tree Neriidae is shown as rendering the former Pseudopomyzidae paraphyletic (Figs. 110.1, 4-6; 111.2). This is surprising as most studies (including the morphological analysis here) indicate that the former Pseudopomyzidae and Cypselosomatidae s.s. are closely related if not synonyms. However, only two out of the six genes were successfully sequenced for Cypselosoma gephyrae, so these anomalous results probably reflect a molecular dataset that is inadequate for a meaningful comparison of the molecular and morphological evidence.

The molecular analysis recovered only *Micropeza* (Micropezinae) as the basal lineage of Micropezidae, even though Jackson (2019) suggests that Calobatinae (including *Compsobata* and *Cnodacophora*) is the basal micropezid lineage, and even though both subfamilies displayed all the hypothesized groundplan characters mentioned in the morphological analysis above. However, both the molecular (ML and BI trees) and morphological analyses did recover Micropezidae as the sister taxon to the remaining families of Nerioidea, in contrast to phylogenies that proposed Cypselosomatidae *s.l.* as the basal lineage of the Nerioidea (McAlpine, 1966).

Lonsdale's (2020) proposed Nerioidea phylogeny, similar to that of Hennig (1971) and Griffiths (1972) but with the addition of Fergusoninidae to the Cypselosomatidae s.l. clade and the addition of Tanypezidae and Strongylophthalmyiidae to the Neriidae + Micropezidae clade, is also not supported by the ML and BI analyses (Figs. 111.1–2). Neither does the morphological analysis recover Strongylophthalmyiidae, Tanypezidae and Fergusoninidae in the superfamily (Fig. 104). However, some of the single-gene trees (12S, 28S, 28S-D2, COI-3P) (Figs. 110.1, 110.2, 110.3, 110.5) did show the Tanypezidae + Strongylophthalmyiidae clade within the

Nerioidea. Tanypezidae and Strongylophthalmyiidae were recovered as closer to Sphaeroceridae than to the Nerioidea in the molecular analyses (ML and BI) (Figs. 111.1–2), while the morphological analysis (Fig. 104) placed the Tanypezidae + Strongylophthalmyiidae clade as the sister group to the Nerioidea. Fergusoninidae was recovered as more closely related to Diopsidae than to Nerioidea in the molecular analysis (Figs. 111.1–2), however Agromyzidae (usually considered to be the closest group to Fergusoninidae) was not included in the molecular analysis. When both Agromyzidae and Fergusoninidae were included in the morphological analysis (Fig. 104), the family Fergusoninidae was recovered as the sister taxon to Agromyzidae, as expected.

The molecular analyses are insufficient to either conclusively refute or strongly support the paraphyly of the former Pseudopomyzidae or its position in a broadly defined Cypselosomatidae s.l. as indicated by the morphological analysis. Future studies will require a more complete set of genera from the Cypselosomatidae s.l. as well as a wider selection of Schizophora outgroups and sequenced genes to obtain a more fully resolved and stable phylogeny. Testing and improving the family level morphological analyses will require first-hand examination of the morphology and anatomy, especially novel character states, of related Schizophora families.

Zoogeography overview

The three extant genera of Cypselosomatidae s.s. are found in the Australian, Oriental and Palaearctic regions: Clisa (2 described species) in Australia, Cypselosoma (2 described and all known undescribed species) in the Oriental and Palaearctic regions, and Formicosepsis (9 described and all known undescribed species) in the Oriental region. This group seems to have a more restricted distribution than the genera formerly included in Pseudopomyzidae and overlaps with only two of them (Tenuia and some Pseudopomyza).

Members of the former Pseudopomyzidae are found worldwide except for the Afrotropical region. These include six extant genera and one fossil genus: *Heloclusia* (1 described species) from southern South America, *Latheticomyia* (7 described and 16 known undescribed species) from the New World, *Polypathomyia* (1 described species) from the eastern Palaearctic, the redefined *Pseudopomyza* from all regions except North America and Africa (Fig. 112), *Pseudopomyzella* (1 described species) from the Neotropics, *Tenuia* (2 described and 1 known undescribed species) from the Oriental and eastern Palaearctic region and *Eopseudopomyza* (2 described species) from Eocene Baltic amber.

Most *Pseudopomyza* species other than those of the *P. nigrimana* species group of *Pseudopomyza s.s.* are found in the Australasian region. The species known from Australia include *P. arenae* McAlpine 2019, *P. medianentis* Yau & Marshall **sp. nov.**, and *P. collessi* McAlpine 1994; those in New Zealand include *P. flavitarsis* (Harrison 1959), *P.*

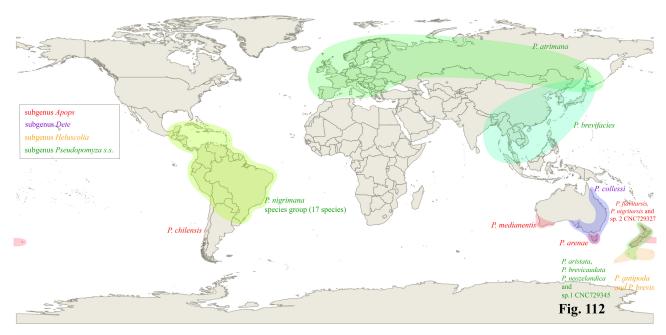


FIGURE 112. Global distribution of the genus *Pseudopomyza*.

antipoda (Harrison 1959), *P. aristata* (Harrison 1959), *P. brevicaudata* (Harrison 1964), *P. brevis* (Harrison 1976), *P. neozelandica* (Malloch 1933), *P. nigritarsis* Yau and Marshall **sp. nov.**, and two undescribed species (**sp. nov.** 1 CNC729345 and **sp. nov.** 2 CNC729327).

Among the New Zealand *Pseudopomyza* species, *P. brevis* and *P. antipoda* are coastal and restricted to oceanic islands. Both have been found in seabird (including shearwaters, petrels and albatrosses) nests and carrion, in coastal plant vegetation and in ground litter. *Pseudopomyza antipoda* is known from seal or sea-lion wallows and shoreline kelp strands (Harrison, 1976) and the Tasmanian *Pseudopomyza arenae* has been collected in beach dunes densely penetrated by burrows of Fairy Penguins and shearwaters (McAlpine, 2019).

The sister taxon of the coastal species *P. arenae* is *P. chilensis*, a species known from two specimens (1 male and 1 female) from a forested area at Pucón, Chile (Araucanía region) at the western base of the Andes. The Western Australian *P. medianentis* (also know from 1 male and 1 female) is another inland species seemingly isolated from the primarily coastal eastern Australian/New Zealand *Pseudopomyza* species.

Outside the Australasian region, *Pseudopomyza brevifacies* is only known from the Oriental region and *P. atrimana* is widespread across the Palaearctic region. The Neotropical *P. nigrimana* species group is diverse and found across Central and South America and in the Caribbean. The absence of this genus from the Nearctic region is surprising, especially considering that the Palaearctic *P. atrimana* is the immediate sister group to the Neotropical *P. nigrimana*-group. It seems very likely that *Pseudopomyza* once occurred in the Nearctic but later became extinct.

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Appendices

Catalog of former Pseudopomyzidae, now Cypselosomatidae in part

Museum acronyms:

AMS, Australian Museum, Sydney, New South Wales, Australia;

CBFC, Colección Boliviana de Fauna, La Paz, Bolivia; CSCA, California State Collection of Arthropods, California Department of Food and Agriculture, Sacramento, California, United States of America;

CMNZ, Canterbury Museum, Christchurch, New Zealand;

CNC, Canadian National Collection of Insects, Arachnids & Nematodes, Ottawa, Ontario, Canada;

HNHM, Hungarian Natural History Museum, Budapest, Hungary;

MIZA (Museo del Instituto de Zoología Agrícola, Maracay, Venezuela);

MNCR, Museo Nacional de Costa Rica, San José (including the collections of INBio, the Instituto Nacional de Biodiversidad = INBC);

MNNC, Museo Nacional de Historia Natural, Santiago, Chile;

MONZ, Museum of New Zealand, Wellington, New Zealand;

MUSM, Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru;

NHMUK, Natural History Museum (British Museum), London, U.K.;

NZAC, New Zealand Arthropod Collection, Landcare Research, Auckland, New Zealand;

QCAZ, Museo de Zoología, Pontificia Universidad Católica del Ecuador, Ouito, Ecuador;

SDEI, Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany;

SMNS, Staatliches Museum für Naturkunde , Stuttgart, Germany;

UNAM, Universidad Nacional Autónoma de México, Mexico City, Mexico;

USNM, United States National Museum, (National Museum of Natural History), Washington D.C., USA; UVGC, Collección de Artrópodos, Universidad de Valle

de Guatemala, Guatemala City, Guatemala;

WAM, Western Australian Museum, Perth, Western Australia, Australia;

ZISP, Russian Academy of Sciences, Zoological Institute, St. Petersburg, Russia;

ZMUM, Moscow State University, Moscow, Russia.

Genus EOPSEUDOPOMYZA Hennig

EOPSEUDOPOMYZA Hennig, 1971: 7. Type species: Eopseudopomyza kuehnei Hennig, 1971, mon.

KUEHNEI† Hennig, 1971: 7. H \circlearrowleft SMNS. Type locality: Baltic amber in SMNS. Distribution: Baltic amber.

SZADZIEWSKII† Hoffeins and Woznica, 2013: 319. HT \circlearrowleft SDEI. Type locality: Baltic amber in collections of C. and H.W. Hoffeins (Hamburg, Germany). Distribution: Baltic and Bitterfeld amber.

Genus HELOCLUSIA Malloch

HELOCLUSIA Malloch, 1933: 184 (Heleomyzidae). Type species: Heloclusia imperfecta Malloch, 1933, mon.

Hennig 1969:591 [as genus of Pseudopomyzidae].

IMPERFECTA Malloch 1933:186. HT & NHMUK. Type locality: "Concepción", Bío Bío, Chile. Distribution: Chile, Argentina.

Genus LATHETICOMYIA Wheeler

LATHETICOMYIA Wheeler, 1956: 306. Type species: Latheticomyia tricolor Wheeler, 1956 (orig. des.).

Hennig 1969: 591 [as genus of Pseudopomyzidae].

TRICOLOR Wheeler 1956: 307. HT & USNM. Type locality: U.S.A., Arizona, Coronado National Forest, Chiricahua Mountains, Ronquist ler Park Campground. Distribution: Costa Rica, Guatemala, Honduras, U.S.A.

LINEATA Wheeler 1956: 310. HT & USNM. Type locality: U.S.A., Arizona, about 25 miles south (airline) of Prescott, Prescott National Forest, Horse Theif Basin Recreation Area. Distribution: U.S.A.

INFUMATA Wheeler 1956: 312. HT & USNM. Type locality: Nicaragua, north of Matagalpa, Santa María de Ostuma. Distribution: Costa Rica, Venezuela, Nicaragua.

LONGITEREBRA Hennig 1969: 592. HT ♀ CNC. Type locality: Peru, Madre de Dios, Avispas. Distribution: Peru.

ROTUNDICORNIS Hennig 1969: 592. HT $\stackrel{\frown}{\hookrightarrow}$ CNC. Type locality: Mexico, Durango, 10 mi W. El Salto. Distribution: Mexico.

PERUANA Marques and Rafael 2016: 428. HT ♂ MUSM. Type locality: Peru, Cusco, 19 km W Quincemil, Río Araza tributary. Distribution: Peru.

XANTHA Marques and Rafael 2016: 430. HT ♂ MUSM. Type locality: Peru, Cusco, 19 km W Quincemil, Río Araza tributary. Distribution: Peru.

Genus POLYPATHOMYIA Krivosheina

POLTPATHOMYIA Krivosheina, 1979: 106. Type species: Polypathomyia stackelbergi Krivosheina, 1979, mon.

STACKELBERGIKrivosheina 1979: 108. HT♀ZISP. Type locality: Russia, Kunashir Island, Mendeleyevo. Distribution: Russia.

Genus PSEUDOPOMYZA Strobl

PSEUDOPOMYZA Strobl 1893: 284. Type species:

Pseudopomyza nitidissima Strobl, 1893 (=Opomyza atrimana Meigen, 1830), mon.

APOPS: See below as subgenus. DETE: see below as subgenus.

HELUSCOLIA: see below as subgenus.

MACALPINELLA Papp, 2005: 189. Type species: Macalpinella brevifacies Papp, 2005 (orig. des.). Reduced to subgenus by Buck & McAlpine, 2010: 823. Synonymized with subgenus Pseudopomyza by **new synonymy**.

PROTOBORBORUS Malloch, 1933: 261. Type species: Protoborborus neozelandicus Malloch, 1933 (orig. des.). Synonymized with Pseudopomyza by McAlpine, 1966: 682.

RHINOPOMYZELLA Hennig, 1969: 596. Type species: Rhinopomyzella nigrimana Hennig, 1969 (orig. des.). Reduced to subgenus by McAlpine, 1994: 182. Synonymized with subgenus Pseudopomyza by **new synonymy**.

Subgenus APOPS McAlpine

APOPS McAlpine 1994:183. Type species: Pseudopomyza flavitarsis Harrison (orig. des.)

ARENAE McAlpine 2019: 88. HT & AMS. Type locality: Australia, Tasmania, Bruny Island (Penguin Rookery), The Neck. Distribution: Australia.

CHILENSIS Yau & Marshall 2022: 79. HT & MNNC. Type locality: Chile, Araucanía, Pucón. Distribution: Chile.

FLAVITARSIS (Harrison, 1959): 121 (Heloclusia). HT & NZAC. Type locality: New Zealand, Auckland, Owairaka. Distribution: New Zealand. Pseudopomyza (Apops) flavitarsis McAlpine 1994: 183.

MEDIANENTIS Yau & Marshall 2022: 84. HT & WAM. Type locality: Australia, Western Australia, Mount Frankland, ~30 km N Walpole. Distribution: Australia.

NIGRITARSIS Yau & Marshall 2022: 115. HT NZAC. Type locality: New Zealand, Waikako. Distribution: New Zealand, Mercury Islands, Poor Knights Islands, Chatham Islands.

Subgenus DETE McAlpine

DETE McAlpine 1994:183. Type species: Pseudopomyza collessi McAlpine (orig. des.)

COLLESSI McAlpine 1994: 185 (Dete). HT & AMS. Type locality: Australia, New South Wales, Wentworth Falls, Blue Mountains. Distribution: Australia.

Subgenus HELUSCOLIA Harrison

HELUSCOLIA Harrison 1959:119 (as subgenus of Heloclusia Malloch, 1933). Type species: Pseudopomyza antipoda Harrison (orig. des.). Synonymized with Pseudopomyza by McAlpine 1966:683. Restituted from synonymy with Pseudopomyza by Yau *et al.*, 2024.

ANTIPODA (Harrison, 1955): 215 (Heloclusia). HT & MONZ. Type locality: New Zealand, Antipodes Island, Ringdove Bay. Distribution: New Zealand. Protoborborus antipodes, Harrison, 1976: 145. Pseudopomyza antipoda, McAlpine, 1994: 182.

BREVIS (Harrison, 1976): 144 (Protoborborus). HT & NZAC. Type locality: New Zealand, Snares Island. Distribution: New Zealand. Pseudopomyza brevis, McAlpine, 1994: 182.

Subgenus PSEUDOPOMYZA Strobl

PSEUDOPOMYZA Strobl 1893:284. Type species: Pseudopomyza nitidissima Strobl (=Opomyza atrimana Meigen, 1830), mon.

ADUNCA Yau & Marshall 2022: 102. HT & QCAZ. Type locality: Ecuador, Pichincha, Quito, 10km NW, Valley nr. Hostería San Jorge. Distribution: Bolivia, Ecuador, Venezuela.

ALBIMANA (Hennig, 1969): 598 (Rhinopomyzella). HT & CNC. Type locality: Brazil, Nova Teutônia. Distribution: Brazil, Costa Rica, Dominican Republic, Ecuador, Grenada, Honduras, Venezuela. Pseudopomyza albimana Yau & Marshall 2022: 104.

AMPLIATA Yau & Marshall 2022: 106. HT & UVGC. Type locality: Guatemala, El Progreso, Cerro Pinalón. Distribution: Guatemala.

ANGUSTIFRONS Yau & Marshall 2022: 107. HT & UVGC. Type locality: Guatemala, Zacapa, 7km N San Lorenzo. Distribution: Guatemala, Mexico.

ARISTATA (Harrison, 1959): 123 (Heloclusia). HT & NZAC. Type locality: New Zealand, Little Barrier Island. Distribution: New Zealand. Pseudopomyza aristata, McAlpine, 1994: 182.

ATRIMANA (Meigen, 1830): 106 (Opomyza). HT & depository unknown (Becker, 1902: 307, types not found). Type locality: Germany. Distribution: Austria, Finland, Germany, Netherlands, Norway, Russia, Slovakia, Spain, United Kingdom.

nitidissima Strobl 1893: 284. HT ♀ depository unknown (Chvála, 2008: 196, probably lost). Type locality: Austria, Seitenstetten.

BINAEVIA Yau & Marshall 2022: 108. HT & MNCR. Type locality: Costa Rica, Cartago, Tapantí National Park. Distribution: Costa Rica.

BREVICAUDATA (Harrison, 1964): 312 (Heloclusia). HT & NZAC. Type locality: New Zealand, Campbell Island, Beeman Camp. Distribution: New Zealand. Protoborborus brevicaudata (Harrison) 1976: 145. Pseudopomyza brevicaudata, McAlpine, 1994: 182.

BREVIFACIES Papp 2005: 189 (Macalpinella). HT & HNHM. Type locality: Taiwan, Nantou Hsien, Shuili, forest undergrowth. Distribution: Bhutan, Japan, Malaysia, Taiwan.

BRUNNEICACUMEN Yau & Marshall 2022: 109. HT & MNCR. Type locality: Costa Rica, Puntarenas, Monteverde Biological Reserve. Distribution: Costa Rica, Guatemala, Venezuela.

CORDATA Yau & Marshall 2022: 111. HT & MNCR.

Type locality: Costa Rica, Puntarenas, Monteverde Biological Reserve. Distribution: Costa Rica, Peru.

CYATHIFORMIS Yau & Marshall 2022: 112. HT & MNCR. Type locality: Costa Rica, Cartago, Tapantí National Park, La Esperanza del Guarco. Distribution. Costa Rica.

FLAVICACUMEN Yau & Marshall 2022: 114. HT & MNCR. Type locality: Costa Rica, Cartago, Hwy 2, km 67. Distribution: Costa Rica, Ecuador, Venezuela.

GAMBIFORMIS Yau & Marshall 2022: 115. HT & USNM. Type locality: Ecuador, Chimborazo, "Linje". Distribution: Ecuador.

INFLEXA Yau & Marshall 2022: 116. HT & MNCR. Type locality: Costa Rica, Cartago, Tapantí-Macizo de la Muerte National Park, La Esperanza del Guarco. Distribution: Costa Rica.

MACHAERA Yau & Marshall 2022: 118. HT & UVGC. Type locality: Guatemala, El Progreso, Cerro Pinalón. Distribution: Guatemala.

NEOZELANDICUS (Malloch, 1933): 262 (Protoborborus). HT ♂ NHMUK (AT ♀ CMNZ). Type locality: New Zealand, Wanganui. Distribution: New Zealand. Pseudopomyza neozelandica, Mathis 1989: 470.

NIGRIMANA(Hennig, 1969): 598 (Rhinopomyzella). HT & CNC. Type locality: Brazil, Nova Teutônia. Distribution: Argentina, Belize, Bolivia, Brazil, Columbia, Costa Rica, Cuba, Dominica, Dominican Republic, Ecuador, Guatemala, Guyana, Honduras, Jamaica, Mexico, Nicaragua, Panama, Peru, Puerto Rico, Trinidad and Tobago, Venezuela. Pseudopomyza nigrimana Yau & Marshall 2022: 137.

PARABINAEVIA Yau & Marshall 2022: 126. HT

♂ MIZA. Type locality: Venezuela, Aragua, Maracay, Rancho Grande Biological Station. Distribution: Peru, Venezuela.

PROBOSCIS Yau & Marshall 2022: 127. HT & MNCR. Type locality: Costa Rica, Limón, Estrella Valley, Pandora. Distribution: Costa Rica, Guatemala.

PROLATA Yau & Marshall 2022: 128. HT & QCAZ. Type locality: Ecuador, Napo, SierrAzul Reserve, 14km W Cosanga. Distribution: Ecuador.

SIMULATRIX Yau & Marshall 2022: 129. HT \circlearrowleft CSCA. Type locality: Bolivia, La Paz, near Mapiri Arroyo Tuhiri. Distribution: Bolivia.

Genus PSEUDOPOMYZELLA Hennig

PSEUDOPOMYZELLA Hennig, 1969: 594. Type species: Pseudopomyzella flava Hennig, 1969, mon.

FLAVA Hennig 1969: 595. HT & CNC. Type locality: Peru, Madre de Dios, Avispas. Distribution: Bolivia, Ecuador, Guatemala, Peru, Venezuela.

Genus TENUIA Malloch

TENUIA Malloch, 1926: 493 (Geomyzidae). Type species: Tenuia nigripes Malloch, 1926 (orig. des.).

NIGRIPES Malloch 1926: 493. HT ♀ depository unknown. Type locality: Baguio, Benguet, Luzon, Philippines. Distribution: Philippines.

SMIRNOVI Shatalkin 1994: 143. HT & ZMUM. Type locality: Primorskiy Kray, Khasan area, "Kedrovaya Pad" Reserve. Distribution: India, Russia.