



# Phylogeny of the old and fragmented genus *Austrocoenosia* Malloch reveals new evidences on the morphology and evolution of the genera *Coenosia* Meigen and *Neodexiopsis* Malloch (Diptera: Muscidae)

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## Abstract

Coenosiini (Diptera: Muscidae) is a large cosmopolitan tribe of muscids, within which *Coenosia* Meigen and *Neodexiopsis* Malloch are the genera with the largest number of species. In this work, we revised for the first time, all the species placed by Malloch (1934) under *Austrocoenosia*, an endemic genus from the Andean Patagonian Forests, whose species are now placed in *Coenosia* and *Neodexiopsis*. We provide detail redescrptions for eight species placed by Malloch (1934) under *Austrocoenosia*, and described two new species (*Coenosia delneneo* **sp. nov.** and *Coenosia patagonica* **sp. nov.**), with high quality photographs detailing new structures of the male and female terminalia. To establish the position of the species of *Austrocoenosia* with respect to *Coenosia* and *Neodexiopsis*, we made a phylogenetic analysis using implied weighting for 36 taxa and 132 morphological characters of adults, including male and female genitalia. We recovered all species of *Austrocoenosia* as *Coenosia* species. We propose the following nomenclature actions: *Austrocoenosia* as a junior synonymy of *Coenosia* (**syn. rest.**); *Coenosia brevicornis* (Malloch) (**comb. nov.**), *Coenosia dubia* (Bigot) (**comb. rest.**); *Coenosia hucketti*, Pont (**nom. nov.**) and *Coenosia nigerrima* (Malloch) (**comb. rest.**). We also propose *Coenosia spumicola* Pont as an unplaced species of *Coenosia* sensu lato. Finally, we updated the geographic distributions for all species and observed several new male and female terminalia structures, which enriched the discussion of the genera and the tribe.

## Key words

Coenosiini, new species, new synonyms, predator, South America

## 1. Introduction

As part of the revision of the muscids of Argentina and Chilean Patagonia (southern South America), Malloch (1934) erected the new genus *Austrocoenosia* Malloch, 1934, within the tribe Coenosiini (Diptera, Muscidae, Coenosiinae) endemic to areas currently considered as part of the Andean biogeographic region (Morrone 2015). This new genus was differentiated from the larger and cosmopolitan genus *Coenosia* Meigen, 1826 only by the presence of one seta on the posterodorsal surface of the hind tibia, in addition to the anterodorsal and anteroventral setae present in *Coenosia* specimens. *Austrocoenosia* included six new species (*Austrocoenosia aurifera* Malloch, 1934; *Austrocoenosia argentifrons* Malloch, 1934; *Austrocoenosia brevicornis* Malloch, 1934; *Austrocoenosia nigerrima* Malloch, 1934; *Austrocoenosia inusitata* Malloch, 1934 and *Austrocoenosia projecta* Malloch, 1934). Malloch (1934) also added two already known species of *Coenosia* as part of *Austrocoenosia*: *Coenosia dubia* (Bigot, 1885) and *Coenosia ignobilis* Stein, 1911. Furthermore, Malloch (1934) designated *A. nigerrima* as the type species of the genus. Several years later, Snyder (1957) described a new species: *Limosia tarsata* Snyder, 1957, collected at the southern extreme of Argentina based on three specimens (one male and two females). Although this author observed the presence of the posterodorsal seta on the hind tibia of the specimens studied, he found it difficult to assign this species to *Austrocoenosia* or *Coenosia*. Snyder (1957) considered that the combination of two preapical setae on the hind femur and the doubtful presence of a posterodorsal seta on the hind tibia were characters similar to those observed in the Nearctic genus *Limosia*, and consequently assigned *tarsata* under this genus. Later, in a catalog of the Diptera of the Americas south of the USA, Pont (1972) placed *Austrocoenosia* as a junior synonymy of *Coenosia* and established new combinations of most of the species presented by Malloch (1934) and Snyder (1957) under *Coenosia* with the exception of *A. brevicornis*, which was placed as a new combination under the New World genus *Neodexiopsis* Malloch, 1920. In a study of *Neodexiopsis* specimens housed in the Museu Nacional do Rio Janeiro, Brazil (MNRJ), Couri and Albuquerque (1979) observed one female specimen of *C. ignobilis* Stein 1911 and one male and several female specimens of *A. nigerrima*, presented a description of the male terminalia of *A. nigerrima*, and, based on the results, proposed a new combination of both species (and consequently of *Austrocoenosia*) under the genus *Neodexiopsis*. Several years later, the type specimens of *C. ignobilis* were studied by Pont (2001), who established that the species belonged to *Coenosia* and not to *Neodexiopsis*. In a similar way, Couri and Nuñez (2001) provided a redescription of *A. argentifrons* with details of the male terminalia, and determined that the species belonged to *Coenosia*. Currently, the species of *Austrocoenosia* are placed under the genera *Coenosia* or *Neodexiopsis* (Carvalho et al. 2005).

The large genus *Coenosia*, with over 360 species, is known from all biogeographic regions (Sorokina 2009), although according to Couri and Pont (2000) more than 60% of its species are distributed in the Old World. Some species of *Coenosia* are currently used as biocontrol agents in greenhouses because they prey over white flies, black fungus gnats and leaf-mining flies (Kühne 2000). The generic concept of *Coenosia* sensu lato only includes the presence of two preapical setae in the third femur. Due to its wide distribution and species richness, a complete revision of *Coenosia* has never been accomplished. In contrast, there are several coexisting regionally focused taxonomic diagnoses of the genus, such as that of Hockett (1934a) for North American species, that of Sorokina (2009) for Siberian species, that of Couri and Pont (2016) for African species, and that of our research group (Patitucci et al. 2021) for southern South American species. In addition, diverse subgroups are used as subgenera in different regions such as the Nearctic region (Hockett and Vockeroth 1987) or the Neotropical region (Patitucci et al. 2021) or as species-group in the Oriental region (Xue and Wang 2014) or the Palearctic region (Hennig 1961).

Regarding *Neodexiopsis*, the other genus in which the species of *Austrocoenosia* were placed, its external morphology is very similar to that of *Coenosia*. The generic concept of *Neodexiopsis* only includes the presence of three preapical setae in the third femur. The genus is restricted to the New World, with a large proportion of the species (87 of the 96 described) distributed in the Neotropical region (Carvalho et al. 2005), many of which were described on the basis of female specimens. Although several taxonomic studies on this genus have been carried out (Snyder 1957, 1958; Couri and Albuquerque 1979; Costacurta et al. 2005; Patitucci and Couri 2018), more comprehensive studies of *Neodexiopsis* are needed.

From the phylogenetic point of view, Hennig (1965) suggested that *Coenosia* could be a non-monophyletic group, whereas Couri and Pont (2000) in their study of the phylogenetic relationships of Coenosiini based on morphological characters did not find synapomorphy characters for *Coenosia* or *Neodexiopsis*. More recently, based on morphological characters of Coenosiini from the Mexican Transition Zone, Gomes et al. (2020) obtained the same result.

As part of a series of studies based on extensive exploration of the Muscidae inhabiting the southern extreme of South America, we have collected new material, revised all the species placed by Malloch (1934) under *Austrocoenosia*, and discovered two new morphospecies that share the characters defined for the last genus. Thus, the main aims of this study were: 1) to assess the position of the species belonging to the genus *Austrocoenosia* proposed by Malloch (1934) with respect to the genera *Coenosia* and *Neodexiopsis*, by developing a hypothesis of phylogenetic relationships among the species of these genera by means of a cladistics analysis, using morphological and genitalia characters of female and male adults of the species; 2) to assess whether *Austrocoenosia* is a monophyletic group as proposed by Malloch (1934) or whether it is

a monophyletic group within the genera *Coenosia* or *Neodexiopsis*; and 3) to provide a taxonomic revision of all *Austrocoenosia* species, describe two new species, update the geographic distributions for all species, and provide high quality photographs detailing new structures of the male and female terminalia. These terminalia structures led to a substantially enriched discussion of the genera.

## 2. Materials and Methods

### 2.1. Source of material

**Study area and sampling methods.** Most of the specimens studied were collected by two of the authors (LDP and PRM) in the following protected natural areas: “Área Natural Protegida Batea Mahuida” (ABM), “Área Natural Protegida Lagunas de Epu Lauquen” (ALE), “Área Natural Protegida Volcán Domuyo” (AVD), “Parque Nacional Lanín” (PNL), “Parque Nacional Lago Puelo” (PNLP); and “Parque Nacional Los Alerces” (PNLA), in Argentine Patagonia. Some of the specimens were collected in “Parque Nacional Nahuel Huapi” (PNNH), as part of the “Darwin Initiative” project (Brooks et al. 2009). A detailed description of the areas studied has been previously presented in Brooks et al. (2009) and Patitucci et al. (2016 and 2021). Specimens collected by the authors were obtained between 2011 and 2018 with two different techniques: 1) active capture with an entomological net over vegetation and 2) passive capture with a Malaise trap.

**Specimens studied.** The specimens collected were identified using the original descriptions (Malloch 1934, Snyder 1957) and photographs of type specimens. To study the morphology of the terminalia, the abdomen of selected specimens was detached and transferred to 90% lactic acid at room temperature for two weeks. After clearing, the genital structures were removed and temporarily mounted on concave glass slides in glycerine. After the study, the dissected parts were placed in a plastic micro vial with glycerine and pinned with the respective specimen. The terminology used for the external morphology followed Cumming and Wood (2017).

All the specimens studied belong to the following institutions. **IFML** – Instituto y Fundación Miguel Lillo, Tucumán, Argentina, **MACN** – Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina, **MLP** – Museo de La Plata, Buenos Aires, Argentina, and **MNRJ** – Museu Nacional, Universidade Federal do Rio Janeiro, Rio de Janeiro, Brazil.

The specimens collected by the authors were deposited at the IFML, MACN, and MLP. High quality images of type specimens were examined. These images are currently deposited at: **CNC** – Canadian National Collection of Insects, Ontario, Canada, **SZNM** – Institute of Systematics and Ecology of Animals, Siberian Branch, Novosibirsk, **ZMHB** – Museum für Naturkunde der Humboldt-Universität, Berlin, Germany, **USNM** – Na-

tional Museum of Natural History, Washington D.C., USA, **BMNH** – Natural History Museum, London, United Kingdom, **UMO** – Oxford University Museum of Natural History, United Kingdom, and **ZMUH** – Universität von Hamburg, Zoologisches Institut und Zoologisches Museum, Hamburg.

The labels of the type specimens examined are cited verbatim, lines separated by a slash, different labels by semicolon, and comments are given in brackets.

### 2.2. Taxonomic work

All known synonyms for each species, as well as a list of generic combinations for the currently valid names are provided.

Species distributions are based on examined material and published records. Countries and localities for specimens examined are given in full.

**Abbreviations. Chaetotaxy.** **acr s** – acrostichal seta, **ad** – anterodorsal seta, **aDC** – anterior presutural dorsocentral seta, **av** – anteroventral seta, **eaDC** – extra anterior presutural dorsocentral seta, **pd** – posterodorsal seta, **pDC** – posterior presutural dorsocentral seta, **pV** – posteroventral seta. **Terminalia.** **cp** – central promontory, **epand** – epandrium, **epiph** – epiphallus, **distiph** – distiphallus; **hypd** – hypandrium, **pap** – pointed apical process, **pgt** – postgonite, **phapod** – phallopodeme, **pregt** – pregonite, **s distiph** – sclerotized distiphallus, **tp** – triangular process.

**Images, measurements, and maps.** Digital photographs were taken using an Olympus DP 25 digital camera mounted on an Olympus SZX 16 stereomicroscope, and a Touptek TC digital camera mounted on a Lancet XSZ-146AT microscope. Images were processed using the Olympus cellSens Standard software and Combine ZM (Alan Hadley, UK).

Scanning Electron Microscopy (**SEM**) images were taken with a Philips XL30 TMP scanning electron microscope at the **MACN**. The structures used were dehydrated through 80, 90, and 99.5% ethanol, and coated with gold-palladium in a Thermo VG Scientific SC 7620 sputter coater. Measurements of the body length (considered as the length between the anterior margin of the head (frons), excluding antenna, to the apex of the abdomen) were digitally obtained with the software Leica Application Suite EZ Version 2.1.0. Distribution maps were created with the QGIS software 2.18.3 (<http://www.qgis.org/pl/site>) and edited with Adobe Illustrator CS6. The shapefiles used are available at ‘Instituto Geográfico Nacional de Argentina’ (<http://www.ign.gov.ar>), ‘Áreas Naturales Protegidas de Neuquén’ (<https://www.anp.gov.ar>), ‘Administración Parques Nacionales’ (<https://mapas.parquesnacionales.gov.ar>), and Romano (2017). The biogeographic regionalization scheme used was that proposed by Morrone (2014, 2015). To facilitate the use of georeferenced biodiversity data, a geospatial table is presented with the new records produced in this study (Table S3).

**Table 1.** Species selected, biogeographic distribution, and source of character coding.

Species	Biogeographic regions	Source of character coding
<i>Coenosia argentifrons</i> (Malloch, 1934) (*)	Andean	MACN, MNRJ; [BMNH]
<i>Coenosia aurifera</i> (Malloch, 1934) (*)	Andean	MACN; [BMNH]
<i>Coenosia bimorpha</i> (Snyder, 1965)	Australasia	Snyder 1965; [USNM]
<i>Coenosia chaetosa</i> Malloch, 1934	Andean	MACN; [BMNH]
<i>Coenosia conflicta</i> Hockett, 1965	Nearctic, Palearctic (Euro-Siberia region)	Sorokina 2009, 2022; [SZNM]
<i>Coenosia curviventris</i> Albuquerque, 1959	Neotropical	Albuquerque 1959; MNRJ
<i>Coenosia delneneo</i> <b>sp. nov.</b>	Andean	MACN
<i>Coenosia doloresae</i> Pont & Gregor, 2008	Palearctic (Mediterranean basin)	Pont and Gregor 2008; [CNC]
<i>Coenosia flavohumeralis</i> Couri & Pont, 2016	Afrotropical	Couri and Pont 2016
<i>Coenosia forcipiungula</i> Xue & Zhang, 2011	Oriental	Xue and Zhang 2011
<i>Coenosia freidbergi</i> Pont & Grach, 2008	Palearctic (Mediterranean basin)	Pont and Grach 2008; [BMNH]
<i>Coenosia ignobilis</i> (Stein, 1911) (*)	Andean	MACN, MNRJ; [ZMUH]
<i>Coenosia inaequalis</i> Malloch, 1934	Andean	MACN, MNRJ; [BMNH], [USNM]
<i>Coenosia inusitata</i> (Malloch, 1934) (*)	Andean	MACN; [USNM]
<i>Coenosia laeta</i> Hockett, 1934	Nearctic	Hockett 1934a; [CNC]
<i>Coenosia longipede</i> Albuquerque, 1956	Neotropical	MNRJ; Albuquerque 1956
<i>Coenosia lucens</i> Couri & Pont, 2016	Afrotropical	Couri and Pont 2016
<i>Coenosia mallochi</i> Patitucci, Couri & Mulieri, 2021	Andean	MACN
<i>Coenosia metalleg</i> Patitucci, Couri & Mulieri, 2021	Andean	MACN
<i>Coenosia patagonica</i> <b>sp. nov.</b>	Andean	MACN
<i>Coenosia projecta</i> (Malloch, 1934) (*)	Andean	MACN, [BMNH]
<i>Coenosia setiventris</i> Stein, 1911	Andean	Couri and Pont 2020
<i>Coenosia spumicola</i> Pont, 1973	Australasia	Pont 1973
<i>Coenosia subgracilis</i> Xue & Cui, 2001	Palearctic (Euro-Siberia region), Oriental	Xue and Cui 2001, Sorokina 2009; [SZNM]
<i>Coenosia tarsata</i> (Snyder, 1957)	Andean	MACN, IFML
<i>Coenosia tausa</i> Hockett, 1934	Nearctic	Hockett 1934b; [USNM]
<i>Coenosia tigrina</i> (Fabricius, 1775)	Nearctic, Palearctic	IFML
<i>Coenosia wulpi</i> Pont, 1972	Mexican transition zone	Couri 2007
<i>Coenosia zhongdianensis</i> Xue & Zhang, 2011	Oriental	Xue and Zhang 2011
<i>Helina australis</i> Carvalho & Pont in Carvalho et al. 1993	Andean	MACN, IFML
<i>Lispidoides inaequifrons</i> Malloch, 1934	Andean	MACN
<i>Neodexiopsis brevicornis</i> (Malloch, 1934) (*)	Andean	MACN; [BMNH]
<i>Neodexiopsis dubia</i> (Bigot, 1885) (*)	Andean	MACN, MNRJ; [UMO]
<i>Neodexiopsis geniculata</i> (Bigot, 1885)	Neotropical	MACN, MNRJ
<i>Neodexiopsis neoaustralis</i> Snyder, 1957	Neotropical	MACN, MNRJ, IFML
<i>Neodexiopsis nigerrima</i> (Malloch, 1934) (*)	Neotropical, Andean	MACN, MNRJ
<i>Neodexiopsis paulistensis</i> Albuquerque, 1956	Neotropical	MACN, MNRJ
<i>Neodexiopsis rufipes</i> (Macquart, 1851)	Neotropical	MACN, MNRJ
<i>Reynoldsia rufoapicata</i> Malloch, 1934	Andean	MACN, MNRJ
<i>Spathipheromyia guttipennis</i> (Thomson, 1869)	Neotropical	MACN, MNRJ; [BMNH]
(*) species considered by Malloch (1934) as part of the genus <i>Austrocoenosia</i> .	Characters of the species were encoded through: 1: observed specimens (acronyms of institutions); 2: literature; and 3: photographs of the type specimens (acronyms of institutions in brackets).	

### 2.3. Phylogenetic work

**Taxon sampling.** The terminal taxa studied are 36 species representative of the genera *Coenosia* and *Neodexiopsis*. These included 29 valid *Coenosia* species: five previously included in *Austrocoenosia*, eight from the Andean biogeographic region, 15 representing the largest possible number of species-groups and geographical regions of the world, and *Coenosia tigrina* (Fabricius, 1775), the type species of *Coenosia*, and seven valid *Neodexiopsis* species: three previously considered in the

genus *Austrocoenosia*, two belonging to the *Neodexiopsis* “*ovata* group”, and *Neodexiopsis rufipes* (Macquart, 1851), the type species of *Neodexiopsis*. The outgroup taxa *Helina australis* Carvalho and Pont in Carvalho et al. 1993, *Lispidoides inaequifrons* Malloch, 1934, *Reynoldsia rufoapicata* Malloch, 1934, and *Spathipheromyia guttipennis* (Thomson, 1868) were chosen based on the phylogenetic hypothesis of the *Coenosini* presented by Couri and Pont (2000). All the species included in the analysis and their geographical distributions are listed in Table 1.

### 2.3.1. Characters and character states

A total of 132 characters from the male and female adults were coded. These were discrete characters, and included: from males: the head and its appendages (0–16), the thorax (17–38), the wings and halteres (39–40), the abdomen (41–53), the legs (54–75), and the terminalia (76–103), and from females: the head, thorax, wings, abdomen, legs and ovipositor (104–131). Characters used by Couri and Pont (2000) are highlighted with (\*), and those modified from Couri and Pont (2000) are highlighted with (\*\*). The distribution of character states in the terminal taxa is indicated in the data matrix in Table S1.

#### Male: head

0. **Distance between right and left fronto-orbital plates:** absent (0);  $1/3 \times$  head width (1); equal or wider than  $1/3 \times$  head width (2). \*\*
1. **Microtrichia of arista:** present in all length (0); present only in basal half (1); absent (2). \*\*
2. **Length of microtrichia of arista:** longer than width of base of arista (0); equal or shorter than width of base of the arista (1). \*
3. **Insertion of antenna in relation to midline of the eye (head in lateral view):** near middle line (0); above middle line (1). \*
4. **Length of postpedicel (head in anterior view):** not reaching epistoma (0); reaching epistoma (1). \*
5. **Number of reclinate orbital setae:** without seta (0); 2–3 (1); 1 (2). \*\*
6. **Number of frontal setae:** 5 (0); 4 (1); 3 (2); 2 (3). \*\*
7. **Width of frons:** longer than wide (0); wider than long (1); similar length and wide (2). \*\*
8. **Frontal triangle:** present (0); absent (1).
9. **Length of frontal triangle:** short, confined within upper half of frons (0); long, confined within lower half of frons (not reaching lunule) (1); long, reaching lunule (2). \*\*
10. **Length of ocellar setae:** longer than the length of the ocellar triangle (0); shorter than the length of the ocellar triangle (1).
11. **Width of gena (head in lateral view):** narrower than the width of postpedicel (0); similar to width of postpedicel (1); higher than the width of the postpedicel (2).
12. **Hook-like prestomal teeth:** absent (0); present (1). \*
13. **Setulae on fronto-orbital plate:** 6 or more extending all over the plate (0) (Fig. 1B); 3 or 5 close to parafacial (1); without setulae (2). \*\*
14. **Prementum of proboscis:** dusted (0); glossy (1). \*
15. **Eye:** bare (0); pilose (1).
16. **Width of parafacial in relation to width of postpedicel (head in lateral view):** narrower (0); similar (1); wider (2).

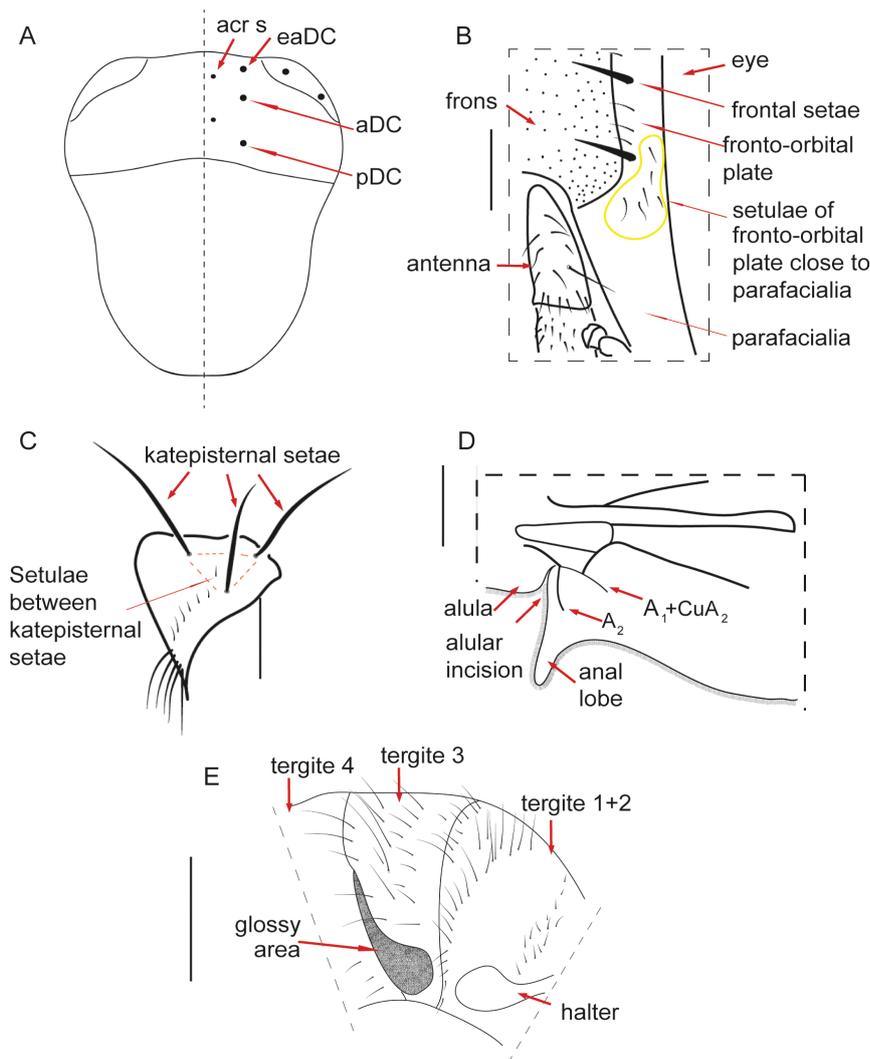
#### Male: thorax

17. **Prealar seta:** present (0); absent (1).\*

18. **Vitta placed on the acrostichal setae:** present (0); absent (1).
19. **Vitta placed on the dorsocentral setae:** present (0); absent (1).
20. **Vitta placed on the intra-alar setae:** present (0); absent (1).
21. **Vitta placed between the acrostichal seta and the dorsocentral setae:** absent (0); present (1).
22. **Vitta placed between the dorsocentral and the intra-alar setae:** absent (0); present (1).
23. **Presutural acrostichal setae:** distributed in pairs (2 or 3 pairs of setae) (0); irregular rows of setae (1).
24. **Length of postsutural acrostichal setae:** all postsutural acrostichal setae with similar length (0); posterior postsutural acrostichal pair longer (1).
25. **Posterior presutural dorsocentral setae placed in the posterior half of the prescutum:** present (0); absent (1) (Fig. 1A).
26. **“Extra” anterior presutural dorsocentral seta:** absent (0); present (1) (Fig. 1A).
27. **Length of extra anterior presutural dorsocentral seta in relation to length of presutural acrostichal setae:** similar (0); longer (1); shorter (2).
28. **Width of extra anterior presutural dorsocentral seta in relation to width of presutural acrostichal setae:** similar (0); wider (1); thinner (2).
29. **Length of extra anterior presutural dorsocentral seta in relation to length of anterior presutural dorsocentral seta:** similar (0); shorter  $1/3$  (1);  $1/2$  longer (2)
30. **Number of postsutural dorsocentral setae:** 4 (0); 3 (1). \*
31. **Number of postsutural intra-alar setae:** 2 (0); 1 (1).
32. **Length of posterior postsutural intra-alar setae in relation to anterior seta:** same length (0); shorter (1); longer (2). \*\*
33. **Length of apical scutellar seta (measured in antero-posterior direction) in relation to length of scutellum:** shorter (0); longer (1).
34. **Setulae between katepisternal setae:** 4 or more (0); 1–3 (1) (Fig. 1C); without setulae (2). \*\*
35. **Position of katepisternal setae:** not forming an imaginary equilateral triangle (0); forming an equilateral triangle (1). \*
36. **Comparative length between the notopleural setae:** similar length (0); anterior longer than posterior (1).
37. **Number of proepimeral setae:** 4 or more (0); 3 setae (1); 2 setae (2).
38. **Katepimeron:** bare (0); setulose (1).

#### Male: wing

39. **Anal angle of the wing forming a prominent lobe:** absent (0); present (1) (Fig. 1D).
40. **Length of lower calypter in relation to upper calypter:** longer (0); equal (1); shorter (2). \*\*



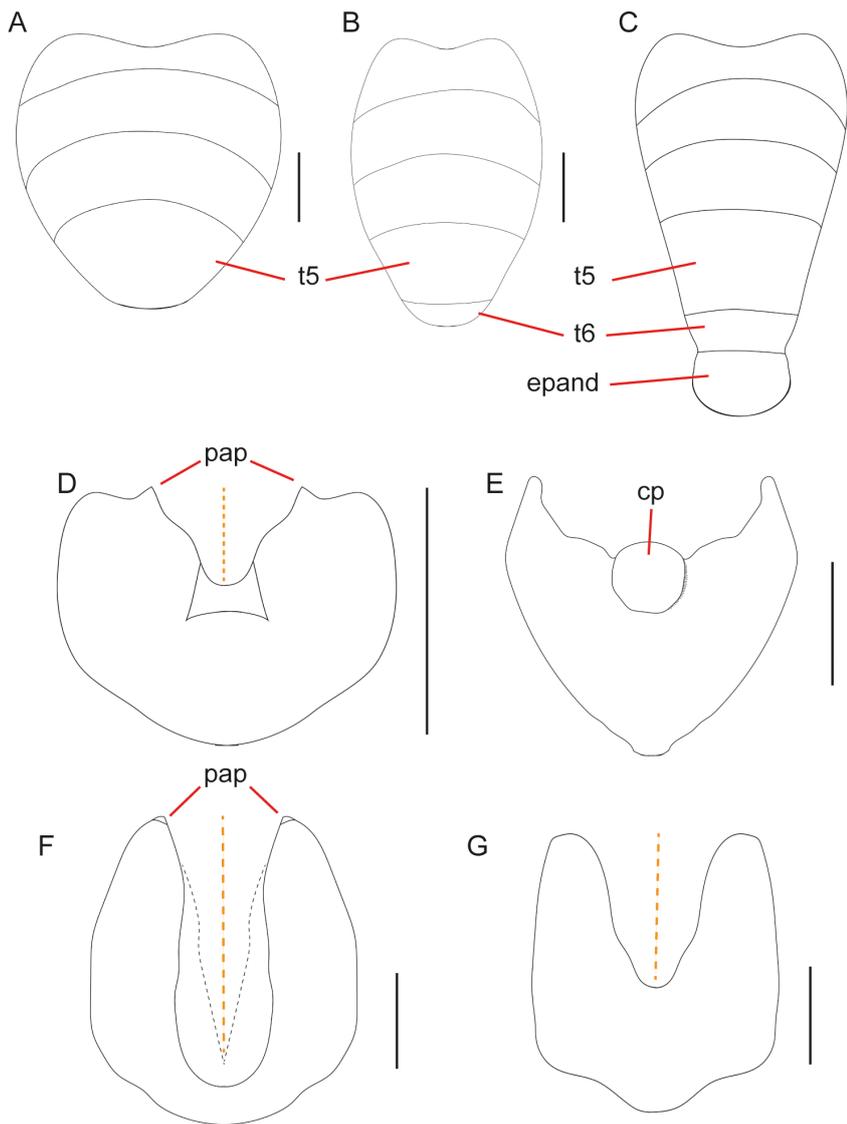
**Figure 1.** **A** Schematic thorax, dorsal view, position of dorsocentral setae on the prescutum. *Coenosia nigerrima*, male. **B** Head, setulae on fronto-orbital plate. *Coenosia dubia*, male. **C** Katepisternum. *Neodexiopsis neoaustralis*, male. **D** Wing, detail of anal region. **E** Abdomen, lateral view. Scale bar: 0.5 mm (A, D–E), 0.1 mm (B), 0.3 mm (C).

#### Male: abdomen

41. Lateral spots on tergite 1+2: absent (0); present (1).
42. Central longitudinal stripe on tergite 1+2: absent (0); present (1).
43. Glossy area between tergites 3 and 4: absent (0); present (1) (Fig. 1E).
44. Lateral spots on tergite 3: absent (0); present (1).
45. Central longitudinal stripe on tergite 3: absent (0); present (1).
46. Lateral spots on tergite 4: absent (0); present (1).
47. Central longitudinal stripe on tergite 4: absent (0); present (1).
48. Lateral spots on tergite 5: absent (0); present (1).
49. Central longitudinal stripe on tergite 5: absent (0); present (1).
50. Tergite 6 in dorsal view: not visible (0) (Fig. 2A); only a small portion visible (1) (Fig. 2B); fully visible (2) (Fig. 2C).
51. Epandrium in dorsal view: not visible (0) (Fig. 2B); visible (1) (Fig. 2C).
52. Epandrium form: not globose (0); globose (1) (Fig. 2C).
53. Sternite 1: bare (0); setulose (1).

#### Male: legs

54. Row of setae on anteroventral surface of fore femur: absent (0); present only on the basal half (1); a complete row (2).
55. Size of claws and pulvilli of the three legs: similar in size (0); fore pair longer than mid and hind pair (1).
56. Setae on anterior surface of mid femur: absent (0); present (1).
57. Number of preapical setae of mid femur (on posterodorsal to posterior surface): 3 (0); 2 (1); 1 (2).
58. Number of setae on median third of posterior to posterodorsal surface of mid tibia: 3–4 (0); 2 (1); 1 (2); 0 (3). \*\*
59. Number of setae on median third of anterodorsal surface of mid tibia: 2 or more setae (0); 1 (1); 0 (2).
60. Length of anterodorsal seta in relation to the length of posterodorsal seta on median third of mid tibia: similar (0); shorter (1); longer (2).
61. Position (in the apical-distal direction) of anterodorsal seta with respect to the position of posterodorsal seta on median tibia: same position (0); apical (1).



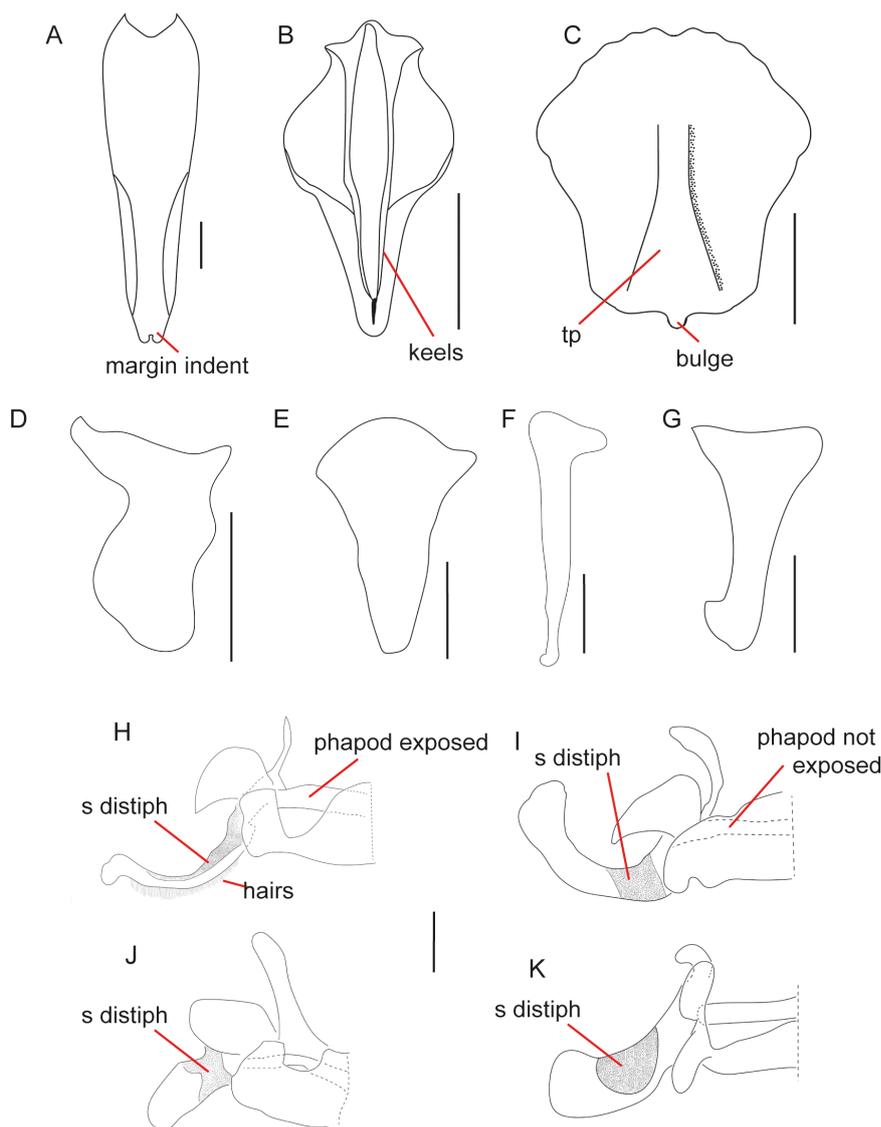
**Figure 2.** Abdomen, male, dorsal view. **A** *Neodexiopsis neoaustralis*, **B** *Coenosia argentifrons*, **C** *Coenosia delneneo* sp. nov. Fifth sternite, male (setae were not drawn). **D** *Coenosia ignobilis*, **E** *Neodexiopsis rufipes*, **F** *Coenosia delneneo* sp. nov., **G** *Coenosia mallochi*. Scale bar: 0.5 mm (A–D, F), 0.2 mm (E, G). Orange dashed lines indicate the length of the concavity.

62. Row of anterodorsal setae on hind femur: present (0); absent (1).  
 63. Row of anterior seta on hind femur: absent (0); present (1).  
 64. Row of anteroventral setae on hind femur: a complete row (0); present only on apical middle (1); without setae (2).  
 65. Anterodorsal preapical setae on hind femur: present (0); absent (1).  
 66. Dorsal preapical setae on hind femur: present (0); absent (1).  
 67. Posterodorsal preapical setae on hind femur: present (0); absent (1).  
 68. Supramedian anterodorsal setae on hind tibia: absent (0); present (1). \*  
 69. Median anterodorsal seta on hind tibia: present (0); absent (1).  
 70. Median posterodorsal seta on hind tibia: absent (0); present (1). \*  
 71. Supramedian posterodorsal seta on hind tibia: present (0); absent (1). \*  
 72. Median anteroventral seta on hind tibia: absent (0); 1 (1); 2 or more (2).

73. Median anterior seta on hind tibia: absent (0); present (1).  
 74. Anterodorsal preapical seta on hind tibia: present (0); absent (1). \*  
 75. Posterodorsal preapical seta on hind tibia: absent (0); present (1). \*

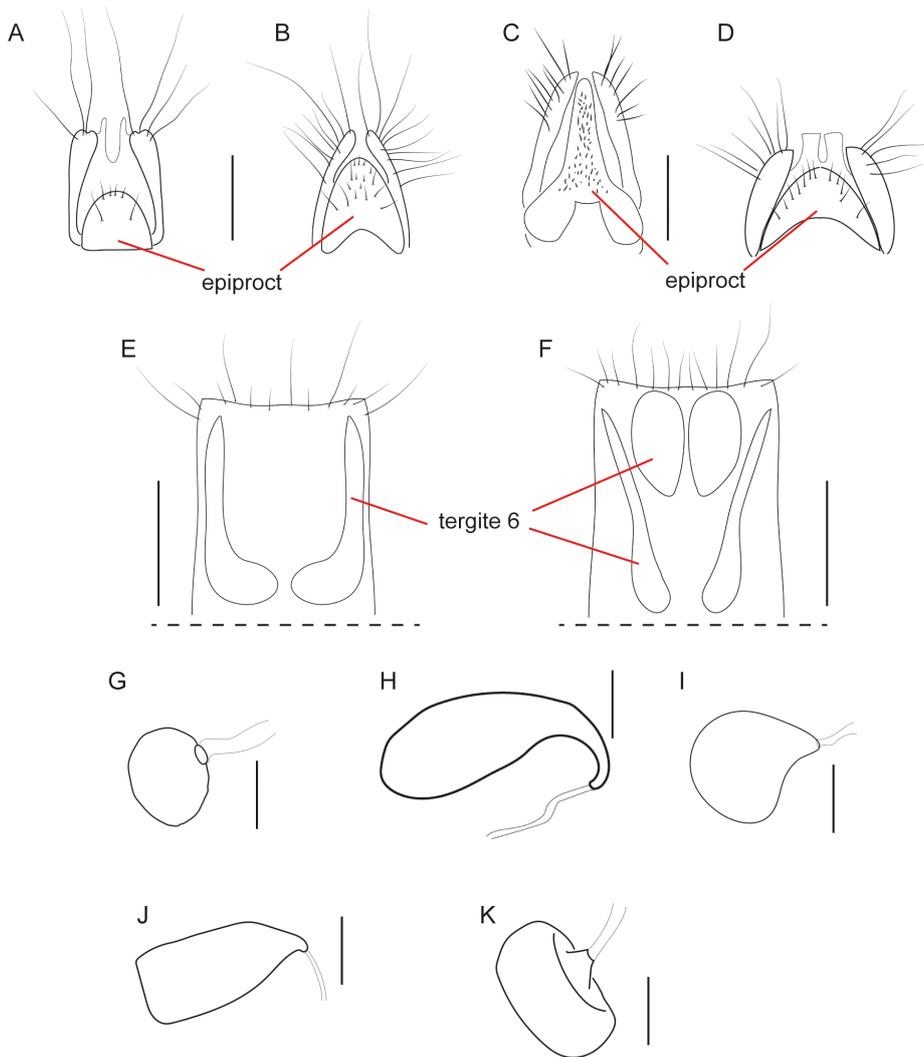
#### Male: terminalia

76. Shape of sternite 5: broader than long (0) (Fig. 2D); as broad as long (1) (Fig. 2E, G); longer than broad (2) (Fig. 2F).  
 77. Pointed apical processes of sternite 5: present (0) (Fig. 2D, F); absent (1).  
 78. Distribution of setae on sternite 5: present throughout the plate (0); present only in the apical half (1). \*  
 79. Sternite 5 central promontory: absent (0); present (1) (Fig. 2E).  
 80. Sternite 5 basal margin: straight (0); convex (1).  
 81. Apical margin of sternite 5: slightly concave (0) (Fig. 2E); concave (the length of the concavity is equal to the length of the basal half of the plate) (1)



**Figure 3.** Male terminalia, cercus. **A** *Coenosia metalleg*, **B** *Coenosia argentifrons*, **C** *Neodexiopsis neoaustralis*. Left surstylus, lateral view. **D** *Coenosia nigerrima*, **E** *Coenosia ignobilis*, **F** *Coenosia inaequalis*, **G** *Spathipheromyia guttipennis*. Phallic complex, distal extreme, lateral view. **H** *Coenosia delneneo* sp. nov., **I** *Coenosia inaequalis*, **J** *Coenosia patagonica* sp. nov., **K** *Spathipheromyia guttipennis*. Scale bar: 0.25 mm (A–B, E), 0.1 mm (C, F), 0.2 mm (D, G), 0.01 mm (H–K).

- (Fig. 2D); strongly concave (“V” form) (2) (Fig. 2G); strongly concave (“U” form) (3) (Fig. 2F).
- 82. Shape of cercus:** as long as wide (0); 1.5–2× as long as wide (1); 2.5–3× as long as wide (2). \*\*
- 83. Cercus divided longitudinal more than half its length:** present (0); absent (1).
- 84. Basal margin vs. apical margin of the cercus:** similar length (0); basal margin longer than apical margin (1).
- 85. Apical margin of cercus:** indented (0) (Fig. 3A); straight (1); with a bulge (2) (Fig. 3C).
- 86. Inner concavity of cercus:** absent (0); present (1). \*
- 87. Keels of cercus:** absent (0); present (1) (Fig. 3B).
- 88. Triangular process on the dorsal surface of the cercus:** absent (0); present (1) (Fig. 3C).
- 89. Distribution of setae on cercus:** only in the basal half (0); only in the apical half (1); throughout the plate (2).
- 90. Dorsal setae on cercus:** hair-like (0); spine-like (1).
- 91. Shape of surstylus:** broad at base and at apex (0) (Fig. 3D); broad at base and tapering towards apex (1) (Fig. 3E); elongated thin (2) (Fig. 3F).
- 92. Length of the surstylus compared to the length of the cercus, in lateral view:** longer than cercus (0); shorter than cercus (1); same length (2).
- 93. Setae in the outer surface of surstylus:** absent (0); present (1).
- 94. Shape of distal extreme of the surstylus, in lateral view:** distal third curved towards cercus (0); tip of distal third curved towards cercus (1); straight (2); curved forwards cercus (3).
- 95. Preapical hook, a sharp prolongation of distal extreme of the surstylus:** absent (0), present (1) (Fig. 3G).
- 96. Shape of hypandrium:** flat, plate type (0); tubular (1). \*
- 97. Distal extreme of tubular hypandrium:** open, exposing the phallapodeme (0) (Fig. 3H); close, not exposing the phallapodeme (1) (Fig. 3I).
- 98. Length of phallapodeme:** shorter than the length of hypandrium (0); similar to the length of hypandrium (1); longer than the length of hypandrium (2).
- 99. Epiphallus:** present (0); absent (1).



**Figure 4.** Female terminalia, epiproct. **A** *Coenosia ignobilis*, **B** *Coenosia inaequalis*, **C** *Reynoldsia rufoapicata*, **D** *Coenosia tarsata*. Sixth tergite. **E** *Coenosia patagonica* sp. nov., **F** *Coenosia tarsata*. Spermatheca. **G** *Helina australis*, **H** *Lispoidea inaequifrons*, **I** *Coenosia aurifera*, **J** *Neodexiopsis neoaustralis*, **K** *Coenosia patagonica* sp. nov. Scale bar: 0.2 mm (A–B, D–F), 0.1 mm (C, G, I–K), 0.5 mm (H).

**100. Length of epiphallus:** similar length to postgonite (0); longer than postgonite (1); shorter than postgonite (2).

**101. Sclerotization of the distiphallus:** complete ring (0) (Fig. 3I); complete ring that narrows in middle section (1) (Fig. 3J); dorsal line (2) (Fig. 3H); dorsal and lateral incomplete ring (3) (Fig. 3K).

**102. Acrophallus:** naked (0); with hairs (1).

**103. Acrophallus hairs:** few hairs at base (0); several hairs placed along the ventral surface (1) (Fig. 3H).

#### Female: head

**104. Length of frontal triangle:** short, confined within upper half of frons (0); long, confined within lower half of frons (not reaching lunule) (1); long, reaching lunule (2).

**105. Height of gena (head in lateral view):** narrower than the width of postpedicel (0); similar to width of postpedicel (1); higher than the width of the postpedicel (2).

**106. Width of parafacial in relation to width of postpedicel:** (head in lateral view): narrower (0); equal (1); wider than the width of the postpedicel (2).

#### Female: thorax

**107. Length of posterior postsutural intra-alar seta in relation to anterior seta:** equal (0); shorter (1); longer (2).

**108. Length of notopleural seta in relation to each other:** similar (0); anterior longer than posterior (1).

#### Female: abdomen

**109. Spots on tergite 1+2:** absent (0); present (1).

**110. Spots on tergite 3:** absent (0); present (1).

**111. Central longitudinal stripe on tergite 3:** absent (0); present (1).

**112. Central longitudinal stripe on tergite 4:** absent (0); present (1).

#### Female: legs

**113. Anterior to anterodorsal seta on median third on fore tibia:** absent (0); present (1).

**114. Row of setae on anteroventral surface on fore femur:** absent (0); present only in the basal half (1); a complete row (2).

- 115. Setae on anterior surface of mid femur:** absent (0); present (1).
- 116. Number of setae on median third of posterior to posterodorsal surface of mid tibia:** three to four setae (0); two setae (1); one seta (2).
- 117. Length of anterodorsal seta in relation to the length of posterodorsal seta on median third of mid tibia:** similar (0); shorter (1); longer (2).
- 118. Row of anteroventral setae on hind femur:** a complete row (0); present only on apical middle (1); without setae (2).
- 119. Dorsal preapical setae on hind femur:** present (0); absent (1).
- 120. Posterodorsal preapical setae on hind femur:** present (0); absent (1).
- 121. Median posterodorsal setae on hind tibia:** absent (0); present (1).
- 122. Median anteroventral setae on hind tibia:** absent (0); one seta (1); two or more setae (2).
- 123. Posterodorsal preapical seta on hind tibia:** absent (0); present (1).

#### Female: ovipositor

- 124. Length and width of the segments of the ovipositor:** longer than wide (0); as long as wide (1); wider than long (2). \*\*
- 125. Microtrichia on sternites 6 and 7:** absent (0); present (1).\*
- 126. Length of female cerci in relation to epiproct:** longer (0); equal or shorter (1).
- 127. Setae of epiproct:** hair-like setae (0); strong spine-like setae (1).
- 128. Shape of epiproct:** equilateral triangle or hemisphere (0) (Fig. 4A); isosceles triangle (1) (Fig. 4B); inverted “Y” letter shape (2) (Fig. 4C); boomerang shape (3) (Fig. 4D).
- 129. Shape of hypoproct:** equilateral triangle (0); isosceles triangle (1).
- 130. Number of tergites on segment 6:** two tergites (0) (Fig. 4E); four tergites (1) (Fig. 4F).
- 131. Spermatheca shape:** sphere (0) (Fig. 4G); hook (1) (Fig. 4H); ovoid (2) (Fig. 4I); bottle (3) (Fig. 4J); erythrocyte (4) (Fig. 4K).

#### 2.3.2. Phylogenetic analysis

Characters were treated as unordered and non-applicable characters were coded as ‘-’, whereas unknown character states were coded as ‘?’ (Strong and Lipscomb 1999). The program TNT 1.0 (Goloboff et al. 2003) was used to search for optimal trees using implied weights with a weighting strength of  $K = 3$ . The high presence of parallelisms and reversals in previous cladistics studies on different taxa of Muscoidea (Couri and Pont 2000; Domínguez and Roig-Juñent 2008, 2017), suggests that the value of  $K$  chosen for the analysis ( $K = 3$ ) ponders the weight of the characters with a high homoplasy, favoring the characters with greater fit. Heuristic, unconstrained searches for optimal trees were conducted using tree bisection reconnection

(TBR) branch swapping in each of 1000 replications of random taxon addition sequences, maintaining up to 10 trees per replication. A second TBR round was applied to each of the optimal trees, to increase confidence of finding all minimum-length topologies. Zero length branches were collapsed and strict consensus trees were generated. The support of groups was estimated using Bremer values, both absolute (Bremer 1994) and relative (Goloboff and Farris 2001), as well as symmetric resampling using 500 replicates ( $P = 0.33$ ) (Goloboff et al. 2003). Bremer supports were calculated by obtaining suboptimal trees in 10 successive stages, saving up to 2000 sub-optimal trees at each stage. At every stage, we searched for suboptimal trees with 0.1 units of fit longer than the optimal tree. Since the fit is a concave function of homoplasy (Goloboff 1993), this means that we searched for trees with 0.1 to 1 units of fit longer than the optimal tree. Finally, as recommended by Goloboff and Farris (2001), relative support values were calculated by considering only the trees within the absolute Bremer support for each group. Values of group support are indicated at each node. Characters in the text are referred with numbers followed a dash and the numbers of the states (e.g., 28-2).

Some groups of species are named as “grades” when they form paraphyletic assemblages on the phylogenetic tree and “clades” when they form monophyletic groups (Fig. 5). This was done to facilitate the description and discussion of our results, but these groupings do not constitute a new classification (Buenaventura and Pape 2017).

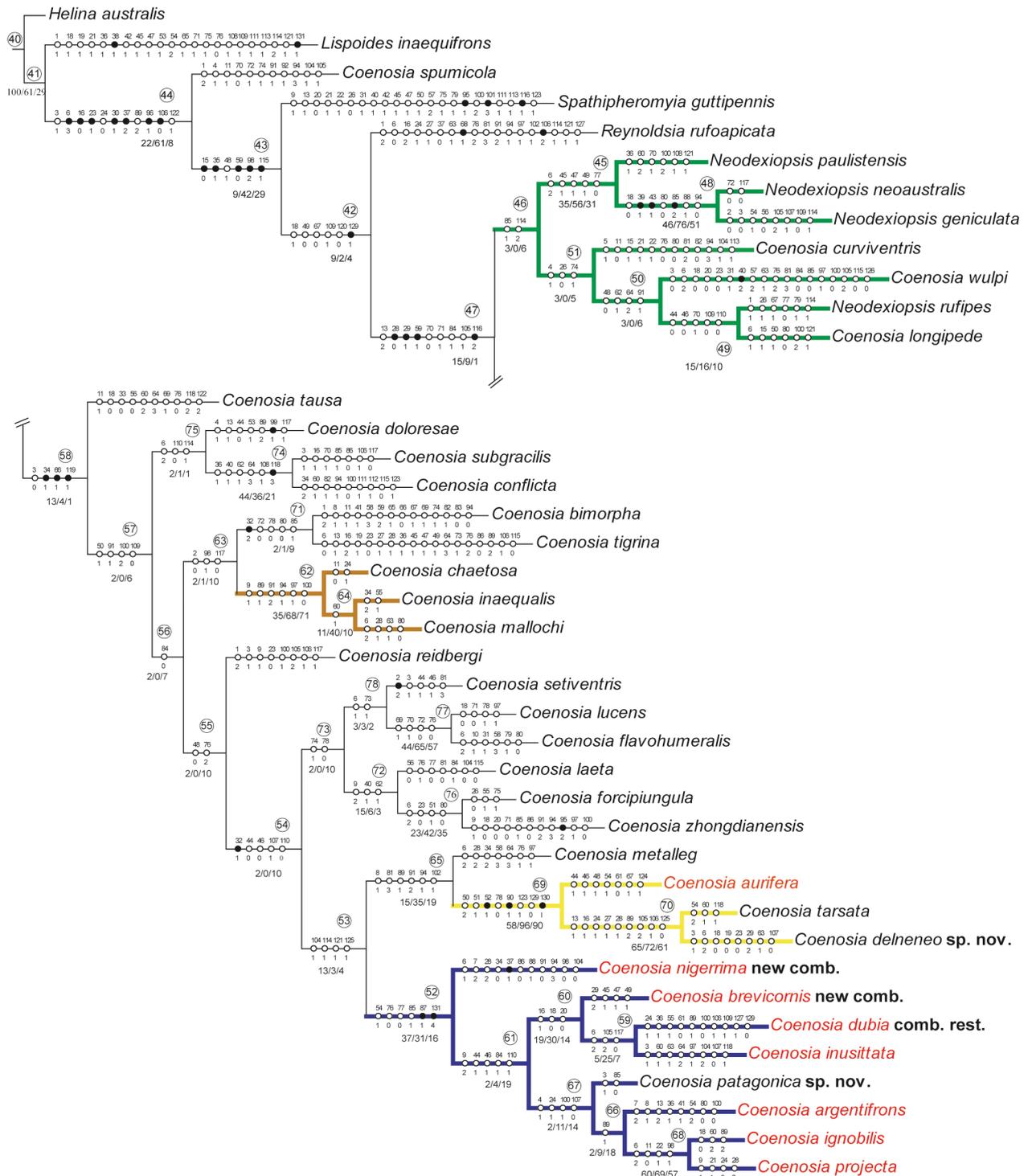
### 3. Phylogenetic results

Searches under implied weights yielded one optimal tree, with a fit of 60.46898 (Fig. 5). Neither of the two valid genera herein studied, *Coenosia* and *Neodexiopsis*, were recovered as monophyletic. Species previously ascribed to *Austrocoenosia* under the original concept of Malloch (1934) were not recovered as a monophyletic genus, but formed an apical monophyletic clade (except *C. aurifera*) (node 53), within *Coenosia*.

The three also shows that *Lispoides inaequifrons* was placed as the sister taxon to all other Coenosiini, with *Coenosia spumicola* at its base, followed by *Spathipheromyia guttipennis* and *Reynoldsia rufoapicata* (Fig. 5).

Clade 47 included all *Coenosia* and *Neodexiopsis* species (except *C. spumicola*), and was supported by nine apomorphies, four of which are exclusive (Table S2). The species of *Neodexiopsis* were grouped in a clade (node 46) with two species of *Coenosia* from the Neotropical region and with *C. wulpi* from the Mexican transition zone (here referred to as *Neodexiopsis* grade (Fig. 5)), supported as a monophyletic group by the character states 85-1 and 114-2 (Table S2).

Clade 58 grouped all the remaining *Coenosia* species included in this study, and was supported by a non-exclusive apomorphy and three synapomorphies (34-1, 66-1,



**Figure 5.** Tree obtained with implied weights ( $k = 3$ ). Absolute, relative Bremer supports and Symmetric resampling values indicated below each node. Species originally described by Malloch (1934) as part of *Austrocoenosia* genus – scientific names in red. *Neodexiopsis* grade – green branches; *Coenosia chaetosa* group – brown branches; *Coenosia aurifera* group – yellow branches; and *Coenosia argentifrons* group – blue branches. Synapomorphies: black circles, homoplasies: empty circles.

and 119-1). The tree also showed *C. tausa* as the sister species to all remaining species of *Coenosia*, followed by two clades (Fig. 5). Clade 75 grouped three species (*C. doloresae*, *C. conflicta*, and *C. subgracilis*), and the sister group of this clade (node 56) is formed by two clades, one of them (clade 63) is divided in two clades: one containing the type species of *Coenosia* (*C. tigrina*) + *C. bimorpha* (node 71), and the other (node 62) includ-

ing the species described by Malloch (1934) as *Coenosia* for the Andean biogeographic region (*C. chaetosa* and *C. inaequalis*), and the recently described *C. mallochi*. This clade was supported by six non-exclusive apomorphies (9-1, 89-1, 91-2, 94-1, 97-1, and 100-0).

*Coenosia reidbergi* was placed as the sister taxon to two geographically distinct groups: the first clade (node 73, Fig. 5) grouped six species of *Coenosia* distributed in

**Table 2.** Homoplasy for each character, expressed as units of fit.

	0	1	2	3	4	5	6	7	8	9
0	--	0.77	0.40	0.77	0.50	0.25	0.81	0.40	0.40	0.77
10	0.25	0.77	--	0.70	--	0.40	0.57	--	0.75	0.77
20	0.67	0.50	0.40	0.62	0.73	--	0.62	0.75	0.62	0.40
30	0.00	0.40	0.00	0.25	0.50	0.00	0.70	0.25	--	0.00
40	0.40	0.67	0.50	0.00	0.67	0.57	0.62	0.57	0.62	0.57
50	0.57	0.25	0.00	0.25	0.77	0.40	0.67	0.25	0.50	0.25
60	0.70	0.57	0.40	0.57	0.62	0.25	0.25	0.57	--	0.40
70	0.70	0.50	0.67	0.25	0.50	0.67	0.75	0.57	0.70	0.40
80	0.75	0.72	0.72	0.40	0.57	0.67	0.57	0.00	0.25	0.78
90	0.0	0.73	0.77	0.57	0.75	--	0.00	0.73	0.50	--
100	0.80	0.40	0.25	--	0.75	0.75	0.62	0.57	0.40	0.62
110	0.57	0.57	0.57	0.40	0.72	0.57	0.00	0.72	0.50	0.00
120	0.25	0.57	0.50	0.50	0.40	0.50	0.70	0.25	0.57	0.50
130	0.00	0.57								

the Palearctic, Ethiopian, and Nearctic regions, and a single Neotropical species (*C. setiventris*), whereas the second clade (node 53, Fig. 5) grouped 12 species of *Coenosia* endemic to the Andean region, including all species previously ascribed to *Austrocoenosia* under Malloch's original concept.

Node 53 grouped two clades. The first clade included *C. metalleg* as the sister taxon of *C. aurifera* + (*C. tarsata* + *C. delneneo* **sp. nov.**) (node 69), and was supported by five non-exclusive apomorphies (50-2, 51-1, 78-0, 123-1, and 129-0) and three synapomorphies (52-1, 90-1, and 130-1). The second clade (node 52) recovered all species previously ascribed to *Austrocoenosia* under Malloch's original concept (except *C. aurifera*), and a new species *C. patagonica* **sp. nov.** supported by four non-exclusive apomorphies (54-1, 76-0, 77-0, and 85-1) and two synapomorphies (87-1 and 131-4) (Fig. 5).

The results of the present study show that many of the characters are highly homoplasious (Table 2), and that support measures were generally low, with few exceptions (Fig. 5). The use of implied weights reduced the possibility of groupings based on strongly homoplasious characters, such as leg chaetotaxy of male and female external morphology, because they were down-weighted during the process.

For lists of character changes, for all nodes, see Table S2.

## 4. Taxonomic work

### *Coenosia* Meigen, 1826

**Type-species.** *Musca tigrina* Fabricius.

**Synonymous list of generic names.** *Caricea* Robineau-Desvoidy, 1830; *Limosia* Robineau-Desvoidy, 1830; *Palusia* Robineau-Desvoidy, 1830; *Oplogaster* Rondani, 1856; *Allognota* Pokorný, 1893; *Dexiopsis*

Pokorný, 1893; *Centriocera* Pokorný, 1893; *Rhynchocoenops* Bezzi, 1918; *Tenuicosta* Stein, 1919; *Macrocoenosia* Malloch, 1920; ***Austrocoenosia* Malloch, 1934: 217. Type-species, *nigerrima* Malloch. syn. rest.; *Hebdomostilda* Enderlein, 1936; *Mesodiplectra* Enderlein, 1936; *Psephidocera* Enderlein, 1936; *Diatinoza* Enderlein, 1936; *Platyochiracra* Enderlein, 1936; *Adiplectra* Enderlein, 1936; *Trilasia* Karl, 1936; *Lamprocoenosia* Ringdahl, 1945; *Leucoenosia* Ringdahl, 1945; *Xanthorhinia* Ringdahl, 1945.**

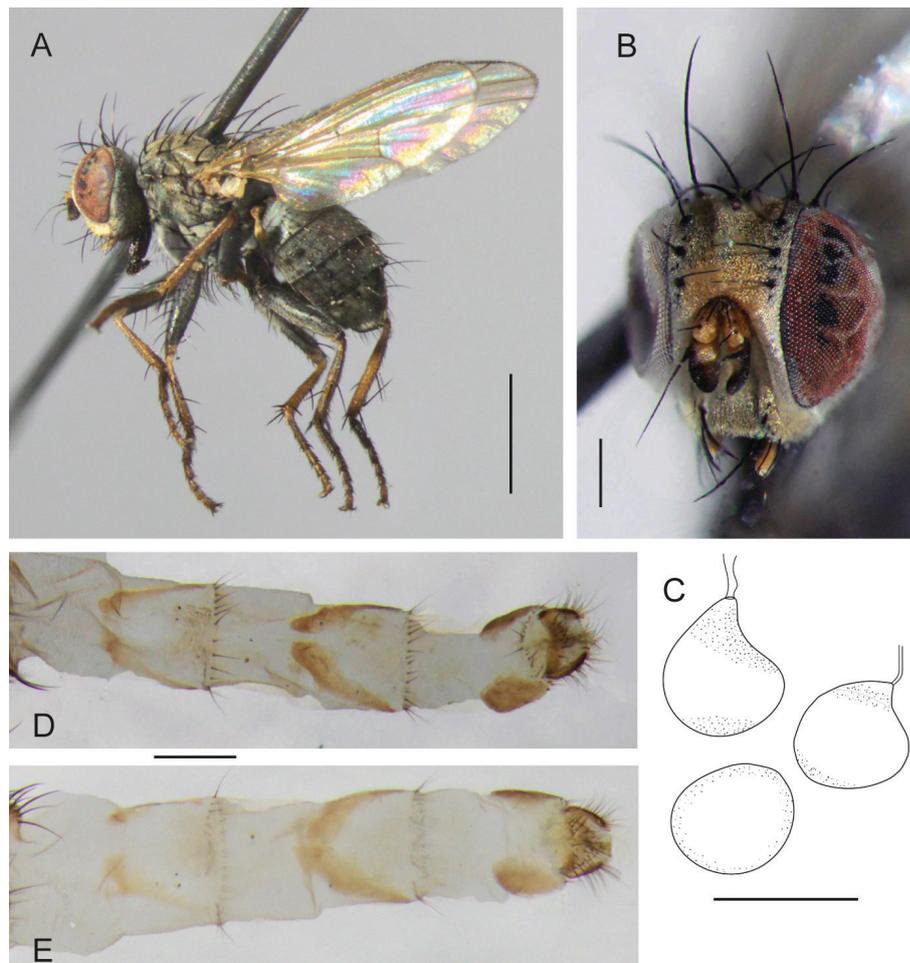
**Diagnosis of the *Coenosia aurifera* group.** The *Coenosia aurifera* group is defined by the combination of the following characters: grey species, with grey or brownish-yellow pollinosity [except head of males of *C. aurifera* with golden pollinosity]; frons longer than wide; dorsocentrals 1+3, with an eaDC, that is usually less than one third or fifth of length of the aDC [except *C. delneneo* **sp. nov.**, with eaDC is half (or more) of length of aDC]; mid tibia with one ad and one pd median setae; hind femur with one preapical ad and one pd [dorsal in some specimens of *C. aurifera*] setae; hind tibia with one long ad seta and one fine av setae, a pd seta with variable length. Males can be characterized by tergite 6 and epadrium visible on dorsal view, and cercus longer than broad with strong spines. Female ovipositor presents tergite 6 with four plates.

The *Coenosia aurifera* group here proposed includes *C. aurifera*, *C. delneneo* **sp. nov.**, and *C. tarsata*. This group seems to be biogeographically circumscribed to the Andean chains, especially to the Subantarctic sub-region and the south extreme of the Andean sub-regions.

**Descriptions.** To avoid lengthy and redundant descriptions, the characters listed below are present in all species of *C. aurifera* group. — **Male. Head:** Dichoptic; eyes bare. 3–4 pairs of frontal setae, 1 pair of reclinate orbital setae. Frons longer than wide, frontal triangle not visible, with the same color of the frons [except female of *C. aurifera* with a visible triangle] (Fig. 7B). Inner vertical setae strong and longer than outer vertical setae. Ocellar



**Figure 6.** *Coenosia aurifera*, male. **A** lateral view, **B** head, frontal view, **C** thorax, dorsal view, **D** abdomen, dorsal view, **E** abdomen, lateral view, **F** fifth sternite, **G** cercus, dorsal view, **H** cercus and surstylus, lateral view, **I** detail of cercus, distal tip, **J** phallic complex, lateral view, **K** detail of phallic complex, distal tip. Scale bar: 1 mm (A), 0.2 mm (B, E–H), 0.5 mm (C, D), 0.05 mm (I), 0.01 mm (J, K). Distiphallus, brush of fine hairs – red arrow.



**Figure 7.** *Coenosia aurifera*, female. **A** Lateral view, **B** head, frontal view, **C** spermathecae, **D** ovipositor, dorsal view, **E** ovipositor, ventral view. Scale bar: 1 mm (A), 0.2 mm (B, D–E), 0.1 mm (C).

setae strong and long. Occiput with three rows of setae: a posterior row at dorsal middle of head, a central row complete, and an anterior row at ventral middle of head. Gena with black hairs, and with height greater than the width of the postpedicel. Antenna inserted at the mid-level of the eye in lateral view. Palpus filiform. **Thorax:** Without vitta; anterior and posterior spiracles grey. Chaetotaxy: intra-alars 1+2, posterior postsutural seta shorter; supra-alars 1+1; postpronotals 2; notopleurals 2. Prealar absent. Scutellum with one long basal and one long apical pair of setae, similar in size: katapisternals 1+1+1, forming an equilateral triangle; anepimeron, katepimeron, and meron bare, proepisternals 2; proepimeral 2, lower seta downcurved. Prosternum bare. **Wing:** Hyaline; veins bare, except costal vein; lower calypter glossiform, twice longer than the upper one. Tegula yellow. Halter yellow. **Legs:** Fore tibia with one median posterior seta. Mid femur with 2 preapical setae on pd to posterior surface. Hind femur with one preapical ad setae and one pd (dorsal in some *C. aurifera* specimens) setae. Hind tibia with one long ad seta, a long pd seta, and one shorter av setae. Similar sized claws and pulvilli of the three legs. **Abdomen:** Tergite 6 visible in dorsal and lateral view. Epandrium globose, wider than tergite 6 in dorsal view. Sternite 1 bare. Sternite 5 longer than broad with basal margin convex. **Terminalia:** Cercus longer than broad, sclerotized, with strong spine, and apical margin concave with 2 teeth strongly sclerotized. Surstyli longer than broad, straight,

and curved at tip. Hypandrium tubular longer than wide, distal extreme exposing the phapod. Aedeagus with phapod straight, strongly sclerotized, and longer than hypd in lateral view; pregt developed, kidney-shaped, ventrally fused with the hypd; pgt developed, epiphalus slightly sclerotized, and distiph tubular, with a sclerotized ring at base and extending on dorsal surface to tip, and with a brush of fine hair on ventral surface. — **Female. Ovipositor:** Tergites 6 with two long and wide sclerotized plates and two square plates, epiproct with “boomerang” shape, with hair-like setae, shorter than cercus; hypoproct triangular, setulose, with several strong setae on distal margin.

### *Coenosia aurifera* (Malloch, 1934)

**Male (Fig. 6A).** Length. Body: 3.56–3.70 mm, wing: 2.89–3.02 mm. **Head** (Fig. 6B): Frons at vertex about one third of the head width. Frons, fronto-orbital plate, parafacial and gena yellow with golden pollinosity. Fronto-orbital plate without setulae, close to parafacialia. Antenna light brown with yellow pollinosity; arista brown with its longest microtrichia shorter than its basal diameter. Palpus yellow. **Thorax:** (Fig. 6C). Grey with light brown pollinosity. Chaetotaxy: acr s strong and biseriata; anterior presutural acr s longer than the eaDC; dorsocentrals 1+3, eaDC is less than one fifth of the aDC. Anepisternum with a series of 4–5 strong setae; katepisternum with 1–2

setula. **Wing:** Both calypters whitish hyaline with white margins. **Legs:** Coxae and femora grey. Trochanters, apex of femora, tibiae, and tarsus yellow. Fore femur with a row of strong pd setae, and a row of strong pv setae. Mid femur with 2 strong setae on ventral surface, and 2–3 setae on anterior surface; mid tibia with one ad and one pd median setae, both setae with the same length and position. Hind femur with a row of ad and a row of av setae, and two long setae on ventral surface, with two preapical setae (ad and dorsal); hind tibia with 4 preapical setae (ad, dorsal, pd, ventral). **Abdomen:** (Fig. 6D, E). Grey with brown spots on tergites 3–5. Sternite 5 with apical margin with a thin “U” shape and without membrane; setae concentrated on the lobes and some long and strong on apical margin (Fig. 6F). **Terminalia:** Cercus with strong spine on apical third (Fig. 6G–I).

**Female (Fig. 7A).** Length. Body: 3.80–4.06 mm, wing: 3.00–3.12 mm. Differs from male as follows: **Head:** (Fig. 7B). Frons black with golden pollinosity, frontal triangle white, reaching lunule; fronto-orbital plate, parafacial and gena yellow with silver pollinosity. Antenna yellow, with distal part of postpedicel dark brown. **Thorax:** Chaetotaxy: acr s strong and biseriate; anterior presutural acr s shorter than the eaDC. **Ovipositor:** Segments with similar length and width. Tergites 7 with two long and sclerotized plates running laterally towards ventral surface; tergite 8 with two wide and square plates (Fig. 7D). Sternites 6 and 7 without plates; sternite 8 divided into two small and slightly sclerotized plates each with 5–6 setae on distal margin (Fig. 7E). Three spermathecae, oval shape (Fig. 7C).

**Type material. Holotype.** Male; BMNH [pinned, damaged, head glued on card]. Original labels: “♂ [handwritten] / Holo- / type [printed]” on white circular paper, red frame; “Argentina: / Terr. Rio Negro. / F.& M. Edwards / B.M. 1927–63.” printed on white paper; “Bariloche. / 28.xi–1xii.1926.” printed on white paper; “Austrocoenosia / auriceps / Type [handwritten] / det. JRMALLOCH [printed]” on white paper, black frame: <https://data.nhm.ac.uk/object/bde2c2d5-9453-4a8a-bb92-96b869e9f9c9/1678838400000>. — **Paratype.** Female; BMNH [glued on card, in good condition]. Original labels: “♀ [handwritten] / Allo- / type [printed]” on white circular paper, red frame; “Argentina: / Terr. Rio Negro. / F.& M. Edwards / B.M. 1927–63.” printed on white paper; “Bariloche. / 28.xi–1xii.1926.” printed on white paper: <https://data.nhm.ac.uk/object/b070de6e-f7a5-4b84-b436-5a3dfcc85ba1/1678924800000>.

**Additional material examined.** ARGENTINA — **Río Negro province** • 1 female; Bariloche, Los Repollos; 22 Jan 2019; 650 m a.s.l.; –41.849378, –71.416898; Agüero leg.; over *Mulinum spinosum*; MACN • 1 male; El Bolson, Piltriquitron; Jan 2012; 1190 m a.s.l.; –41.972377, –71.478712; Mulieri & Patitucci leg.; MACN. — **Neuquén province** • 2 females; ABM; Jan 2013; 1400 m a.s.l.; –38.845457, –71.093002; Mulieri & Patitucci leg.; MACN • 2 males; Pampa Lonco Luan, Ruta 13; 09 Feb 2018; 1522 m a.s.l.; –38.897919, –70.890376; Patitucci leg.; MACN.

**Distribution (Fig. 12A).** ARGENTINA: Neuquén (new record), Río Negro.

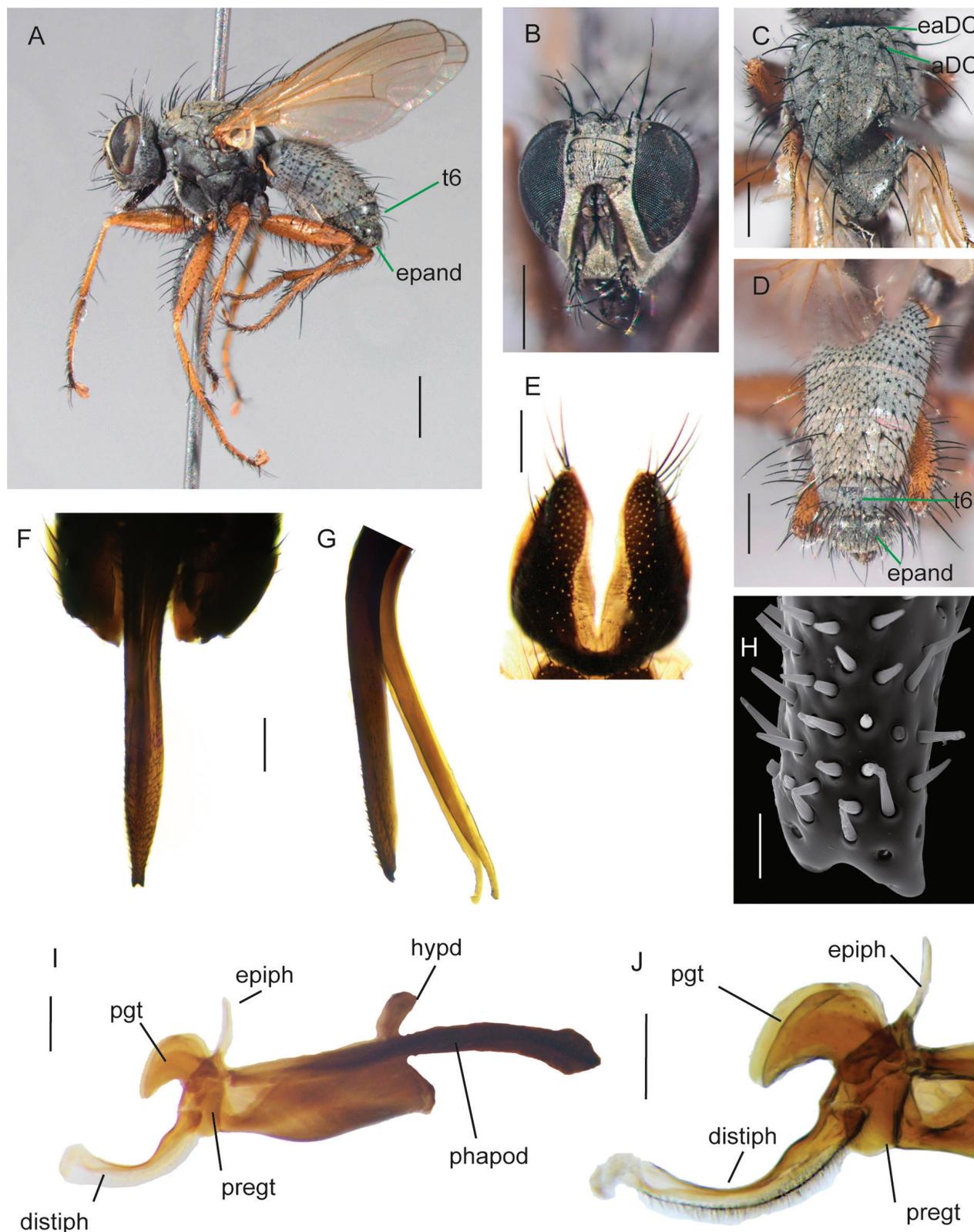
**Remarks.** *Coenosia aurifera* was described with male and female specimens by Malloch (1934) as part of the genus *Austrocoenosia*. This author highlighted its striking coloration and the unique shape of the male abdomen. Our observation also showed morphological (male abdomen, cercus, and female ovipositor) and phylogenetic evidence to distinguish this species from the remaining species of *Austrocoenosia* presented by Malloch.

### *Coenosia delneneo* sp. nov.

<https://zoobank.org/1863B9FA-097C-4465-9289-DE7B93737D43>

**Male (Fig. 8A).** Length. Body: 5.56–5.90 mm, wing: 4.1–4.69 mm. **Head:** (Fig. 8B). Frons at vertex about one third of the head width. Frons, fronto-orbital plate, parafacial and gena black with yellow-grey pollinosity. Frons, fronto-orbital plate with 1–3 little setulae, close to parafacialia. Antenna dark brown, apex of pedicel with yellow pollinosity; arista brown with its longest microtrichia hardly longer than its basal diameter. Palpus black. **Thorax:** (Fig. 8C). Grey with light brown pollinosity. Chaetotaxy: acr s strong and biseriate; anterior presutural acr s shorter than the eaDC; dorsocentrals 1+3, eaDC is half (or more) of length of the aDC. Anepisternum with a series of 4–5 strong setae; katepisternum with 2–3 setula. **Wing:** Both calypters whitish hyaline with white margins. **Legs:** Coxae grey. Fore femur yellow with a black large spot on dorsal to posterior surface. Trochanters, femora, tibiae, and 1–4 tarsomeres yellow. Fifth tarsomere black. Fore femur with a row of strong pd setae, and a row of strong pv setae. Mid femur with a row of strong setae on ventral surface, and 5–6 setae on anterior surface; mid tibia with one ad and one pd median setae with the same length, ad seta positioned below of the pd seta. Hind femur with a complete row of ad and a complete row of av setae, two setae on anterior surface at middle, and a row of setae on ventral surface, hind tibia with 3 preapical setae (ad, dorsal, ventral). **Abdomen:** (Fig. 8D). Grey without spots, tergite 6 and epand brighter than the other tergites. Sternite 5 with apical margin concave (“U” shape) and membrane; setae concentrated on the lobes and some long and strong on apical margin (Fig. 8E). **Terminalia:** Cercus with strong spines on apical middle (Fig. 8F, G).

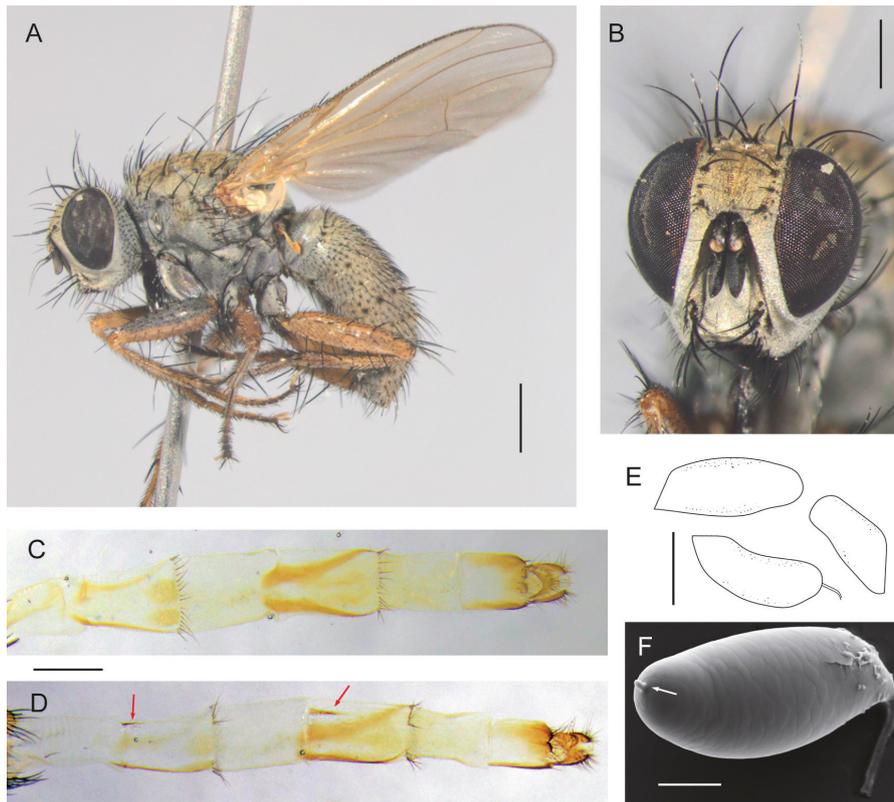
**Female (Fig. 9A, B).** Length. Body: 5.70–6.00 mm, wing: 4.8–5.12 mm. Differs from male as follows: **Legs:** Mid tibia with one ad and one pd median setae, both setae with the same length and position. **Ovipositor:** Segments longer than wide. Tergites 7 and 8 with two long and wide sclerotized plates (Fig. 9C). Sternites 6 and 7 with one short and thin plates; sternite 8 divided into two small and sclerotized plates each with 4–5 setae on distal margin (Fig. 9D). Three spermathecae, oval shaped, with a small prominence at the opposite end of the insertion of the tracheola (Fig. 9E, F).



**Figure 8.** *Coenosia delneneo* sp. nov., male. **A** Lateral view, **B** head, frontal view, **C** thorax, dorsal view, **D** abdomen, dorsal view, **E** fifth sternite, **F** cercus, **G** cercus and surstylus, lateral view, **H** detail of cercus, distal tip (SEM), **I** phallic complex, lateral view, **J** detail of phallic complex, distal tip. Scale bar: 1 mm (A), 0.5 mm (B–E), 0.2 mm (F, G), 0.02 mm (H), 0.01 mm (J, K).

**Type material.** *Holotype*. Male; MACN [pinned]. Original labels: “Arg. Neuquén, Aluminé / Río Aluminé 896 m / 39°14'26.03”S 70°54'43.93” / JAN2013 Olea, Mulieri & Patitucci leg.” print. on white paper; “MACN-En / 34728” print. on white paper; “Holotype” print. on red paper, black frame. — *Paratypes*. One male; MACN [pinned]. Original

labels: “Arg. Neuquén, Aluminé / Río Aluminé 896 m / 39°14'26.03”S 70°54'43.93” / JAN2013 Olea, Mulieri & Patitucci leg.” print. on white paper; “MACN-En / 34729” print. on white paper; “Paratype” print. on red paper, black frame. Seven females; MACN [pinned]. Original labels: “Arg. Neuquén, Aluminé / Río Aluminé 896 m / 39°14'26.03”S



**Figure 9.** *Coenosia delneneo* sp. nov., female. **A** Lateral view, **B** head, frontal view, **C** ovipositor, dorsal view, **D** ovipositor, ventral view, **E** spermathecae, **F** details of spermathecae (SEM). Scale bar: 1 mm (A), 0.5 mm (B–D), 0.2 mm (E), 0.05 mm (F). Sixth and seventh sternites – red arrows, spermathecae small prominence – white arrow.

70°54'43.93" / JAN2013 Olea, Mulieri & Patitucci leg." print. on white paper; "MACN-En / 34721 [to] 37427" print. on white paper; "Paratype" print. on red paper, black frame. Two males and one female; MLP [pinned]. Original labels: "Arg. Neuquén, PN Lanín / Huechulafquen 1070 m (transecta) / 39°47'33.25" 71°12'56.26"W / 13-XII-2013 Mulieri leg." print. on white paper, "Paratype" print. on red paper, black frame. One male and 2 females; IFML [pinned]. Original labels: "Arg. Neuquén, Ruta 13 / Pampa de Lonco Luan / 1522 m a.s.l. transecta / -38.897919 -70.890376 / 09.II.2018 Patitucci leg." print. on white paper, "Paratype" print. on red paper, black frame.

**Additional material examined.** ARGENTINA — **Río Negro province** • 1 female, 1 male; El Bolson, Piltriquitron; -41.972377, -71.478712; 1190 m a.s.l.; 12 Jan 2012; Mulieri & Patitucci leg.; MACN. — **Neuquén province** • 2 females; Arroyo Guyapa, Ruta 13, -38.859349, -70.472570; 1240 m a.s.l.; 07 Feb 2018; Mulieri & Patitucci leg.; MACN • 1 male; Primeros Pinos, Portezuelo La Atravezada; -38.891693, -70.652192; 1876 m a.s.l.; 08 Feb 2018; Mulieri leg.; MACN • 3 females; Ruta 23; -39.809776, -71.030665; 16 Dec 2013; Mulieri & Patitucci leg.; MACN.

**Distribution (Fig. 12B).** ARGENTINA: Neuquén, Río Negro.

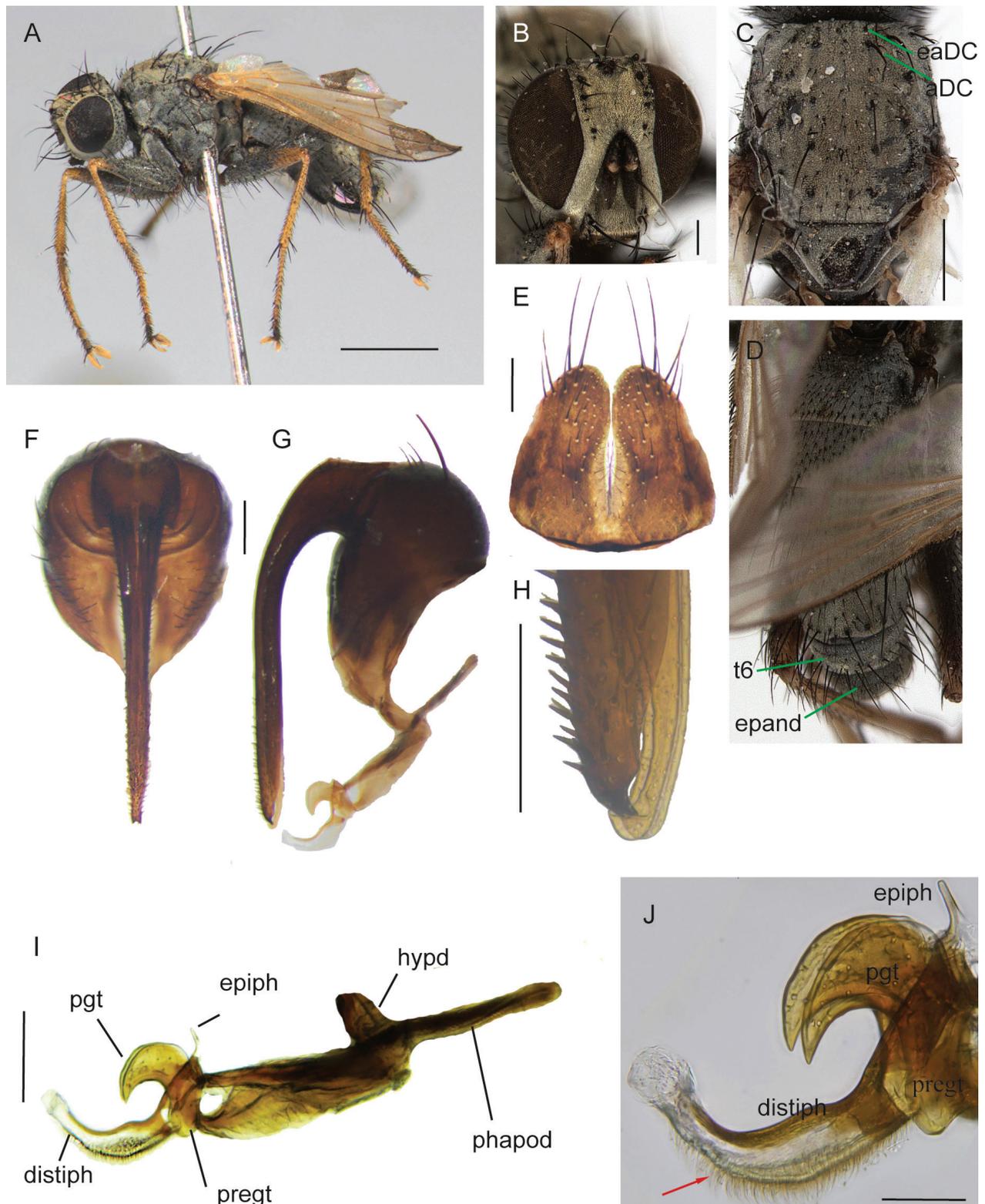
**Etymology.** The name "delneneo" refers to an expression in Spanish to the vulgar name (neneo) of the plant *Mulinum spinosum* Pers., where several specimens were collected.

**Remarks.** *Coenosia delneneo* sp. nov. is distinguished from its congeners by the following combination of characters: gena height greater than the width of the postpedicel, thorax and abdomen gray without vitta or spots, fore

femur yellow with a black large spot on dorsal to posterior surface, fifth tarsomere black, dorsocentrals 1+3, with an extra short presutural pair which is half (or more) of the length of the presutural seta, hind tibia with one long ad seta, a long pd seta, and one fine av setae, and cercus longer than broad and with strong spines. Male: tergite 6 and epandrium visible and brighter, distiph with a brush of fine hair on ventral surface. Female: ovipositor in tergites 6 with two long and wide sclerotized plates and two square strongly sclerotized plates, and epiproct with "boomerang" shape. In Stein's key (1911), *C. delneneo* comes close to *Coenosia pilitibia* Stein 1911, but differs in the chaetotaxy of the mid tibia. In Malloch's key (1934), *C. delneneo* comes close to *C. ignobilis* Stein, 1911, but the coloration of the fore femur and the shape of the abdomen can separate it from the latter.

### *Coenosia tarsata* (Snyder, 1957)

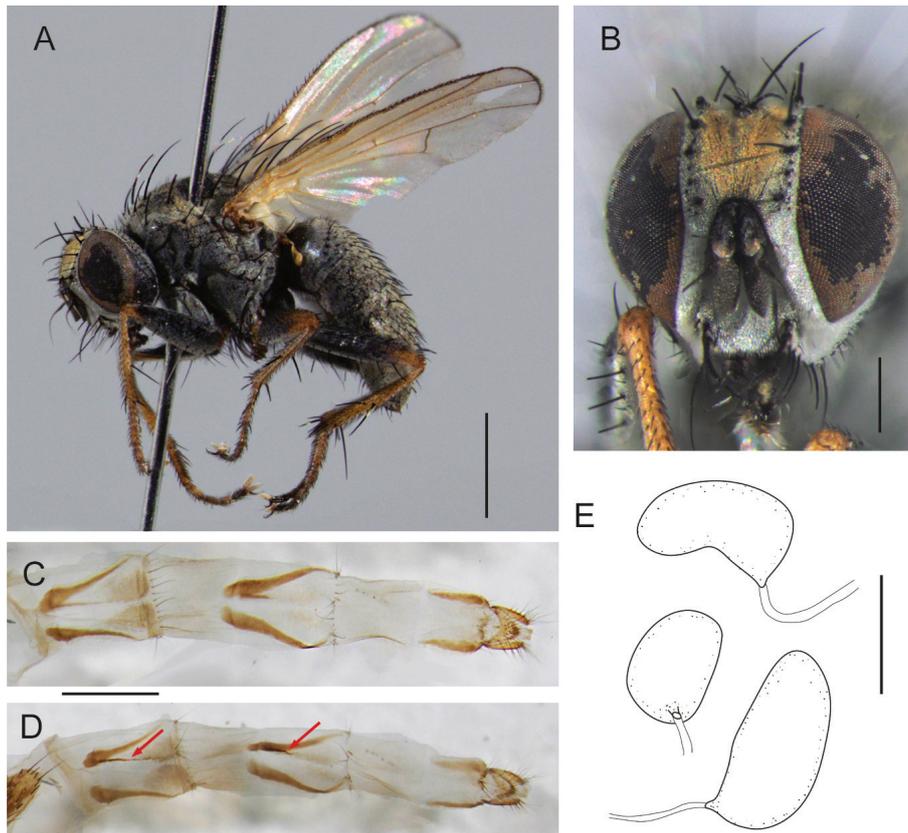
**Male (Fig. 10A).** Length. Body: 3.6–4.75 mm, wing: 2.4–3.0 mm. **Head** (Fig. 10B): Frons at vertex about more than one third of the head width. Frons, fronto-orbital plate, parafacial and gena black with yellow-grey pollinosity. Fronto-orbital plate with 1-3 little setulae, close to parafacialia. Antenna dark-brown, apex of pedicelo yellowish, apical angle of postpedicel acute; arista brown with its longest microtrichia shorter than its basal diameter. Palpus black. **Thorax:** (Fig. 10C). Black with brownish-gray. Chaetotaxy: acrostichals with irregular length and biseriata, anterior presutural acrs shorter than the eaDC; dorsocentrals 1+3, eaDC is less than one third of the aDC. Anepisternum with a series of 3–4 strong



**Figure 10.** *Coenosia tarsata*, male. **A** Lateral view, **B** head, frontal view, **C** thorax, dorsal view, **D** abdomen, dorsal view, **E** fifth sternite, **F** cercus, dorsal view, **G** cercus, surstylus and phallic complex, lateral view, **H** detail of cercus and surstylus, distal tip, **I** phallic complex, lateral view, **J** detail of phallic complex, distal tip. Scale bar: 1mm (A), 0.5 mm (B–D), 0.2 mm (E–G), 0.1 mm (H–J). Distiphallus, brush of fine hairs – red arrow.

setae; katapisternum with 3–4 setula. **Wing:** Both calypters hyaline with yellow margins. **Legs:** Coxae black with grey pollinosity; trochanters yellow; femora black with grey pollinosity; apex of femora, tibiae, and 1–4 tarsomeres yellow. Fifth tarsomere black (Fig. 10A). Fore

femur with a row of dorsal, posterior, and ventral setae; first tarsomere with a strong ventral seta. Mid femur with 5–6 setae on anterior surface, 2–3 av setae on basal third, and 3–5 pv setae on basal half; mid tibia with one ad and one pd median, ad seta shorter and positioned below of



**Figure 11.** *Coenosia tarsata*, female. **A** Lateral view, **B** head, frontal view, **C** ovipositor, dorsal view, **D** ovipositor, ventral view, **E** spermathecae. Scale bar: 1 mm (A), 0.2 mm (B), 0.5 mm (C–D), 0.1 mm (E). Sixth and seventh sternites – red arrows.

the pd seta. Hind femur with 3 setae on anterior surface, a row of pv setae on basal third, and a row of 5 av setae distanced from each other; hind tibia with 3 preapical setae (ad, dorsal, ventral). **Abdomen:** Grey without spots. Sternite 5 with apical margin concave with a thin “U” shape and with membrane; setae presented throughout the plate (Fig. 10E). **Terminalia:** Cercus with strong spines on apical middle (Fig. 10F–J).

**Female (Fig. 11A, B).** Length. Body: 4.3–50 mm, wing: 4.1–4.6 mm. Differs from male as follows: **Head:** Frons with golden pollinosity. **Ovipositor:** Segments longer than wide. Tergites 7 and 8 with two long and wide sclerotized plates (Fig. 11C). Sternites 6 and 7 with one short and thin plate; sternite 8 divided into two small and sclerotized plates each with 4–5 setae on distal margin (Fig. 11D). Three spermathecae, oval shaped (Fig. 11E).

**Type material. Holotype.** Male; IFML [pinned, both in good condition]. **Paratype.** Female [pinned, both in good condition]. See Patitucci et al. (2011) for original labels.

**Additional material examined.** ARGENTINA — Neuquén province • 2 females, 1 male; Primeros Pinos, Portezuelo La Atravezada; –38.891693, –70.652192; 1876 m a.s.l.; 08 Feb 2018; Mulieri & Olea leg.; MACN.

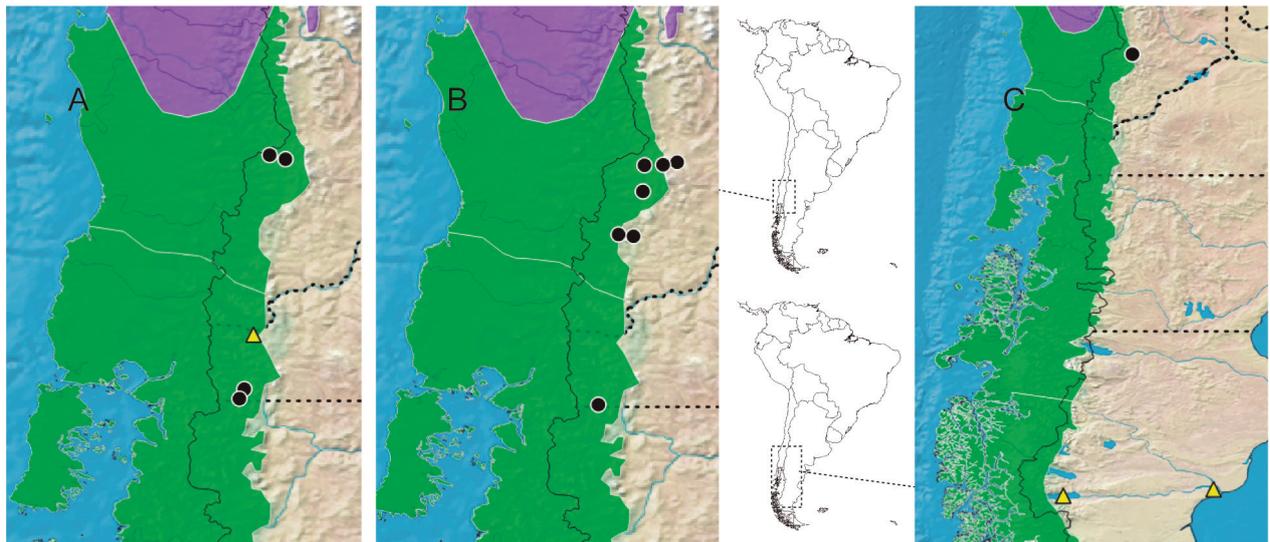
**Distribution (Fig. 12C).** ARGENTINA: Neuquén (new record), Santa Cruz.

**Remarks.** Snyder (1957) described *C. tarsata* with one male and two female specimens from Santa Cruz prov-

ince, Argentina. In his work (op. cit.), the author used the classification proposed by Hockett (1934a) and placed the species under the genus *Limosia*. Snyder (1957) found it difficult to use the generic diagnosis of *Coenosia* and *Austrocoenosia* proposed by Malloch (1934) for the species of Patagonia, because he could not establish the presence of the pd seta on the hind tibia. In Stein’s key (1911), *C. tarsata* comes close to *Coenosia pilitibia* Stein 1911, but differs in the chaetotaxy of the mid tibia. In Malloch’s key (1934), *C. tarsata* comes close to *A. ignobilis* (Stein, 1911), but the coloration of fore femur and the shape of the abdomen can separate both species.

**Nomenclature note.** Hockett (1965) described a new species *Coenosia (Limosia) tarsata* with several female and male specimens from the Nearctic region. Since the specific epithet *tarsata*, had been previously used by Snyder (1957) for *Limosia tarsata*, *tarsata* Hockett is a junior secondary homonymy. In some web sites (<http://diptera.org/Nomenclator/Details/50641>, <https://fr.wikipedia.org/wiki/Coenosia>), we found a new proposed name, *Coenosia hocketti* Pont, 1988, but found no publication establishing the replacement name (Adrian Pont per. commu.). So, here we formally propose the replacement name *Coenosia hocketti* Pont.

**Diagnosis of the *Coenosia argentifrons* group.** The *Coenosia argentifrons* group is defined by the combination of the following characters: Black or grey species, with grey or brownish pollinosity [except head of males of *C. argentifrons* with silver pollinosity]; frons longer than wide [except *C. argentifrons* and *C. nigerrima* with sim-



**Figure 12.** Geographical distribution. **A** *Coenosia aurifera*, **B** *Coenosia delneneo* sp. nov., **C** *Coenosia tarsata*. Central Chilean subregion – violet, Subantarctic subregion – green; new records – black dots, previous records – yellow triangle.

ilar length and width]; dorsocentrals 1+3, with an eaDC, that is usually less than one third or fifth of length of the aDC [except *C. brevicornis* with eaDC is half of length of aDC]; mid tibia with one ad and one pd median setae; hind femur with one preapical ad and one pd setae; hind tibia with one long ad seta and one fine av seta, a pd seta. Male terminalia can be characterized by cercus longer than broad with two longitudinal keels. Female spermathecae, with erythrocyte shape.

The *Coenosia argentifrons* group here proposed includes *C. argentifrons*, *C. brevicornis*, *C. dubia*, *C. ignobilis*, *C. inusitata*, *C. nigerrima*, *C. patagonica* sp. nov., and *C. projecta*. This group includes all the species originally assembled by Malloch (1934) under the genus *Austrocoenosia* (with the exception of *C. aurifera*) and a new species. This group seems to be biogeographically circumscribed to the Andean chains, especially in the Central Chilean and Subantarctic sub-regions of South America.

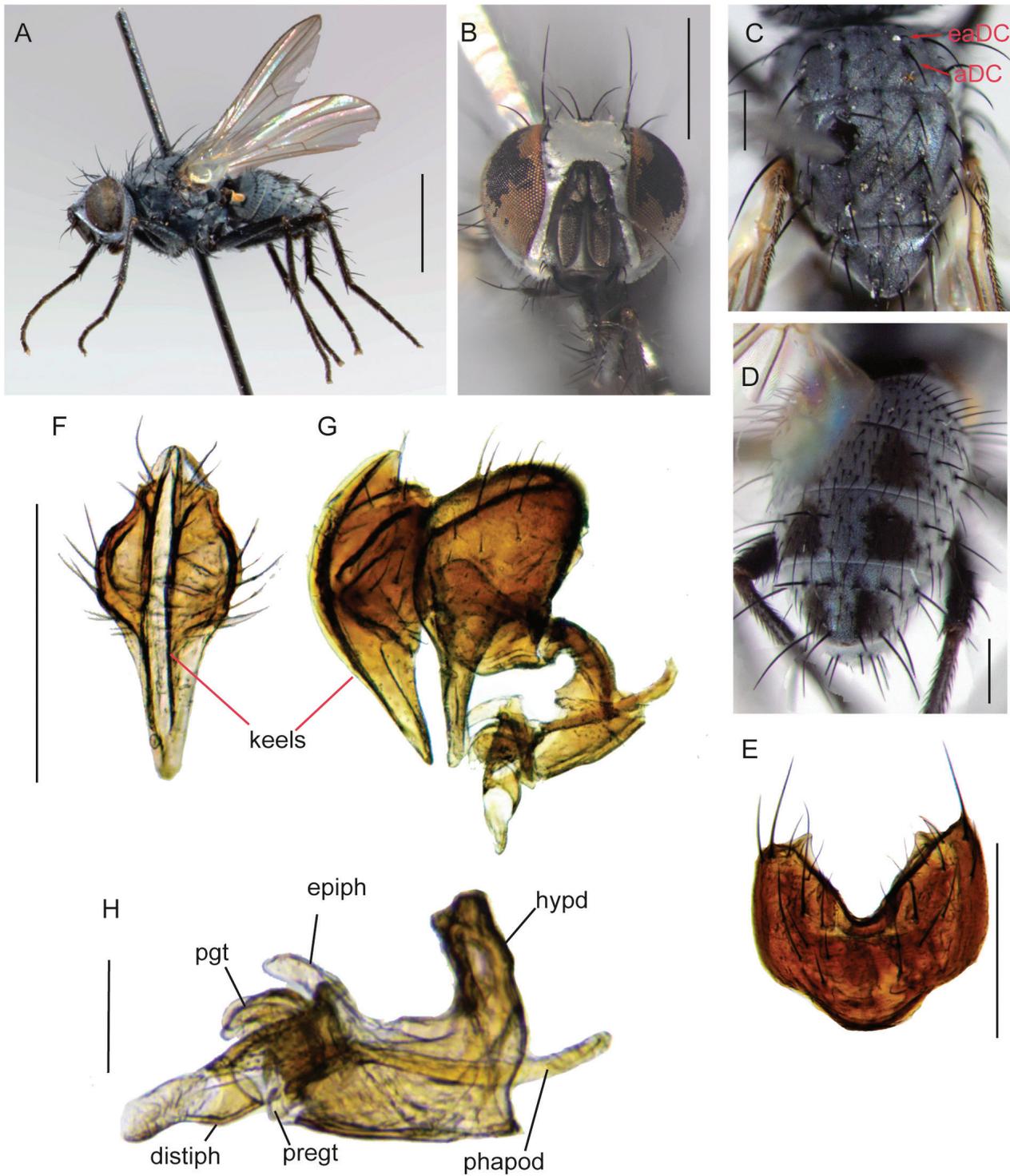
**Descriptions.** To avoid lengthy and redundant descriptions, the characters listed below are present in all species of *C. argentifrons*-group. — **Male. Head:** Dichoptic; eyes bare. 1 pair of reclinate orbital setae. One vertical seta strong and longer than outer vertical setae. Ocellar setae strong and long. Occiput with three rows of setae: a posterior row at dorsal middle of head, a central row complete, and an anterior row at ventral middle of head. Gena with strong black setae. Palpus filiform, black or dark brown. **Thorax:** Chaetotaxy: intra-alars 1+2, posterior postsutural seta shorter; supra-alars 1+1; postpronotals 2; notopleurals 2. Prealar absent. Scutellum with one long basal and one long apical pair of setae, similar in size: katapisternals 1+1+1, forming an equilateral triangle; anepimeron, katepimeron, and meron bare; proepisternals 2; proepimeral 2, lower seta downcurved. Anepisternum with a series of 4–5 strong setae. Prosternum bare. **Wing:** Hyaline; veins bare, except costal vein; lower calypter glossiform, twice at

longer than upper. **Legs:** Fore tibia with one median posterior seta. Hind femur with one preapical ad setae and one pd seta. Hind tibia with one long ad seta and one fine av setae, 3 preapical setae (ad, dorsal, ventral). **Abdomen:** Sternite 1 bare. **Male. Sternite 5** with basal margin convex, and with two-pointed apical process. **Terminalia:** Cercus longer than broad, sclerotized, with hair-like setula, and two longitudinal keels. Aedeagus with phapod slightly curved, strongly sclerotized, and longer than hypod in lateral view; pregt kidney-shaped, ventrally fused with the hypod. — **Female. Ovipositor:** Segments longer than wide. Three spermathecae, “erythrocyte” shaped.

### *Coenosia argentifrons* (Malloch, 1934)

**Male. Thorax:** (Fig. 13A, C). Chaetotaxy: dorsocentrals 1+3, eaDC is less than one fifth of the aDC. Katapisternum with 2–3 setulae. **Abdomen:** (Fig. 13D). Grey with sub-triangular lateral dark-brown marks on tergites 3–5. Tergite 6 poorly visible in dorsal view. Sternite 5 with similar wide and length, apical margin concave with “V” shape; setae long on all the plate (Fig. 13E). **Terminalia:** Cercus, curved in lateral view, keels placed from distal to apical margin, apical margin straight. Surstyli longer than broad, straight (Fig. 13F, G). Hypandrium tubular longer than wide, distal extreme exposing the phallapodema. Aedeagus with pregt developed; pgt developed; epiphallus slightly sclerotized, and distiph tubular, and slightly sclerotized at base, and without fine hair on ventral surface (Fig. 13G, H). — **Female:** Unknown.

**Type material. Holotype.** Male; BMNH [pinned, glued on card, in good condition]. Original labels: “♂ [handwritten] / Holo- / type [printed]” on white circular paper, red frame; “Argentina: / Terr. Rio Negro. / F.& M. Edwards / B.M. 1927–63.” printed on white paper; “Bariloche: / 25-28.x.1926.” printed on white paper; “Austrocoenosia / argentifrons / Type [handwritten] / det. JRMALLOCH [printed]” on white paper,

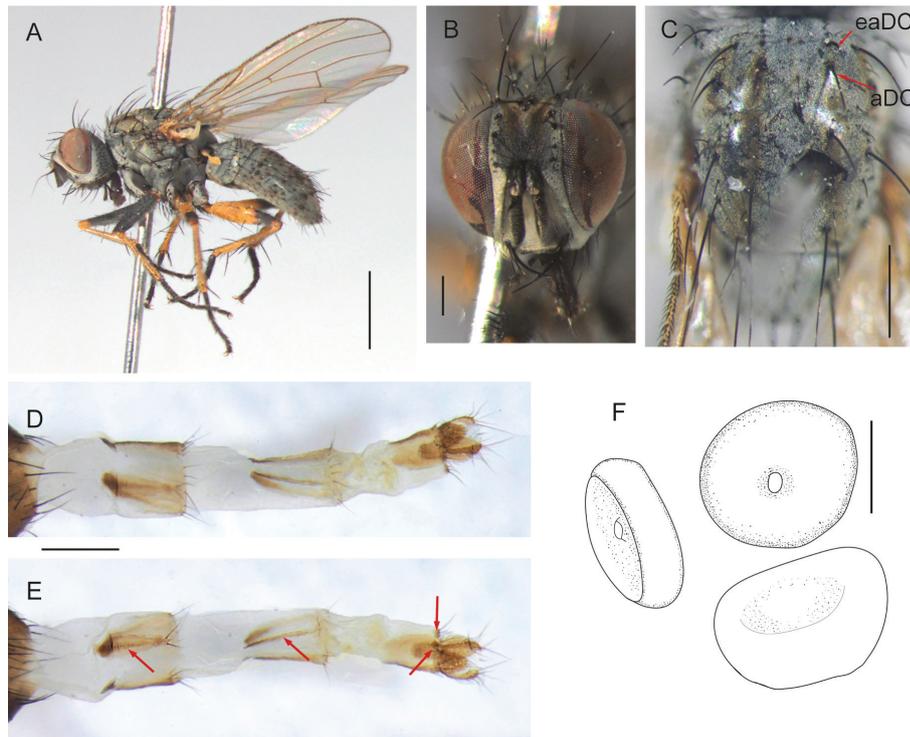


**Figure 13.** *Coenosia argentifrons*, male. **A** Lateral view, **B** head, frontal view, **C** thorax, dorsal view, **D** abdomen, dorsal view, **E** fifth sternite, **F** cercus, dorsal view, **G** cercus, surstylus and phallic complex, lateral view, **H** phallic complex, lateral view. Scale bar: 1 mm (A), 0.5 mm (B–G), 0.02 mm (H).

black frame. <https://data.nhm.ac.uk/object/52fe9b69-4be6-4b8b-b54c-5683508ac9d9/1678924800000>

**Additional material examined.** ARGENTINA — **Chubut province** • 81 males; PNLA, Cabaña La Cascada; –42.888499, –71.592376; 532 m a.s.l.; Feb 2013; Olea, Mulieri & Patitucci leg.; Malaise trap; MACN; • 6 males; PNLA, Lago Verde; –42.717506, –71.725197; 539 m a.s.l.; 24 Oct 2014; Patitucci leg.; MACN • 13 males; PNL, Gendarmería; –42.097468, –71.681953; 200 m a.s.l.; 07–11 Jan 2012; Mulieri &

Patitucci leg.; Malaise trap; MACN; • 1 male; PNL, Intendencia; –42.085077, –71.614662; 12 Jan 2011; Mulieri & Patitucci leg.; MACN • 1 male; PNL, La Playita; –42.099032, –71.607425; 205 m a.s.l.; 09 Jan 2012; Patitucci leg.; MACN • 1 male; PNL, Rio Azul; –42.0916, –71.6155; 17 Jan 2011; Mulieri leg.; MACN • 3 males, same locality; 13 Jan 2012; –42.0908, –71.6247; Mulieri & Patitucci leg.; MACN. — **Neuquén province** • 1 male; ABM, –38.845457, –71.093002; 1400 m a.s.l.; Jan 2013; Mulieri & Patitucci leg.; MACN • 3 males; ALE; –36.816253, –71.081845; 1502 m a.s.l.; 12 Feb 2018; Mulieri &



**Figure 14.** *Coenosia brevicornis*, female. **A** Lateral view, **B** head, frontal view, **C** thorax, dorsal view, **D** ovipositor, dorsal view, **E** ovipositor, ventral view, **F** spermathecae. Scale bar: 1 mm (A), 0.2 mm (B), 0.5 mm (C–D), 0.1 mm (E). Sixth, seventh, and eighth sternites – red arrows.

Patitucci leg.; MACN • 2 males; AVD, Aguas Calientes; –36.678063, –70.606343; 1760 m a.s.l.; 13 Feb 2018; Patitucci leg.; MACN • 3 males; Las Ovejas; –36.992243, –70.749499; 1260 m a.s.l.; 13 Feb 2018, Patitucci & Compagnucci leg.; MACN • 7 males; Pampa Lonco Luan, Ruta 13; –38.897919, –70.890376; 1522 m a.s.l.; 09 Feb 2018; Patitucci leg.; MACN • 1 male; Primeros Pinos; –38.891693, –70.652192, 08 Feb 2018; Patitucci leg.; MACN 1 male; PNL, Laguna Pudu-Pudu; –40.364956, –71.468841; 1000 m a.s.l.; Feb 2013; Mulieri leg.; MACN • 8 males; PNL, Ñorquinco; –39.146931, –71.232717; 1070 m a.s.l.; 09 Jan 2013; Olea, Mulieri & Patitucci leg.; Malaise trap; MACN; • 2 males; PNL, Seccional Bandurrias; –40.144240, –71.342986; 864 m a.s.l.; Feb 2013; Mulieri & Patitucci leg.; Malaise trap; MACN • 1 male; San Martín de los Andes, Truran Kura; 18 Oct 1986, Gentilli leg.; IFML • 1 male; Villa Pehuenia; –38.884694, –71.166337; 1170 m a.s.l.; Feb 2018, Patitucci leg.; MACN. — **Río Negro province** • 17 males; PNNH, Mallín Playa Negra; –41.357809, –71.571683; 797 m a.s.l.; 19 Jan–05 Feb 2009; Garré & Montes de Oca leg.; MLP; Malaise. **CHILE** — **Región de Coquimbo** • 2 males; Valle dos Piuquenes, –30.4333, –70.4167; 7–12 Feb 1964; Peña leg.; MNRJ. — **Región Metropolitana de Santiago** • 1 male; Quebrada de La Plata, La Rinconada; 25–29 Dec 1966; Stange leg.; IFML.

**Distribution (Fig. 27A).** ARGENTINA: Chubut (new record), Neuquén (new record), Río Negro. CHILE: R. de La Araucanía, R. de Coquimbo, R. Metropolitana de Santiago (new record).

**Remarks.** Malloch (1934) described *C. argentifrons* from several specimens from Argentina and Chile. This species can be distinguished from its congeners by the striking silver front (Fig. 13B). Later, Couri and Nuñez (2001) provided a complete redescription with details of male terminalia, and observed, for the first time, longitudinal median keels in the cercus. Our observations also showed this particular structure (keels) in all the species of the *C. argentifrons* group.

### *Coenosia brevicornis* (Malloch, 1934) new comb.

**Female. (Fig. 14A).** Length. Body: 3.44 mm, wing: 3 mm. **Head** (Fig. 14B): Frons at vertex about one third of the head width. Frons black with brownish pollinosity; fronto-orbital plate, parafacial and gena black with grey pollinosity; 4 pairs of frontal setae. Frons longer than wide, with frontal triangle short, light grey, not reaching lunula. Gena with similar height to the width of the postpedicel. Antenna black, apex of pedicelum yellow, apical angle of postpedicel acute; in lateral view inserted at the mid-level of the eye; arista swollen at base, with his longest hairs hardly longer than its basal diameter. **Thorax:** (Fig. 14C). Black with grey pruinescent, with two brown vitta along dorsocentral setae and intra-alar setae; anterior and posterior spiracles grey. Chaetotaxy: acrostichals irregular; dorso-centrals 1+3, eaDC is half of length of the aDC. Katepisternum with 3 setulae. **Wing:** Tegula yellow. Both calypters hyaline with white margins; halter yellow. **Legs:** Fore femur black with yellow apex, mid and hind femora yellow with a black band at apical third, tibiae yellow, tarsus black. Fore femur with a row of dorsal, posterior, pv, and an av row at basal half. Mid femur with 5–6 setae on anterior surface on basal half, 2–3 pv and 2–3 av setae on basal third, 2 preapical setae on pd to posterior surface; mid tibia with one long ad seta and one short pd median seta, ad seta positioned below of the pd seta. Hind femur with a row of ad and a row of av setae, 3 pv setae on basal third. Similar size of claws and pulvilli of the three legs. **Abdomen:** Grey, tergites 3–4 with two brown spots and tergites 3–5 with a thin central longitudinal stripe. **Ovipositor:** Tergites 6 and 7 with two parallel sclerotized plates, tergite 8 with two short and round sclerotized plates over distal margin; epiproct triangular, with hair-like setae, shorter than cercus

(Fig. 14D). Sternites 6 and 7 with one central sclerite; sternite 8 divided into two small and linear sclerotized plates, each with setulae on distal margin; hypoproct triangular, setulose (Fig. 14E). Spermathecae (Fig. 14F).

**Type material. Holotype.** Male; BMNH [pinned, glued on card, fore legs missing]. Original labels: “♂ [handwritten] / Holo- / type [printed]” on white circular paper, red frame; “Chile: / Chiloe I. / F.& M. Edwards / B.M. 1927–63.” printed on white paper; “Ancud. / 17-19.xii.1926.” printed on white paper; “Austrocoenosia / brevicornis / Type [handwritten] / det. JRMAL-LOCH [printed]” on white paper, black frame. <https://data.nhm.ac.uk/object/8ffc5add-f61d-4dca-949b-600039c04740/1678924800000>

**Additional material examined.** ARGENTINA — Chubut province • 1 female; PNLA, Lago Verde; –42.717506, –71.725197; 539 m a.s.l.; 24 Oct 2014; Mulieri leg.; MACN.

**Distribution (Fig. 27D).** ARGENTINA: Chubut (new record). CHILE: R. de los Lagos.

**Remarks.** *Coenosia brevicornis* was described by Malloch (1934) with a single male specimen from Ancud, Chile. Some structures, such as one eaDC with half the length of the aDC, the coloration of the legs, and the profile of the head, allow distinguishing *C. brevicornis* from its congeners. After the original publication, a new combination, *Neodexiopsis brevicornis*, was established by Pont (1972). During our sampling campaigns, we collected only one female specimen with the same characters that distinguish *C. brevicornis* from its congeners and that are consistent with the general morphology of the male holotype. In addition, the female specimen possesses an erythrocyte-shape spermatheca, similar to that observed in all species of the *C. argentifrons* group. We propose the new combination.

### *Coenosia dubia* (Bigot, 1885) comb. rest.

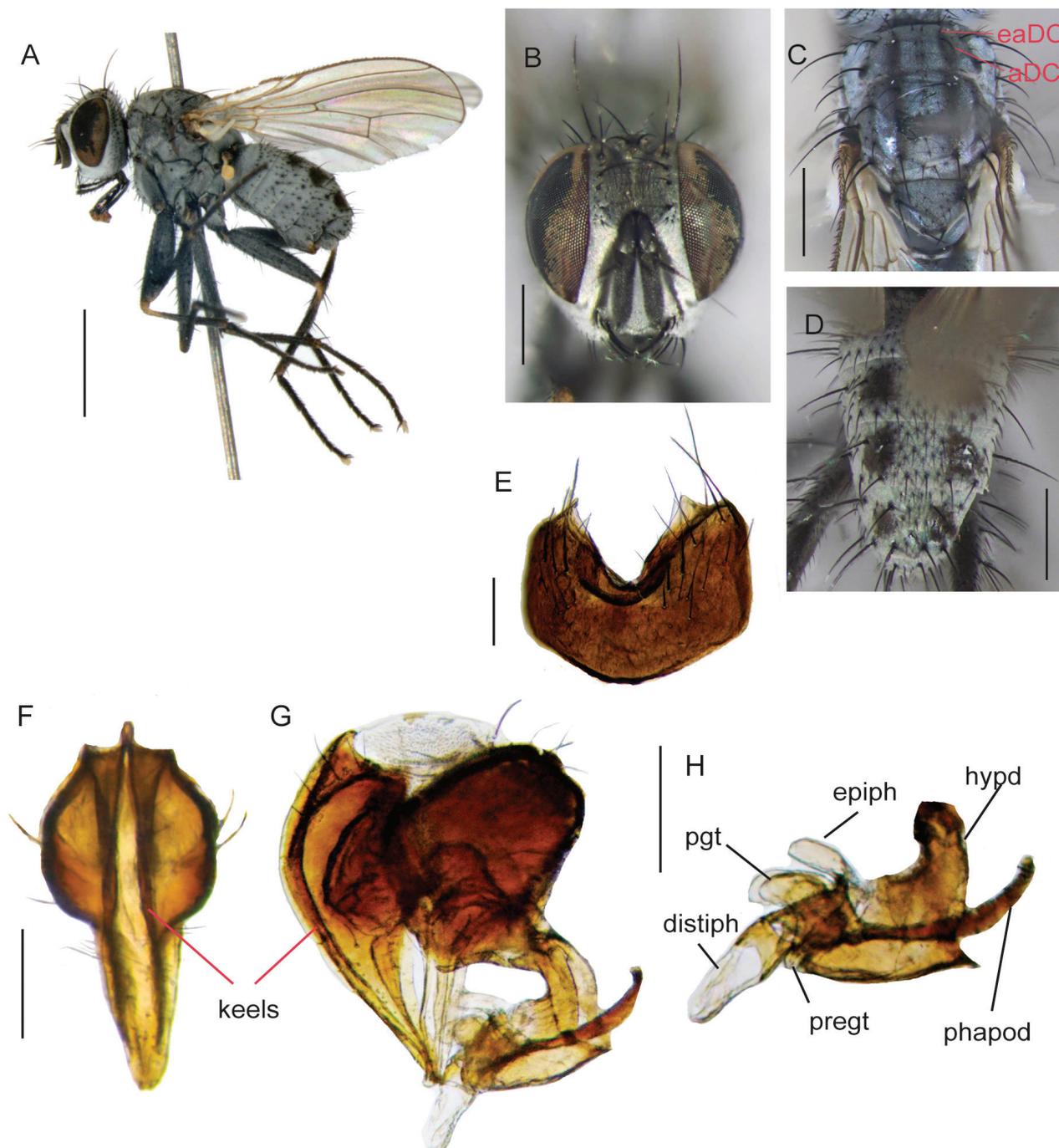
**Male (Fig. 15A).** Length. Body: 3.98–4.22 mm, wing: 3.70–4.00 mm. **Head:** (Fig. 15B). Frons at vertex about one third of the head width. Frons, fronto-orbital plate, parafacial and gena black with silver-grey pollinosity; 3–4 pairs of frontal setae. Frons longer than wide, with frontal triangle long, light grey, reaching lunula. Gena higher than the width of postpedicel. Fronto-orbital plate with 3–5 little setulae, close to parafacialia. Antenna black, apical angle of postpedicel acute; in lateral view inserted at the mid-level of the eye; arista with its longest microtrichia with similar length than its basal diameter. **Thorax:** (Fig. 15C). Black with grey pollinosity, with three fine dark-brown vitta along acrostichal and dorsocentral rows of setae; anterior and posterior spiracles grey. Chaetotaxy: acr s short and strong, the anterior presutural pair shortest as the anterior presutural dorsocentral seta; dorsocentrals 1+3, eaDC is less than one third of the aDC. Katepisternum with 2–3 setulae. **Wing:** Tegula

black. Both calypters whitish hyaline with white margins; halter yellow. **Legs:** Black with grey pollinosity, apex of femora yellow. Fore femur with a row of strong pd, a row of strong pv setae, and a row of av setae at basal third. Mid femur with a row of fine ventral setae, 3–4 strong setae on anterior surface, and 2 preapical setae on pd to posterior surface; mid tibia with one ad and one pd median setae, both setae with the same length and position. Hind femur with ad and av rows of setae. Fore claws and pulvilli longer than mid and hind pairs. **Abdomen:** (Fig. 15D). Grey with sub-triangular lateral dark-brown marks on tergites 1+2–5 (more evident on 3–5). Tergite 6 poorly visible in dorsal view. Sternite 5 broader than long, apical margin concave, with a depressed area at the base, and without membrane; setae concentrated on the lobes and some long and strong on apical margin (Fig. 15E). **Terminalia:** Cercus curved in lateral view, keels placed from distal to apical margin, wider at the base and thinner before apical tip, apical margin straight. Surstylus longer than broad, straight, barely sclerotized (Fig. 15F, G). Hypandrium tubular, wider than long, distal extreme exposing the phapod. Aedeagus with pregt developed barely sclerotized; pgt developed; epiphallus slightly sclerotized, and distiph tubular, slightly sclerotized at base, and without fine hair on ventral surface (Fig. 15G, H).

**Female (Fig. 16A, B).** Length. Body: 4.4–4.7 mm, wing: 4.10–4.33 mm. Differs from male as follows: **Thorax:** (Fig. 16C). Black with grey pollinosity, with five fine dark-brown vitta along acrostichal, dorsocentral and intralar rows of setae; **Ovipositor:** Tergites 6, 7, and 8 with two long and wide sclerotized plates; epiproct triangular, with spine-like setae, shorter than cercus (Fig. 16E). Sternites 6 and 7 with one long and wide plate; sternite 8 with one central plate and two small and sclerotized plates each with 4–5 setae on distal margin; hypoproct triangular, setulose, with several strong setae on distal margin (Fig. 16F). Spermathecae (Fig. 16G).

**Type material.** The type specimen is housed in Oxford University Museum of Natural History (UMO), United Kingdom. <https://oumnh.ox.ac.uk/collections-online/#/item/oum-catalogue-381555>. Pont (2000:11) observed that the holotype is in very poor condition “...head, abdomen, right fore leg, right mid leg, and both hind legs missing...”, and suggested that this species was correctly recognized by Malloch (1934: 218).

**Additional material examined.** ARGENTINA. — Chubut province • 36 females, 14 males; PNLA, Arroyo Torcido; –42.761319, –71.750590; 520 m a.s.l.; 26 Oct 2014; Mulieri, Patitucci & Torretta leg.; MACN • 5 males; PNLA, Cabaña La Cascada; –42.888499, –71.592376; 532 m a.s.l.; Feb 2013; Mulieri, Patitucci & Olea leg.; MACN; Malaise • 2 females; PNLA, Delta Río Stange; –42.873631, –71.780310; 500 m a.s.l.; 06 Feb 2013; Mulieri, Patitucci & Olea leg.; MACN • 1 male; PNLA, Lago Futalaufquen; –42.840982, –71.632934; 529 m a.s.l.; 05 Feb 2013; Mulieri, Patitucci & Olea leg.; MACN • 4 females, 13 males; PNLA, Lago Verde; –42.717506, –71.725197; 539 m a.s.l.; 24 Oct 2014; Mulier & Patitucci leg.; MACN • 8 females, 3 males; PNLP, Gendarmeria II; –42.0994, –71.6845; 205 m a.s.l.; 11 Jan 2012; Mulieri & Patitucci leg.; MACN • 1 female, 1 male (in copula); PNLP, Intendencia, –42.085077, –71.614662; 195 m a.s.l.; 13 Jan 2011; Mulieri leg.;

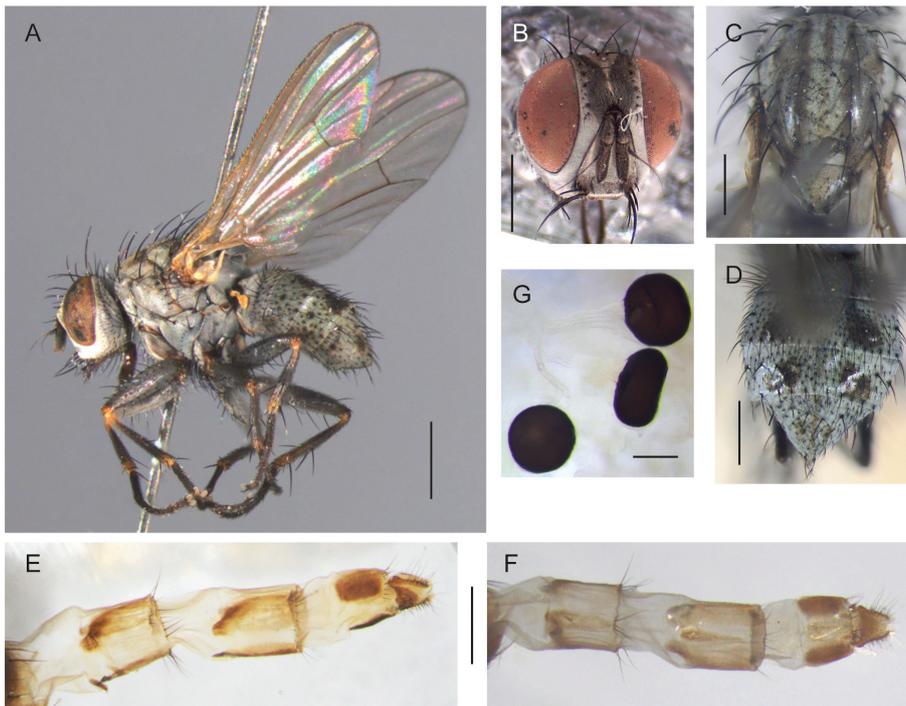


**Figure 15.** *Coenosia dubia*, male. **A** Lateral view, **B** head, frontal view, **C** thorax, dorsal view, **D** abdomen, dorsal view, **E** fifth sternite, **F** cercus, dorsal view, **G** cercus, surstylus and phallic complex, lateral view, **H** phallic complex, lateral view. Scale bar: 1 mm (A), 0.5 mm (B–D), 0.02 mm (E–G), 0.1 mm (H).

MACN • 2 females, PNLP, La Playita; –42.099032, –71.607425; 205 m a.s.l.; 09 Jan 2012; Patitucci leg.; MACN • 2 females, 1 male; PNLP, Los Hitos; –42.097993, –71.684775; 200 m a.s.l.; 14 Jan 2011; Mulieri & Patitucci leg.; MACN • 104 females, 16 males; PNLP, Río Azul; –42.0916, –71.6155; 184 m a.s.l.; 16–17 Jan 2011; Mulieri & Patitucci leg.; MACN • 3 females; PNLP, Río Turbio; –42.228541, –71.666482; 204 m a.s.l.; 12 Jan 2011; Mulieri leg.; MACN. – **Neuquén province** • 2 females; Arroyo Carreri, Ruta 13; –38.885904, –70.433105; 1160 m a.s.l.; 07 Feb 2018; Patitucci leg.; MACN • 3 females; PNL, Ñorquinco; –39.146931, –71.232717; 1070 m a.s.l.; 09 Jan 2013; Mulieri, Patitucci & Olea leg.; MACN. – **Río Negro province** • 1 female, 2 males; Bariloche; Dec 1926; Shannon leg.; Malloch det.; MNRJ.

**Distribution (Fig. 27F).** ARGENTINA: Chubut (new record), Neuquén, Río Negro. CHILE: R. de Bio Bio, R. de los Lagos, R. Metropolitana de Santiago.

**Remarks.** Bigot (1885) described *Anthomyia dubia* with only one female specimen from an unspecified location of Chile. Later, Stein (1907) observed this specimen and proposed a synonym with *Coenosia mediocris* Stein (1919). After that, Malloch (1934) recognized *dubia* with a large series of male and female specimens from Argentina and Chile, presented a very brief description, and considered it as part of *Austrocoenosia*. Later, Couri and Albuquerque



**Figure 16.** *Coenosia dubia*, female. **A** Lateral view, **B** head, frontal view, **C** thorax, dorsal view, **D** abdomen, dorsal view, **E** ovipositor, dorsal view, **F** ovipositor, ventral view, **G** spermathecae. Scale bar: 1 mm (A), 0.5 mm (B–F), 0.1 mm (G).

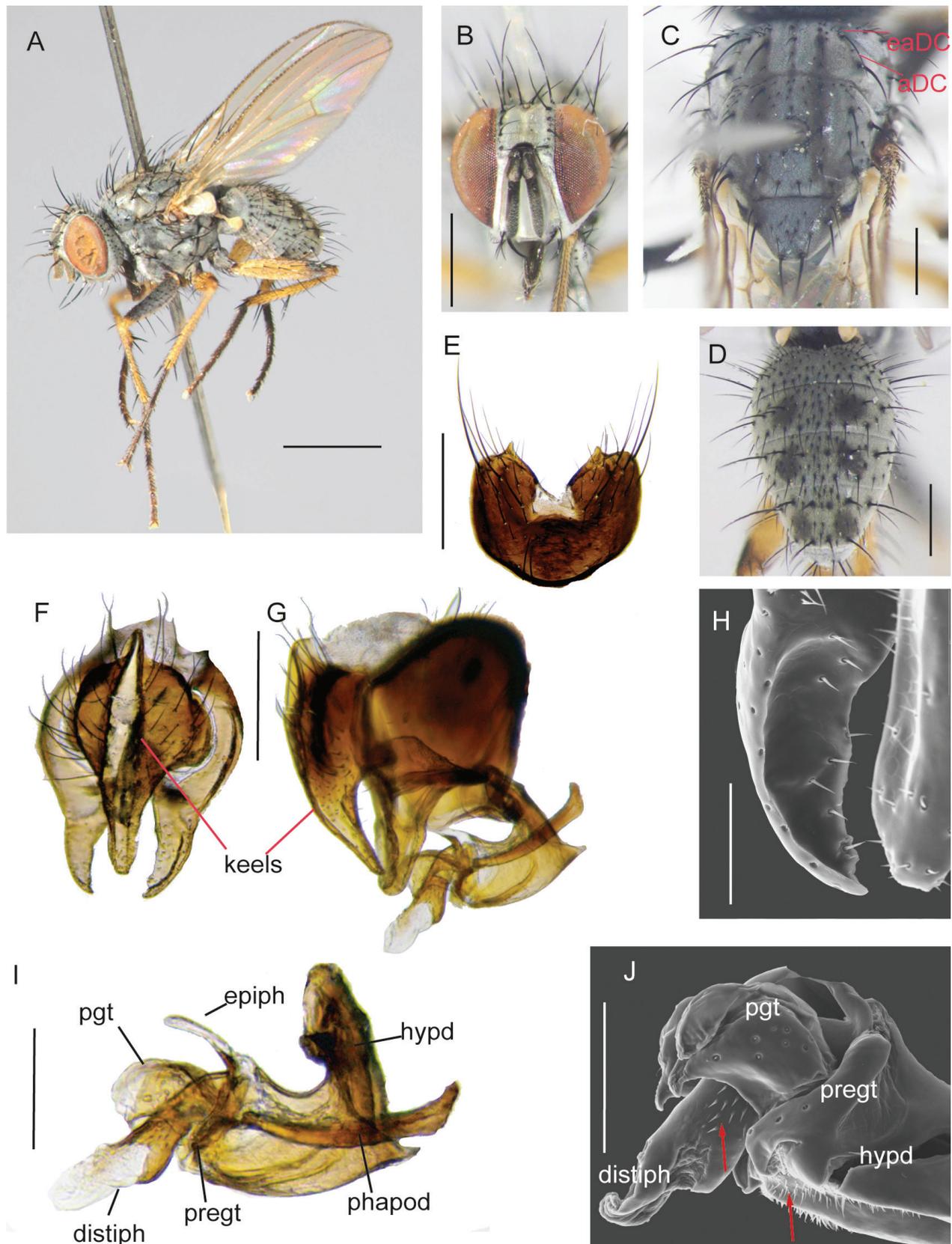
que (1979) included the species as part of the genus *Neodexiopsis*, establishing the current name. Then, Pont (2000, 2001) established that *mediocris* Stein and *dubia* Bigot are two different species, and later (Pont 2012) resolved a possible homonymy with the species *Caenosia dubia* Macquart, 1835. Recently, Couri and Pont (2020) presented a good redescription of the type specimens of *C. mediocris*. In the present study, we compared with our specimens of *C. dubia* and found several differences, including the coloration and the hind tibia chaetotaxy. We also found morphological and phylogenetic evidence to consider *C. dubia* as part of the *C. argentifrons* group, and revalidated the combination *Coenosia dubia*.

### *Coenosia ignobilis* Stein, 1911

**Male (Fig. 17A).** Length. Body: 3.05–3.27 mm, wing: 3.00–3.10 mm. **Head:** (Fig. 17B). Frons at vertex about one third of the head width. Frons, fronto-orbital plate, parafacial and gena dark brown with grey pollinosity; 3–4 pairs of frontal setae. Frons longer than wide, with frontal triangle long, light grey, reaching lunula. Gena height less than the width of postpedicel. Fronto-orbital plate with 3–5 little setulae, close to parafacialia. Antenna black, apical angle of postpedicel acute; in lateral view inserted at the mid-level of the eye; arista with its longest microtrichia with similar length than its basal diameter. **Thorax:** (Fig. 17C). Black with grey pollinosity, with a dark-brown vitta along acrosticals setae and a vitta between dorsocentral and intra-alar rows of setae; anterior and posterior spiracles grey. Chaetotaxy: acr s short and irregular, the anterior presutural acr s with similar length to the eaDC; dorsocentrals 1+3, eaDC is less than one third of the aDC. Katapisternum with 2–3 setulae. **Wing:** Tegula black. Both calypters whitish hyaline with white

margins; halter yellow. **Legs:** Black, apex of fore femur, basal half of mid and hind femora, and tibiae yellow; tarsus black. Fore femur with a row of strong pd, a row of strong pv setae, and a row of av setae at basal third. Mid femur with 5–6 setae on anterior surface on basal half, 2–3 pv and 2–3 av setae on basal third, 2 preapical setae on pd to posterior surface; mid tibia with one ad and one pd median setae, ad seta longer and placed more apically than pd seta. Hind femur with a complete row of ad and a row of av setae on apical half, with three pv seta on basal third, apical most is the longest of the three. Similar size of claws and pulvilli of the three legs. **Abdomen:** (Fig. 17D). Black, with grey pruinosity, tergites 3–5 with two dark brown spots. Tergite 6 partly visible in dorsal view. Sternite 5 broader than long, apical margin concave with a “U” shape, and with membrane; setae concentrated on the lobes and some long and strong on apical margin (Fig. 17E). **Terminalia:** Cercus curved in lateral view, keels only on basal two-thirds, apical margin straight (Fig. 17F, G). Surstylus longer than broad, wide at base and tapering towards apex, straight, sclerotized (Fig. 17H). Hypandrium tubular, wider than long, distal extreme exposing the phapod, and with several hairs on ventral surface. Aedeagus with pregt developed and sclerotized; pgt developed; epiphalus slightly sclerotized, and distiph tubular, sclerotized at base, and with spines on lateral surface (Fig. 17G, I–J).

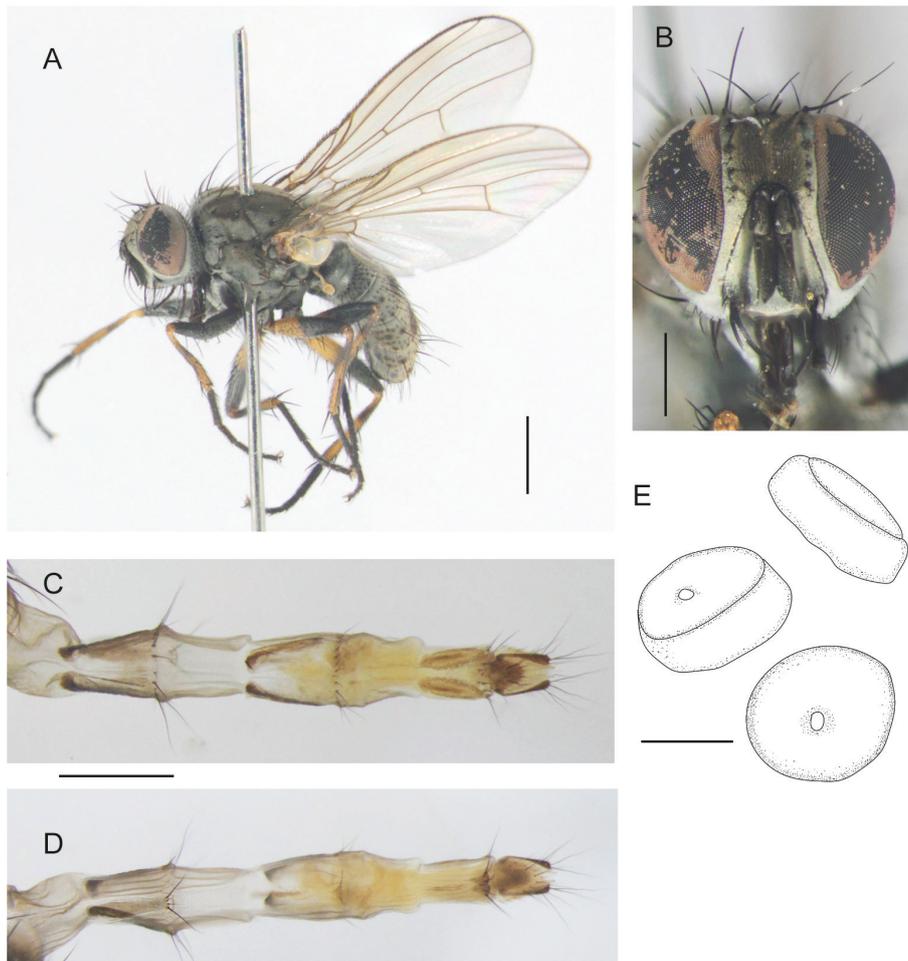
**Female (Fig. 18A, B).** Length. Body: 3.70–4.40 mm, wing: 3.50–4.24 mm. Differs from male as follows: **Legs:** Mid and hind femora more yellow, hind tibia with one long ad, one short av, and one long pd setae on middle third. **Ovipositor:** Tergites 6, 7, and 8 with two long and wide sclerotized plates; epiproct triangular, with hair-like setae, shorter than cercus (Fig. 18C). Sternites 6 and 7 with one long and wide plate; sternite 8 with one central



**Figure 17.** *Coenosia ignobilis*, male. **A** Lateral view, **B** head, frontal view, **C** thorax, dorsal view, **D** abdomen, dorsal view, **E** fifth sternite, **F** cercus and surstylus, dorsal view, **G** cercus, surstylus and phallic complex, lateral view, **H** detail of surstylus, distal tip (SEM), **I** phallic complex, lateral view, **J** detail of phallic complex, distal tip (SEM). Scale bar: 1 mm (A), 0.5 mm (B–G), 0.05 mm (H), 0.1 mm (I–J). Hairs on ventral surface of hypd and spines on lateral surface of distiph – red arrows.

plate and two small, linear, and sclerotized plates each with 4–5 setae on distal margin; hypoproct triangular,

setulose, with several strong setae on distal margin (Fig. 18D). Spermathecae (Fig. 18E).



**Figure 18.** *Coenosia ignobilis*, female. **A** Lateral view, **B** head, frontal view, **C** ovipositor, dorsal view, **D** ovipositor, ventral view, **E** spermathecae. Scale bar: 1 mm (A), 0.5 mm (B–D), 0.1 mm (E).

**Type material. Paratype.** Male; ZMUH [pinned, in good condition]. Original labels: “PARALECTOTYPE ♂ / *Coenosia / ignobilis* / Stein, 1911 / Des.A.C. Pont 1999” printed, on white paper; “*Coenosia / ignobilis* / Typo Stein” handwritten, on white paper; “Type” printed on red paper; “Chile [printed] / 20.IX.02 [handwrite] / Quillota [printed]” on green paper.

**Additional material examined.** ARGENTINA — **Chubut province** • 2 females; PNLA, Cabaña La Cascada; –42.888499, –71.592376; 532 m a.s.l.; Feb 2013; Mulieri, Patitucci & Olea leg.; MACN • 5 females, 5 males; PNLA, Seccional Lago Verde; –42.718803, –71.727470; 538 m a.s.l.; Oct 2014; Mulieri & Patitucci leg.; MACN • 1 female; PNLA, Puerto Mermoud; –42.723248; –71.748801; 521 m a.s.l.; 25 Oct 2014; Torretta leg.; MACN • 3 males; PNLP, Gendarmería; –42.097468, –71.681953; 200 m a.s.l.; 07–11 Jan 2012; Mulieri & Patitucci leg.; MACN • 1 male; PNLP, Intendencia; –42.085077, –71.614662; 195 m a.s.l.; 16 Jan 2011; Mulieri & Patitucci leg.; MACN • 1 female, 9 males; PNLP, La Playita; –42.099032, –71.607425; 205 m a.s.l.; 09 Jan 2012; Patitucci leg.; MACN • 1 female; PNLP, Río Azul; –42.0916, –71.6155; 184 m a.s.l.; 17 Jan 2011; Mulieri & Patitucci leg.; MACN • 2 females; PNLP, Río Turbio; –42.228541, –71.666482; 204 m a.s.l.; 12 Jan 2011; Mulieri & Patitucci leg.; MACN. — **Neuquén province** • 1 female; Cerro Chapelco; –40.197050, –71.298453; 1400 m a.s.l.; 15 Feb 1983; M. Gentili & P. Gentili leg.; IFML • 4 females, 1 male; San Martín de los Andes, Truran Kura; 1000 m a.s.l.; 27 Sep 1986; M. Gentili & P. Gentili leg.; IFML. — **Río Negro province** • 3 males; PNNH, Lago Guillermo; –41.358807, –71.515071; 833 m a.s.l.; 14 Sep–01 Oct 2008; Garré & Montes de Oca leg.; MLP; Malaise. CHILE — **Región de la Araucanía**

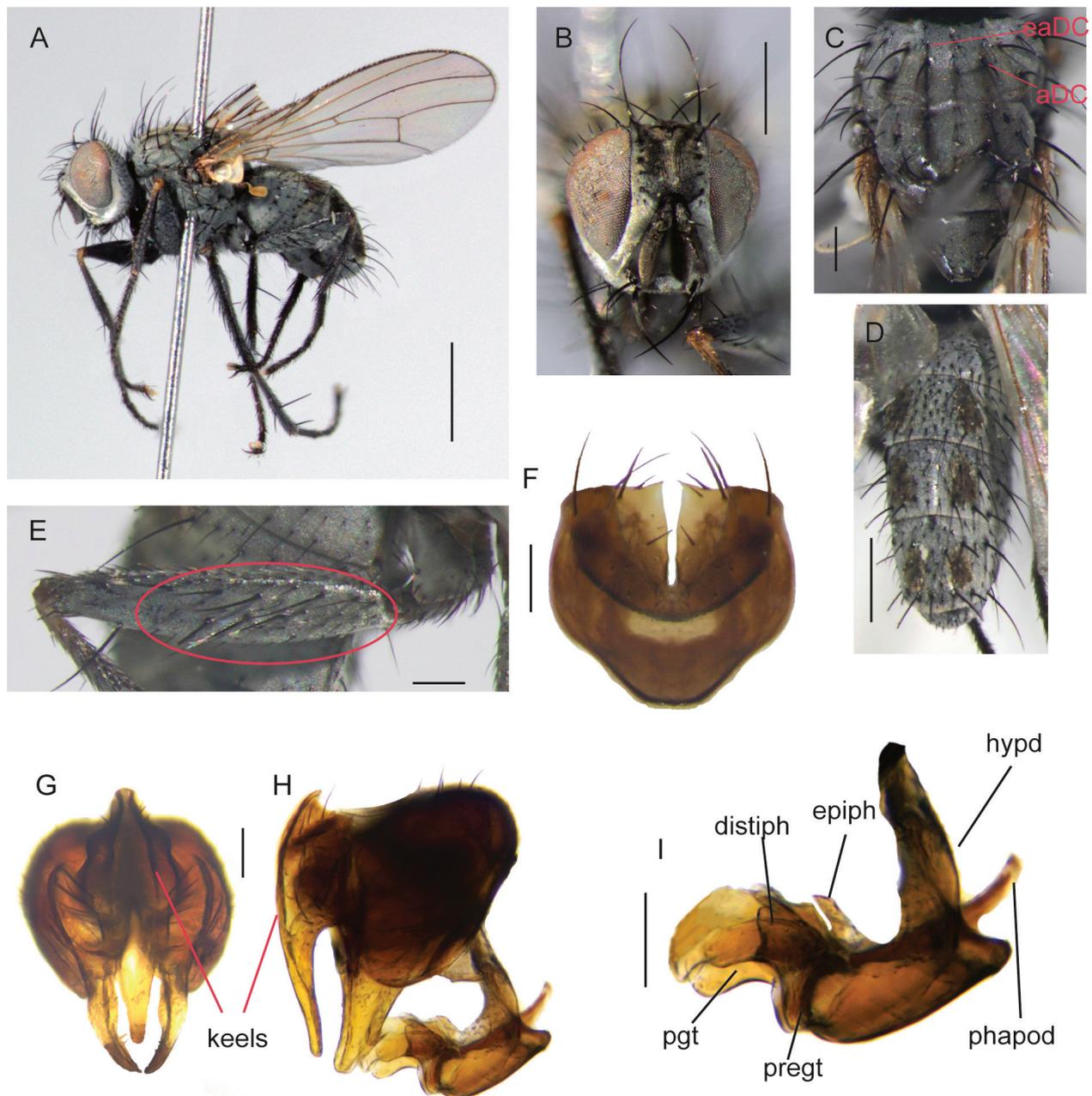
• 1 female; Angol; –37.7800, –72.7500; 15 Sep 1926; JR Malloch det.; SM Lopes leg. MNRJ.

**Distribution (Fig. 27G).** ARGENTINA: Chubut (new record), Neuquén (new record), Río Negro. CHILE: Arch. Juan Fernandez, R. de la Araucanía, R. de Valparaíso.

**Remarks.** Stein (1911) described *Coenosia ignobilis* with male and female specimens from Chile. Later, Malloch (1934) studied a large series of male and female specimens from Argentina and Chile, presented a brief description, and considered it as part of *Austrocoenosia*. Later, Couri and Albuquerque (1979) observed a female specimen from the series of specimens studied by Malloch (op. cit), and included the species as part of the genus *Neodexiopsis*. Pont (2001) designated lectotypes and paralectotypes and established the original combination *Coenosia ignobilis*. Recently, Couri and Pont (2020) presented a redescription of the paralectotype housed in ZMUH.

### *Coenosia inusitata* (Malloch, 1934)

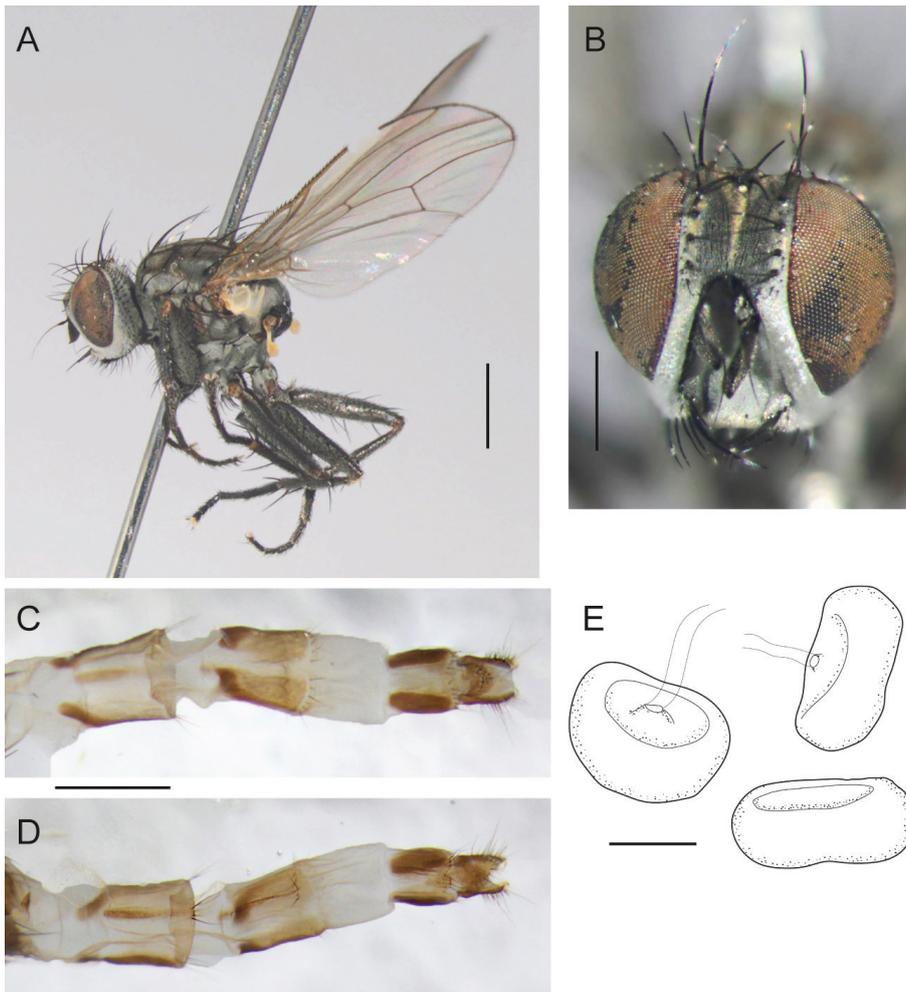
**Male (Fig. 19A).** Length. Body: 4.43–4.8 mm, wing: 4.05–4.24 mm. **Head:** (Fig. 19B). Frons at vertex about one third of the head width. Frons, fronto-orbital plate, parafacial and gena black with grey pollinosity; 4–5 pairs



**Figure 19.** *Coenosia inusitata*, male. **A** Lateral view, **B** head, frontal view, **C** thorax, dorsal view, **D** abdomen, dorsal view, **E** hind femur, anterior surface, **F** fifth sternite, **G** cercus and surstylus, dorsal view, **H** cercus, surstylus and phallic complex, lateral view, **I** phallic complex, lateral view. Scale bar: 1 mm (A), 0.5 mm (B, D), 0.2 mm (C, F), 0.1 mm (G–I). Hind femur, setae on anterior surface – red circle.

of frontal setae. Frons longer than wide, with frontal triangle long, light grey, reaching lunula. Gena higher than the width of postpedicel. Fronto-orbital plate with 1–3 setula, close to parafacialia. Antenna black, apical angle of postpedicel acute; in lateral view inserted over the mid-level of the eye; arista with its longest microtrichia shorter than its basal diameter. **Thorax:** (Fig. 19C). Black with grey pollinosity, with three black vitta at dorsocentral and acrosticals rows of setae; anterior and posterior spiracles grey. Chaetotaxy: acr s short and irregular, the anterior presutural acr s longer than the anterior presutural dorsocentral seta (eaDC); dorsocentrals 1+3, eaDC is less than one third of the aDC. Katepisternum with 2–3 setulae. **Wing:** Tegula black. Both calypters whitish hya-

line with white margins; halter yellow. **Legs:** Black with grey pollinosity, apex of femora yellow. Fore femur with a row of strong pd, a row of strong pv setae, and a row of av setae at basal third. Mid femur with 5–6 setae on anterior surface on basal half, 2 long setae on ventral surface, 2 preapical setae on pd to posterior surface; mid tibia with one ad and one pd setae on median third, ad seta shorter and positioned below pd seta. Hind femur with a complete row of ad setae and a row of anterior setae which are positioned in dorsalventral direction (Fig. 19E), with 1–2 pv seta on basal third. Similar size of claws and pulvilli of the three legs. **Abdomen:** (Fig. 19D). Black, with grey pruinosity, tergites 3–5 with two dark brown spots. Tergite 6 not visible in dorsal view. Sternite 5 broader than



**Figure 20.** *Coenosia inusitata*, female. **A** lateral view, **B** head, frontal view, **C** ovipositor, dorsal view, **D** ovipositor, ventral view, **E** spermathecae. Scale bar: 1 mm (A), 0.5 mm (B–D), 0.1 mm (E).

long, apical margin strong concave, with a depressed area at the base, and without membrane; setae concentrated on the lobes and some long and strong on apical margin (Fig. 19F). **Terminalia:** Cercus curved in lateral view, keels only on basal half, apical margin straight. Surstylus longer than broad, curved at apex, sclerotized (Fig. 19G, H). Hypandrium tubular, wider than long, distal extreme not exposing the phapod. Aedeagus with pregit developed sclerotized; pgt developed; epiphalus sclerotized, and distiph tubular, sclerotized at base, and without spine on ventral surface (Fig. 19H, I).

**Female (Fig. 20A, B).** Length. Body: 4.5 mm, wing: 4.3 mm. Differs from male as follows: **Legs:** Hind femur without a row of anterior setae which are located descendant in dorsalventral direction. **Ovipositor:** Tergites 6, 7, and 8 with two long and wide sclerotized plates; epiproct triangular, with spine-like setae, shorter than cercus (Fig. 20C). Sternites 6 and 7 with one long and thin plates; sternite 8 with one thin central plate and two small and sclerotized plates each with 4–5 setae on distal margin; hypoproct triangular, setulose, with several strong setae on distal margin (Fig. 20D). Spermathecae (Fig. 20E).

**Type material. Holotype.** Male; USNM [pinned, in good condition] Original labels: “Angol – Chile [printed] / 19 Sept. 1926 [handwritten]” on white paper; “USNMENT / [QR code] / 01556237” printed

on white paper; “Type No. [printed] / 49881 [handwritten] / U.S.N.M. [printed]” on red paper; “Coenosia / inusitata / Type [handwritten] / det. JRMALLOCH [printed]” on white paper, black frame. <http://n2t.net/ark:/65665/3663fd640-e048-4b9e-aa65-308c2c8e518b>

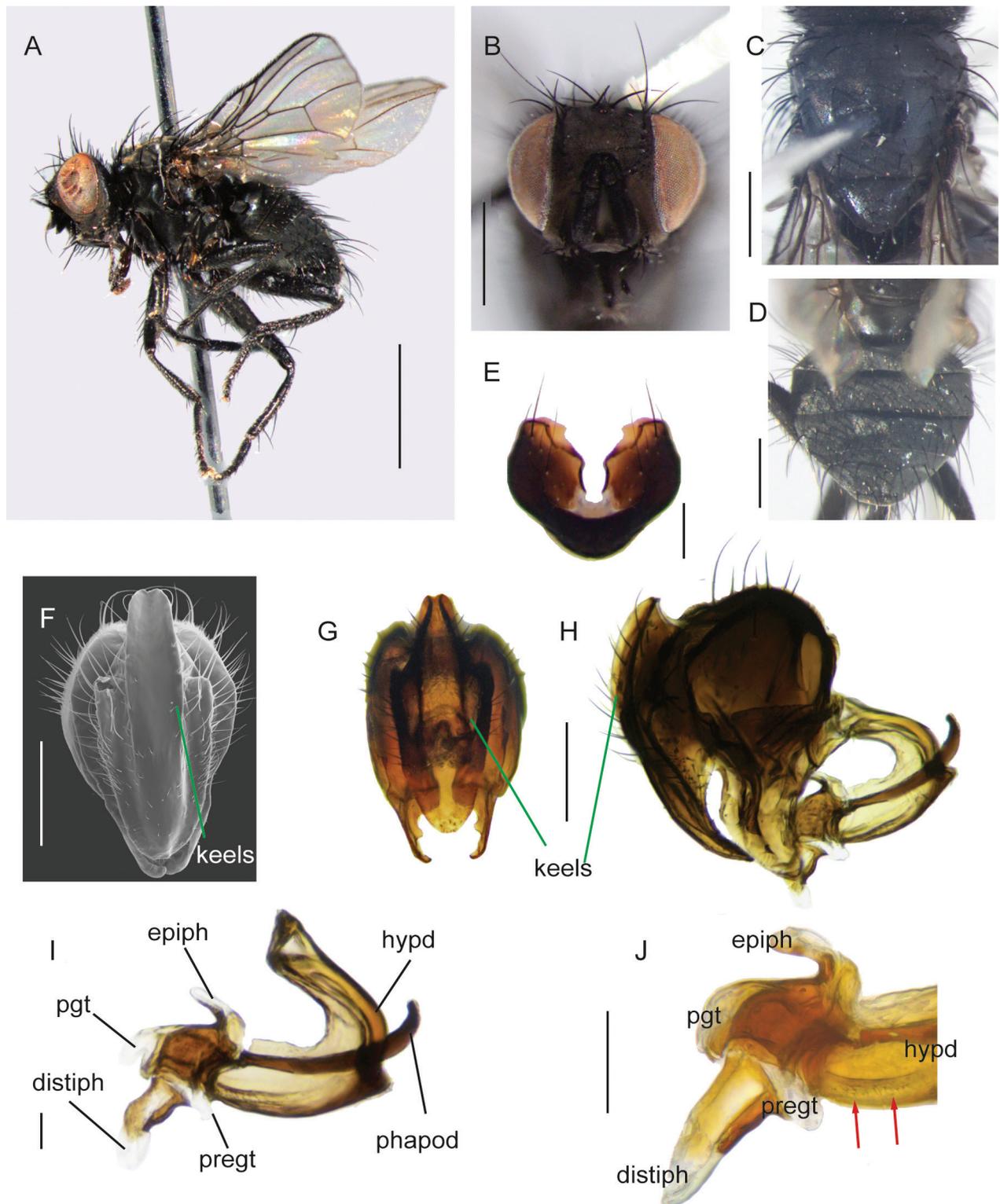
**Additional material examined.** ARGENTINA — Neuquén province • 1 female, 1 male; Alumine, Río Aluminé; –39.234610, –70.910481; 896 m a.s.l.; 12 Jan 2013; Mulieri, Patitucci & Olea leg.; MACN • 4 males; Arroyo Carreri, Ruta 13; –38.885904, –70.433105; 1160 m a.s.l.; 07 Feb 2018; Olea & Patitucci leg; MACN.

**Distribution (Fig. 27B).** ARGENTINA: Neuquén (new record). CHILE: R. de la Araucanía.

**Remarks.** *Coenosia inusitata* was described by Malloch (1934) with male and female specimens from Angol, Chile. Specimens captured by LDP and PRM were collected in open areas (steppe), close to rivers. The abdomen of only female specimen collected was photographed and then removed for the dissection of the terminalia.

### *Coenosia nigerrima* (Malloch, 1934) comb. rest.

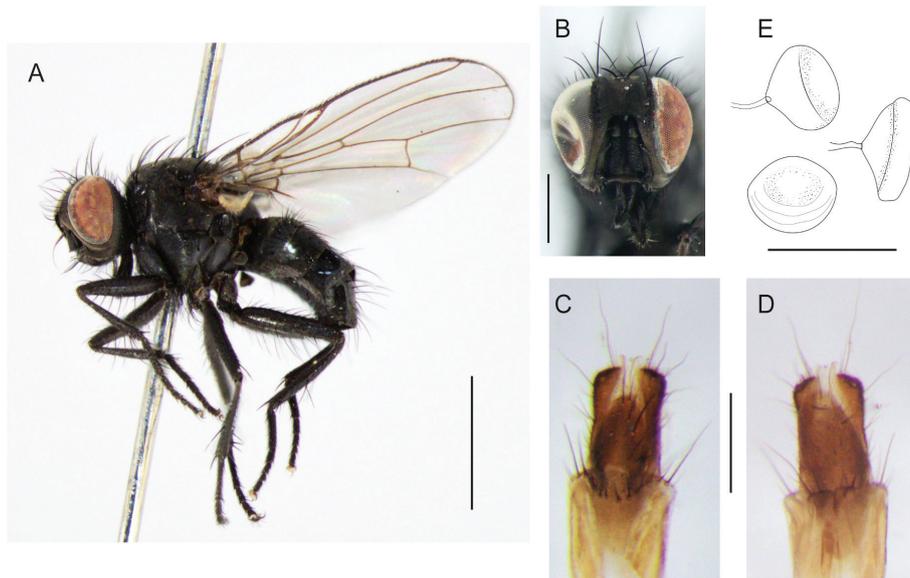
**Male (Fig. 21A).** Length. Body: 3.40–3.94 mm, wing: 2.80–3.49 mm. **Head:** (Fig. 21B). Frons, fronto-orbital



**Figure 21.** *Coenosia nigerrima*, male. **A** Lateral view, **B** head, frontal view, **C** thorax, dorsal view, **D** abdomen, dorsal view, **E** fifth sternite, **F** cercus, dorsal view (SEM), **G** cercus and surstylus, dorsal view, **H** cercus, surstylus and phallic complex, lateral view, **I** phallic complex, lateral view, **J** phallic complex, detail of distal tip. Scale bar: 1 mm (A), 0.5 mm (B–D), 0.2 mm (E–H), 0.05 mm (I–J). Hypandrium, spicules on ventral surface – red arrows.

plate, parafacial and gena black. 5–6 pairs of frontal setae. Frons at vertex about one third of the head width. Frons with similar length and width, with frontal triangle short, black, not reaching lunule. Gena with a similar width to the postpedicel. Fronto-orbital plate with 6–8 short setulae, close to parafacialia. Parafacial in lateral

view narrow. Antenna black; in lateral view inserted over the mid-level of the eye; arista with its longest microtrichia shorter than its basal diameter. Palpus black. **Thorax:** (Fig. 21C). Black with brown pollinosity, without vitta; anterior and posterior spiracles black. Chaetotaxy: acr s strong and biseriata; anterior presutural pair lon-



**Figure 22.** *Coenosia nigerrima*, female. **A:** Lateral view, **B** head, frontal view, **C** ovipositor, dorsal view, distal tip, **D** ovipositor, ventral view, distal tip, **E** spermathecae. Scale bar: 1 mm (A), 0.5 mm (B–D), 0.2 mm (E).

ger than the extra pair of presutural dorsocentral (eaDC); dorsocentrals 1+3, eaDC is less than one fifth of the aDC. Katepisternum with 2–3 setulae. **Wing:** Tegula black. Both calypters hyaline with black margins; halter black. **Legs:** Coxae, trochanters, femora, tibiae, and tarsus black. Fore femur with a row of strong pd to pv setae, and a row of strong av setae on basal third. Mid femur with 1–2 long setae on ventral surface, a row of setae on anterior surface, and 2 preapical setae on pd to posterior surface; mid tibia with one ad and one pd median setae, with the same length and ad seta positioned below pd seta. Hind femur with a row of ad and a row of av setae, with one preapical ad seta and one pd seta. Hind tibia similar size of claws and pulvilli of the three legs. **Abdomen:** (Fig. 21D). Black without spots. Tergite 6 not visible in dorsal or lateral view. Sternite 5 broader than long, apical margin concave with a thin “U” shape reduced towards the base, and without membrane; few setae concentrated on the lobes and some long and strong on apical margin (Fig. 21E). **Terminalia:** Cercus curved in lateral view, and two longitudinal keels only on basal half, apical margin straight. Little spines on inner surface. Surstylus broad at base and at apex, curved, with a pointed process at apical third in inner surface (Fig. 21F–H). Hypandrium tubular longer than wide, with several little spicules close to pregt. Aedeagus with pgt developed and poor sclerotized; epiphalus slightly sclerotized, and distiph tubular, strongly sclerotized at base (Fig. 21I, J).

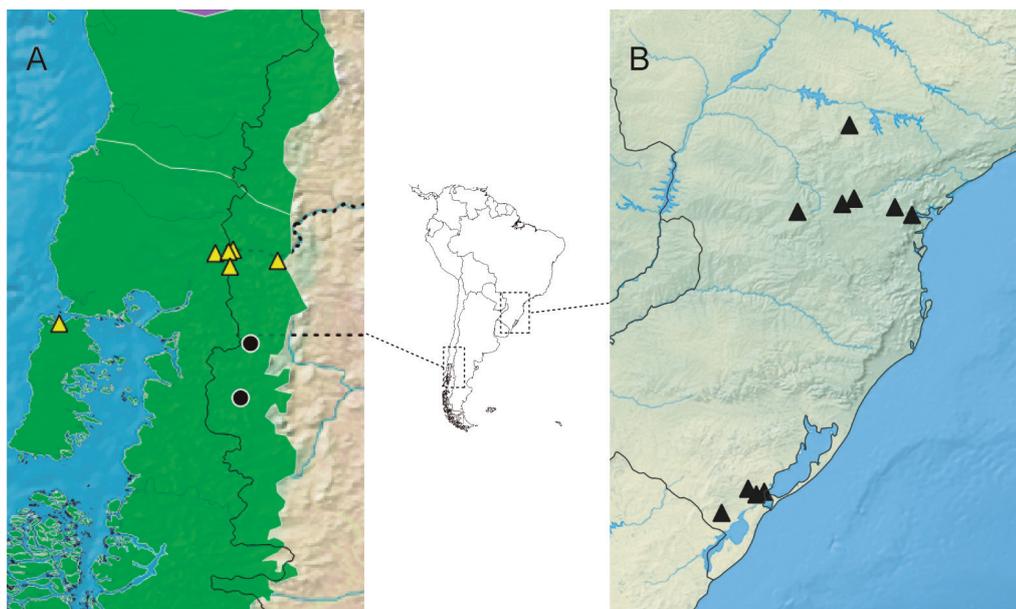
**Female (Fig. 22A, B).** Length. Body: 3.75–4.10 mm, wing: 3.60–4.30 mm. Differs from male as follows: **Wing:** Both calypters hyaline with white margins. **Ovipositor:** Tergites 6, 7 and 8 with 2 long and wide sclerotized plates; epiproct triangular, with hair-like setae, cercus longer than epiproct (Fig. 22C). Sternites 6 and 7 with long plates; sternite 8 with a central long plate and 2 small plates each with 4–5 setae on distal margin; hypoproct triangular, with several short setae on distal margin (Fig. 22D). Spermathecae (Fig. 22E).

**Type material. Paratypes.** Two females; MNRJ. [pinned, without abdomen] Original labels: “Casa Pangué / Llanquihue / Chile Dec 1926 / R& E. Shannon” print. on white paper, “Paratypo” print. on green paper, black frame; “♀” handwr. on white paper. “M.N.R.J [print.] / 4401 [handwr.]” on white paper, black frame. **Paratype:** male; MNRJ. [glued on card, without abdomen]. Original labels: “Casa Pangué / Llanquihue / Chile Dec 1926 / R& E. Shannon” print. on white paper, “Neodexiopsis / nigerrima (Mall.) [handwr.] / S.M. Lopes det. [print.]” on white paper. “Paratypo” print. on green paper, black frame; “♀” handwr. on white paper. “M.N.R.J [print.] / 4401 [handwr.]” on white paper, black frame.

**Additional material examined.** ARGENTINA — **Chubut province** • 2 females, 10 males; PNLA, Seccional Lago Verde; –42.718803, –71.727470; 538 m a.s.l.; Oct 2014, Mulieri Patitucci & Torretta leg.; MACN; Malaise • 1 female; PNLP, Pitranto Grande; –42.0963, –71.6129; 200 m a.s.l.; 11 Jan 2011; Patitucci leg.; MACN. – **Neuquén province** • 2 females; PNL, Pucara; –40.1551565, –71.63161488; Jan 1952; Schajovskoi leg.; MACN.

**Distribution (Fig. 23).** ARGENTINA: Chubut (new record), Neuquén (new record), Río Negro. CHILE: R. de Bio Bio, R. de los Lagos.

**Remarks.** Malloch (1934) described *C. nigerrima* with females and male specimens from Argentina and Chile, and proposed it as the type species of *Austrocoenosia*. Also, this author highlighted the dark black coloration and the absence of marks on the thorax and abdomen, characters that differentiate this species from the remaining *Austrocoenosia* species. Later, Pont (1972) transferred the species to *Coenosia*. After that, Couri and Albuquerque (1979) presented drawing of the female and male terminalia, and transferred the species to *Neodexiopsis*. The general black coloration, and the strongly sclerotized male terminalia make it difficult to correctly identify the species. In the specimens studied in the present work, we observed some differences (presence of keels on the cercus, shape of the surstylus) from the drawings presented by Couri and Albuquerque (1979). We found morphological and phylogenetic evidence to consider this species as



**Figure 23.** Geographical distribution of *Coenosia nigerrima*. **A** Subantarctic subregion records (Argentina, Chile), **B** Atlantic forest region records (Brazil). Biogeographic subantarctic subregion – green area, new records – black circle; bibliographic records – yellow triangle; bibliographic records in Brazil – black triangle.

part of the *C. argentifrons* group, and thus restored the previous combination proposed by Pont (1972) *Coenosia nigerrima*.

Regarding its distribution, several authors (Costacurta et al. 2003; Rodríguez-Fernández et al. 2006; Krüger et al. 2010; Fogaça et al. 2020) recorded this species in the South of Brazil (Fig. 23B). Since species of the *C. argentifrons* group presents restricted distribution in the Central Chilean and Subantarctic subregions; it would be interesting to examine the specimens collected in southern Brazil to establish similarities and differences.

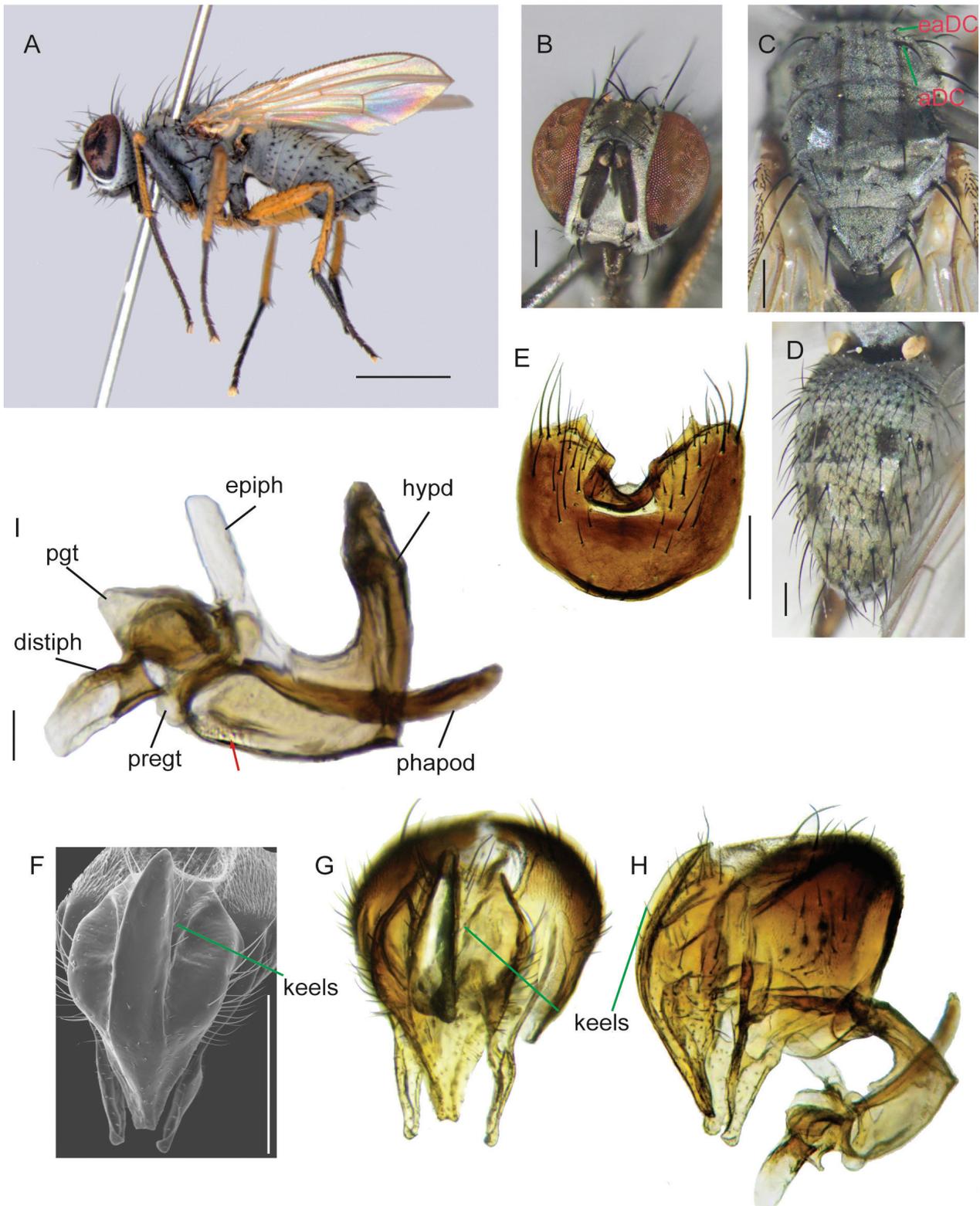
### *Coenosia patagonica* sp. nov.

<https://zoobank.org/CC840C06-5DAF-4F70-8D3E-65B16D060624>

**Male (Fig. 24A).** Length. Body: 3.75–4.2 mm, wing: 3.70–4.0 mm. **Head:** (Fig. 24B). Frons at vertex about one third of the head width. Frons, fronto-orbital plate, parafacial and gena black with grey pollinosity; 3–4 pairs of frontal setae. Frons longer than wide, with frontal triangle long, light brown, reaching lunula. Gena height similar to the width of postpedicel. Fronto-orbital plate with 3–5 little setulae, close to parafacialia. Antenna black, apical angle of postpedicel acute; in lateral view inserted at the mid-level of the eye; arista with its longest microtrichia shorter than its basal diameter. **Thorax:** (Fig. 24C). Black with grey pollinosity, with two thin dark-brown vitta at dorsocentral rows of setae; anterior and posterior spiracles grey. Chaetotaxy: acr s short and irregular, the anterior presutural acr s with similar length to the extra anterior presutural dorsocentral seta (eaDC); dorsocentrals 1+3, eaDC is less than one third of the aDC. Katepisternum with 1–2 setulae. **Wing:** Tegula yellow.

Both calypters whitish hyaline with white margins; halter yellow. **Legs:** Coxae grey. Fore femur grey with apical tip yellow, mid and hind femora yellow with a black apical ring or a dorsal band. Tibiae yellow. Tarsus black. Fore femur with a row of strong pd, a row of strong pv setae, and a row of av setae at basal third. Mid femur with 4–5 setae on anterior surface on basal half, 2–3 pv and 2–3 av setae on basal third, 2 preapical setae on pd to posterior surface; mid tibia with one ad and one pd median setae, with similar length, ad positioned below of the pd seta. Hind femur with a complete row of ad and a row of av setae, with 2–3 pv setae on basal third. Similar size of claws and pulvilli of the three legs. **Abdomen:** (Fig. 24D). Black, with grey pruinosity, tergites 1+2–5 with two dark brown spots. Tergite 6 not visible in dorsal. Sternite 5 broader than long, apical margin concave with a “U” shape, with a depressed area at the base, and without membrane; setae concentrated on the lobes and some long and strong on apical margin (Fig. 24E). **Terminalia:** Cercus curved in lateral view, keels present at basal half, apical margin little concave. Surstylus longer than broad, narrowing towards the apex, straight, sclerotized (Fig. 24F–H). Hypandrium tubular, wider than long, with several spines on ventral surface. Aedeagus with pregt developed sclerotized; pgt developed; epiphalus long and not sclerotized, and distiph tubular, sclerotized at base, and without spine on ventral surface (Fig. 24H, I).

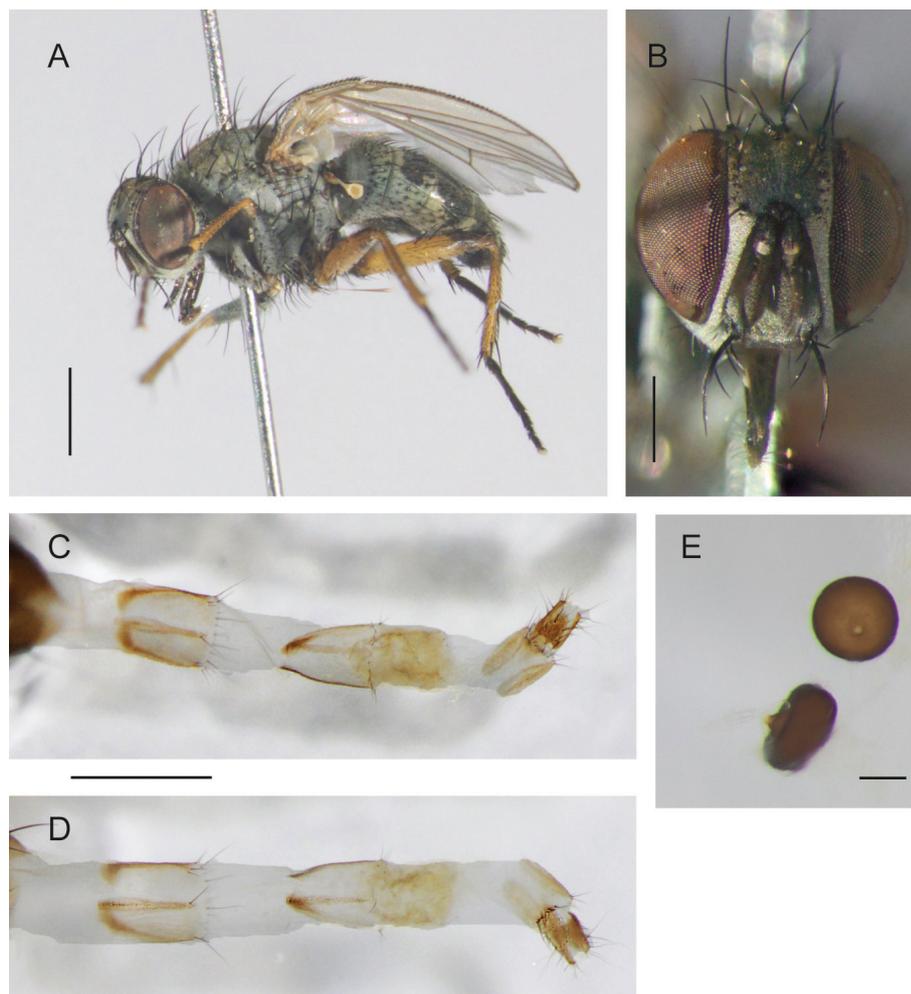
**Female (Fig. 25A, B).** Length. Body: 3.95–4.40 mm, wing: 3.55–4.10 mm. Differs from male as follows: **Thorax:** Chaetotaxy: acr s long and irregular, the anterior presutural pair longer than the anterior presutural dorsocentral seta. Katepisternum with 6–8 setula. **Ovipositor:** Tergites 6 and 7 with two long and thin sclerotized plates, tergite 8 with two long and wide sclerotized plates; epiproct triangular, with hair-like setae, shorter than cer-



**Figure 24.** *Coenosia patagonica* sp. nov. male. **A** Lateral view, **B** head, frontal view, **C** thorax, dorsal view, **D** abdomen, dorsal view, **E** fifth sternite, **F** cercus and surstylus, dorsal view (SEM), **G** cercus and surstylus, dorsal view, **H** cercus, surstylus and phallic complex, lateral view, **I** phallic complex, lateral view. Scale bar: 1 mm (A), 0.5 mm (B–D), 0.2 mm (E–H), 0.05 mm (I). Hypandrium, spicules on ventral surface – red arrows.

cus (Fig. 25C). Sternites 6 and 7 with one long and wide plate; sternite 8 with two small, linear, and sclerotized plates each with 4–5 setae on distal margin; hypoproct triangular, setulose, with several strong setae on distal margin (Fig. 25D). Spermathecae (Fig. 25E).

**Type material examined. Holotype.** Male; MACN [pinned]. Original labels: “Arg. Chubut Parque Nacional / Lago Puelo (Gendarmeria Malaise) / 42°05,947’ S 71°40,937’ W / I-2012 Mulieri & Patitucci leg.” print. on white paper; “MACN-Ent / 34730” print. on white paper, black frame; “Holotype” print. on red paper, black frame. **Paratypes.**



**Figure 25.** *Coenosia patagonica* sp. nov., female. **A** Lateral view, **B** head, frontal view, **C** ovipositor, dorsal view, **D** ovipositor, ventral view, **E** spermathecae. Scale bar: 1 mm (A), 0.2 mm (B), 0.5 mm (C, D), 0.1 mm (E).

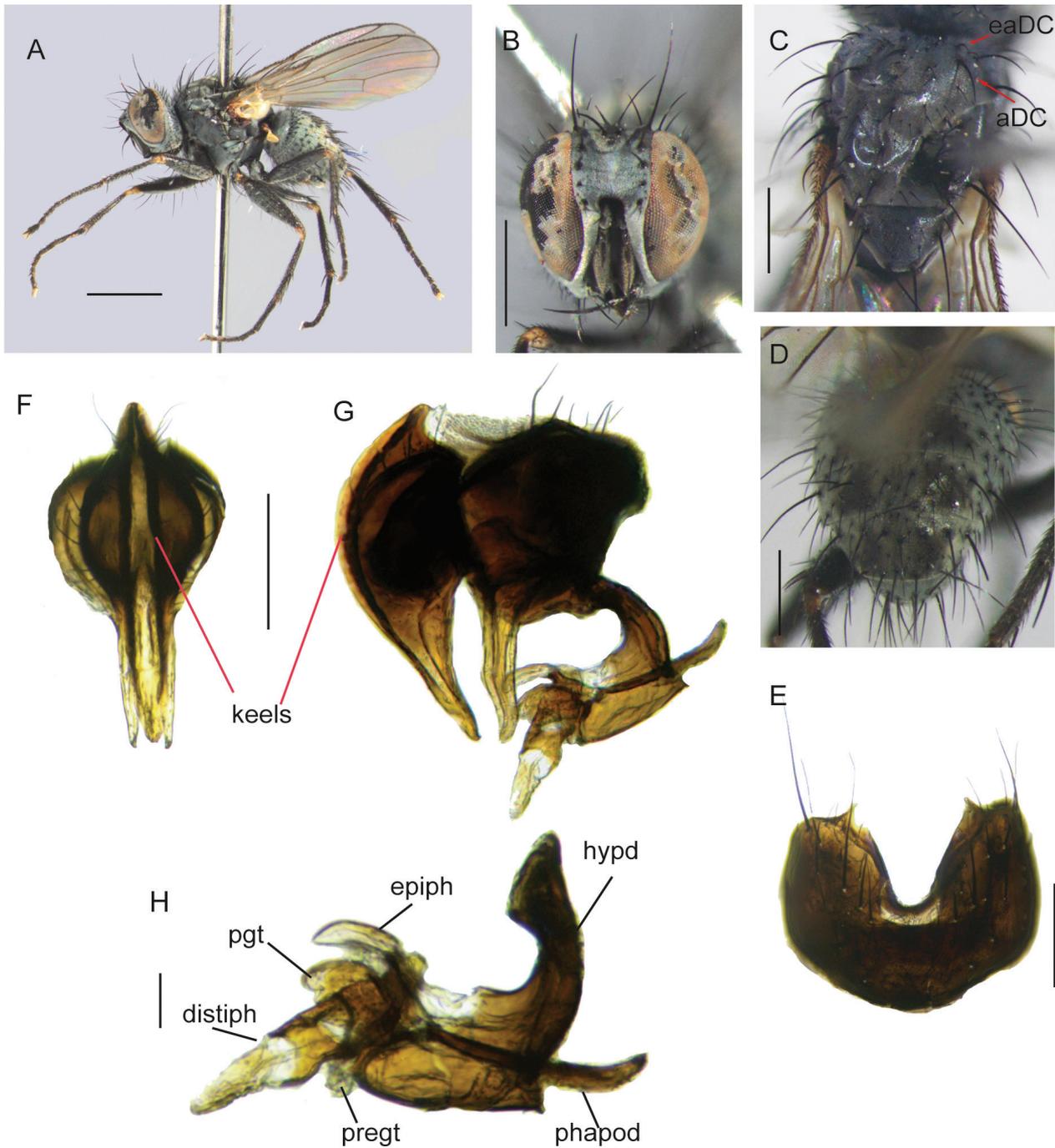
Four females, 5 males; MACN [pinned]. Original labels: “Arg. Chubut Parque Nacional / Lago Puelo (Gendarmería Malaise) / 42°05,947’ S 71°40,937’ W / I-2012 Mulieri & Patitucci leg.” print. on white paper; “MACN-Ent / 34731 [to] 34739” print. on white paper, black frame; “Paratype” print. on red paper, black frame (MACN). **Paratypes.** One female and 1 male; MLP [pinned]. Original labels: “Arg. Neuquén, Villa Pehuenia / 1187 m a.s.l. Malaise / 38.884503, -71.166194 / 9/11.II.2018 Mulieri leg.” Print. on white paper, “Paratype” print. on red paper, black frame. One female; MLP [pinned]. Original labels: “Arg. Río Negro, PNN Huapí / Mallín Playa negra 797 m / -41,357809, -71,571683 / 19/ I-05/II/2009 / Garré & M.de Oca leg. / ARG.DWN-280 / Malaise trap. MLP” print. on white paper, “Paratype” print. on red paper, black frame. **Paratypes.** Two females; IFML [pinned]. Original labels: “R. Argentina / Neuquén / Truran Kura / 8 km NW S.M. de los / andes- 1.000 m.s.n.m. / 18/X/1986 / col. M. y P. Gentili” print. on white paper, black frame; “Trampa / Malaise” print. on white paper; “Colección / Inst. Fund. M. Lillo / (4000) S.M. de Tucumán / Tucumán – Argentina” print. on green paper; “Paratype” print. on red paper, black frame. 4 females, pinned, labels: “R. Argentina / Neuquén / Truran Kura / 8 km NW S.M. de los / andes- 1.000 m.s.n.m. / 25/X/1986 / col. M. y P. Gentili” print. on white paper, black frame; “Trampa / Malaise” print. on white paper; “Colección / Inst. Fund. M. Lillo / (4000) S.M. de Tucumán / Tucumán – Argentina” print. on green paper; “Paratype” print. on red paper, black frame. 1 female, IFML [pinned]. Original labels: “R. Argentina / Santa Cruz / Lago Argentino / Brazo Rico / 12-19-II-1980 / col. A. Willink” print. on white paper, black frame; “Trampa / Malaise” print. on white paper; “Colección / Inst. Fund. M. Lillo / (4000) S.M. de Tucumán /

Tucumán – Argentina” print. on green paper; “Paratype” print. on red paper, black frame.

**Additional material examined.** ARGENTINA – Chubut province • 2 females, 13 males, PNLA, Cabaña La Cascada; -42.888499, -71.592376; 532 m a.s.l.; Feb 2013; Mulieri, Patitucci & Olea leg.; MACN. – Neuquén province • 2 males; Las Ovejas; -36.992243, -70.749499; 1262 m a.s.l.; 13 Feb 2018; Compagnucci & Patitucci leg.; Malaise trap; MACN • 2 females, 1 male; PNL, Ñorquinco; -39.146931, -71.232717; 1070 m a.s.l.; 09 Jan 2013; Mulieri, Patitucci & Olea leg.; MACN.

**Distribution (Fig. 27C).** ARGENTINA: Chubut (new record), Neuquén (new record), Río Negro (new record), Santa Cruz (new record).

**Remarks.** *Coenosia patagonica* sp. nov. is distinguished from its congeners by the coloration of its legs and its chaetotaxy. In addition, the male cercus has keels present at the basal half and the apical margin little concave, and surstylus longer than broad, whereas the female ovipositor is in tergite 8 with two long and wide sclerotized plates. In Stein’s key (1911), *C. patagonica* comes close to *Coenosia rotundiventris* Stein 1911, but differs in the coloration of legs. In Malloch’s key (1934), *C. patagonica* comes close to *C. ignobilis* Stein, 1911, but the coloration of the hind femur and the male terminalia can separate it from the latter.

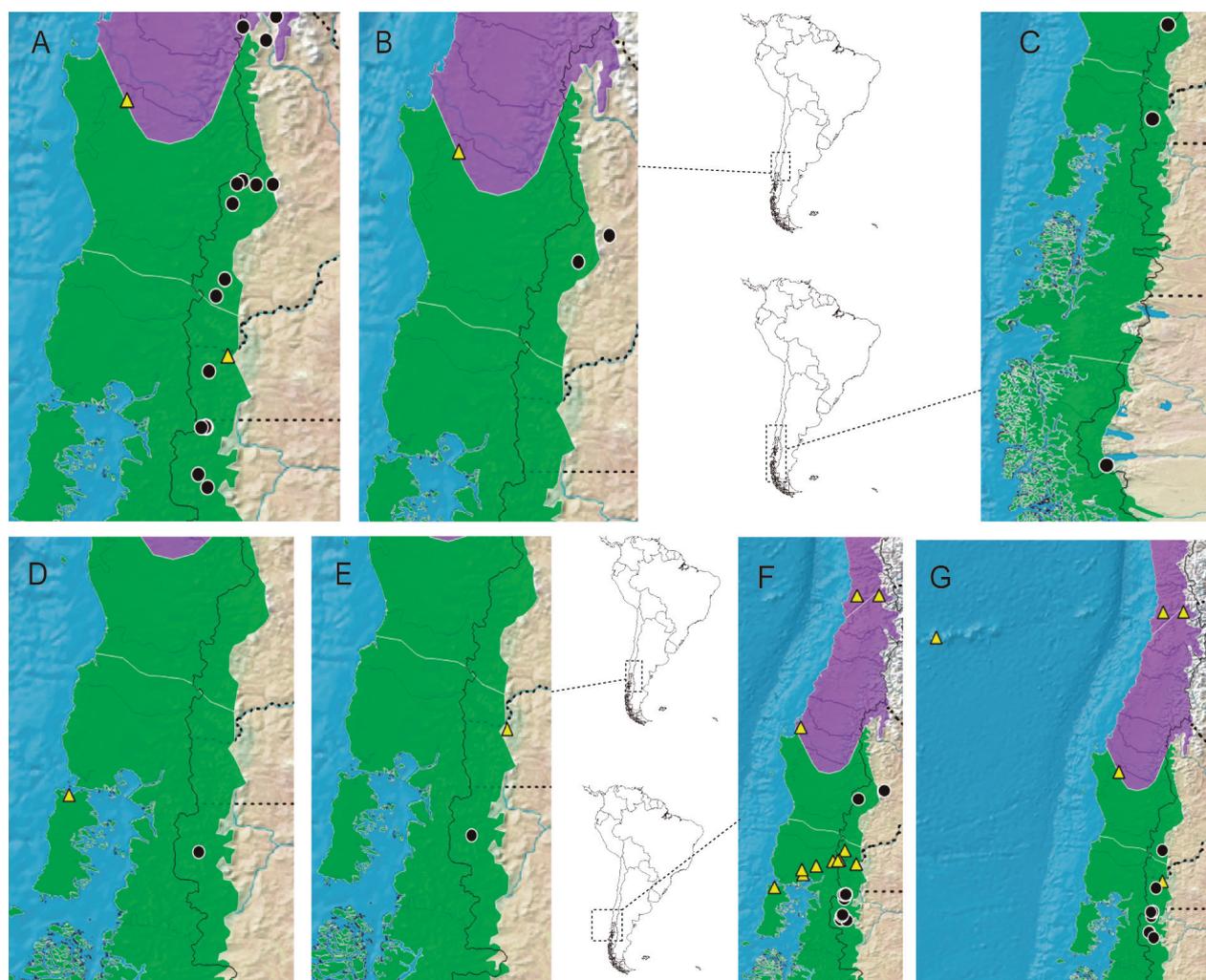


**Figure 26.** *Coenosia projecta*, male. **A** Lateral view, **B** head, frontal view, **C** thorax, dorsal view, **D** abdomen, dorsal view, **E** fifth sternite, **F** cercus and surstylus, dorsal view, **G** cercus, surstylus and phallic complex, lateral view, **H** phallic complex, lateral view. Scale bar: 1 mm (A), 0.5 mm (B–D), 0.2 mm (E–G), 0.05 mm (H).

### *Coenosia projecta* (Malloch, 1934)

**Male (Fig. 26A).** Length. Body: 2.80–3.04 mm, wing: 2.25–2.48 mm. **Head:** (Fig. 26B). Frons at vertex about one third of the head width. Frons, fronto-orbital plate, parafacial and gena black with grey pollinosity; 3–4 pairs of frontal setae. Frons longer than wide, with frontal triangle long, light grey, reaching lunula. Gena narrow, narrower than the width of postpedicel. Fronto-orbital plate with 3–5 little setulae, close to parafacialia. Antenna black, apical angle of postpedicel acute; in lateral view inserted over the mid-level of the eye; arista with

its longest microtrichia shorter than its basal diameter. **Thorax:** (Fig. 26C). Black with grey pollinosity, with three black vitta at dorsocentral and acrostichal rows of setae; anterior and posterior spiracles brown. Chaetotaxy: acr s short and irregular, the anterior presutural acr s longer than the anterior presutural dorsocentral seta (eaDC); dorsocentrals 1+3, eaDC is less than one third of the aDC. Katepisternum with 3–4 setulae. **Wing:** Tegula black. Both calypters whitish hyaline with white margins; halter yellow. **Legs:** Black with grey pollinosity, apex of femora yellow. Fore femur with a row of strong pd, a row of strong pv setae, and a row of av setae at



**Figure 27.** Geographical distribution. **A** *Coenosia argentifrons*, **B** *Coenosia inusitata*, **C** *Coenosia patagonica* sp. nov., **D** *Coenosia brevicornis*, **E** *Coenosia projecta*, **F** *Coenosia dubia*, **G** *Coenosia ignobilis*. Biogeographic Central Chilean subregion – violet area, biogeographic Subantarctic subregion – green area, new records – black circle, bibliographic records – yellow triangle.

basal third. Mid femur with 5–6 setae on anterior surface on basal half, 3–5 pv setae on basal third and a row of av setae, 2 preapical setae on pd to posterior surface; mid tibia with one ad and one pd median setae, with similar length. ad seta placed apical than pd seta. Hind femur with a complete row of ad and a row of av setae on apical half, with 3–4 pv setae on basal third. Similar size of claws and pulvilli of the three legs. **Abdomen:** (Fig. 26D). Black, with grey pruinosity, tergites 3–5 with two dark brown spots. Tergite 6 not visible in dorsal view. Sternite 5 broader than long, apical margin concave with a “U” shape, with a depressed area at the base, and without membrane; setae concentrated on the lobes and some long and strong on apical margin (Fig. 26E). **Terminalia:** Cercus curved in lateral view, keels placed from distal to basal margin, apical margin straight. Surstylus longer than broad curved at apex, sclerotized (Fig. 26F, G). Hypandrium tubular, wider than long, distal extreme not exposing the phapod, and without spines on ventral surface. Aedeagus with pregt developed and sclerotized; pgt developed; epiphalus slightly sclerotized, and distiph tubular, sclerotized at base, and without hairs on ventral surface (Fig. 26G, H).

**Female.** Unknown.

**Type material. Holotype.** Male; BMNH [pinned, in good condition]. Original labels: “♂ [handwritten] / Holo- / type [printed]” on white circular paper, red frame; “Argentina: / Terr. Río Negro. / F.& M. Edwards / B.M. 1927–63.” printed on white paper; “R. Pichileufu / 24.x.1926.” printed on white paper; “Austrocoenosia / projecta / Type [handwritten] / det. JRMALLOCH [printed]” on white paper, black frame. <https://oumnh.ox.ac.uk/collections-online#/item/oum-catalogue-381555>.

**Additional material examined.** ARGENTINA — Chubut province— 3 males, PNLA, Seccional Lago Verde; –42.718803; –71.727470; 538 m a.s.l.; Oct 2014; Mulieri & Patitucci leg.; MACN.

**Distribution (Fig. 27E).** ARGENTINA: Chubut (new record), Río Negro.

**Remarks.** *Coenosia projecta* was described by Malloch (1934) with one male specimen from Río Negro, Argentina. Malloch (1934: 224 Fig 38b) illustrated some striking long and fine hairs on the ventral surface of the hind femur, but did not mention anything in the description. We did not observe these hairs in the images of the type

specimen or in the specimens collected, so we assume that this was a mistake in the original drawing.

## 5. Discussion

Reconstructing a group characterized by a high number of species and widely distributed in nearly all terrestrial regions remains a severe challenge (Cerretti et al. 2014). Our present analysis allowed providing phylogenetic data on the evolution of *Coenosia* and/or *Neodexiopsis*, which can be tested and supplemented with further studies. In fact, this analysis, which was based on extensive morphological external and genitalia data of female and male adults of a large subset of species, represents the first study performed to elucidate the numerous species of *Coenosia* and *Neodexiopsis*.

The tree obtained was fully resolved, and neither *Coenosia* nor *Neodexiopsis* were recovered as monophyletic units. The same was observed for the genus *Austrocoenosia* previously ascribed under Malloch's original concept.

***Coenosia spumicola*.** *Coenosia* is a large group of Muscidae with many interspecific differences which, according to Huckett and Vockeroth (1987), should be considered as a repository of species, i.e., many of its species have been transferred to or from other genera over the years. Pont (1973) suggested that the position of *C. spumicola* within *Coenosia* was not clear, and suggested that it could belong to the tribe Limnophorini, a conclusion based on the comparison of the external morphology of *C. spumicola* with that of species of Limnophorini, and their shared aquatic habitat. Pont (1973) described the presence of an eaDC seta as a striking structure compared to other *Coenosia* species, although this seta is also present in other Coenosiini (e.g., *Reynoldsia* spp., or some *Coenosia* species). *Coenosia spumicola* also differs substantially from other *Coenosia* species in the width of the frons, which are wider than long, a character state shared in this study with *S. guttipennis*. Couri and Pont (2000) established that this character state (7-1) is a synapomorphy of some Coenosiini genera (*Schoenomyza*, *Schoenomyzina*, *Notoschoenomyza*, and *Spathipheromyia*). Both the width of the frons and the association with an aquatic environment have been recently observed in *Spathipheromyia* spp. (Patitucci et al. 2019) and *Notoschoenomyza sulfuriceps* (Patitucci et al. 2020). Taking into account the results obtained in this study and the information regarding *C. spumicola*, this species could be an example of why *Coenosia* has been considered a repository of species. We agree with Pont (1973) and Couri and Pont (2000) that this species does not belong to *Coenosia* and should be assigned to another genus. Thus, we currently consider *C. spumicola* as an unplaced species, and further studies are needed to resolve its phylogenetic position.

***Neodexiopsis* + *Coenosia* (clade 47).** Although *Coenosia* and *Neodexiopsis* are at present considered as indepen-

dent taxonomic entities, the position of these genera has been discussed by several authors. Huckett (1934a) was the first to modify their status as genera by considering that *Coenosia* sensu stricto, *Hoplogaster*, *Limosia* and *Neodexiopsis* were subgenera within *Coenosia*. However, the characters used by Huckett (1934b) to define *Coenosia* sensu lato were not very informative and, in a later study (Huckett and Vockeroth 1987), this subgeneric classification was disregarded. Later, in a phylogenetic analysis of the Coenosiini performed by Couri and Pont (2000), the relationship of *Coenosia* and *Neodexiopsis* with the other genera of the tribe could not be clarified, and these genera were thus in a large polytomy along with other genera, such as *Bithoracochaeta*, *Stomopogon*, *Plumispina*, etc. More recently, in a phylogenetic analysis that aimed to evaluate the position of a new genus of Coenosiini from the Mexican transition zone, Gomes et al. (2020) did not recover any synapomorphic characters for *Coenosia* or *Neodexiopsis*. Their results also showed that the species of *Coenosia* that they had included in their study were polyphyletic, whereas the species of *Neodexiopsis* formed a monophyletic unit.

Although it was not a primary goal of this study to examine the relationship between *Coenosia* and *Neodexiopsis*, clade 47 included all species of both genera (except for *C. spumicola*) and four of the synapomorphies supporting this clade (28-0, 29-1, 59-1, and 116-2) (Table S2) are characters, previously observed by other authors. Characters 28 and 29 which have been recently re-interpreted, describe the shape of the eaDC (Patitucci et al. 2021). In this study, we considered the following: that the pDC (which is placed in a posterior position with respect to the middle line of the prescutum) has been lost or is at least reduced in Coenosiini, that the aDC has been conserved, and that the eaDC has been added. The presence of the eaDC has been considered and analyzed under different criteria within Coenosiinae: Malloch (1934) compared its width with that of acrs, Snyder (1957) mentioned these setae as “accessory presutal dc setulae”, and Gregor et al. (2002) and Sorokina (2009) compared the aeDC with the aDC. Couri and Pont (2000) analyzed this character considering the number of full sized (i.e., fully developed) setae (considering not full-sized setae as setulae), and hypothesized that the presence of two presutal DC setae was the plesiomorphic state or ground-plan for Muscidae, with a reduction to one seta (without specifying which one) in Coenosiini. These authors also observed several reversals for this character in different branches of their tree. Due to the small size of this seta in most of the species included in our analysis (28-0: width of the eaDC similar to that of the presutal AC; 29-1: length of the eaDC 1/3 or less x length of the aDC), it could be interpreted that the eaDC is a setula and not a developed seta. Since the presence and location of the eaDC are constant in all species included in this study, even in species such as in *R. rufopapicata* and *C. delnenseo* sp. nov. in which the eaDC is 1/2 or more of the length of the aDC, we consider it a developed seta and not a setula.

The two remaining synapomorphies of clade 47 (Fig. 5) are: in males, the presence of a single ad in the middle

third of the hind tibia (59-1), and, in females, a single pd in the middle third of the mid tibia (116-2). Both characters states (59-1 and 116-2) are found in all species of *Coenosia* and *Neodexiopsis* included herein, with the exception of the species of *Coenosia* from the Australasian region (Table 1 and Table S2). Couri and Pont (2000) also observed a reduction in the number of setae on the pd surface of the mid tibia in all Coenosiini, with reversals in some genera of Coenosini (e.g.: *Spathipheromyia*, *Reynoldsia*). Although these character states are not very informative at a generic level within Coenosiini, they could be more informative in studies at species level, as was observed by Nihei and Carvalho (2007), in a phylogenetic analysis of Muscini, where they were also recovered as synapomorphies.

Clade 47 (Fig. 5) was also supported by four non-exclusive apomorphies (Table S2), the reduction of the number of setulae on the fronto-orbital plate (13-2) and the absence of the pd of hind tibia, characters also recovered as apomorphies by Couri and Pont (2000).

***Neodexiopsis* grade (node 46).** The diagnosis/characterization of *Neodexiopsis* proposed by Malloch (1920) (DC 1+3; scutellum with four setae of equal length; hind tibia with three setae (av, ad, and pd)) was quickly modified. Hockett (1934a) placed *Neodexiopsis* as a subgenus of *Coenosia* sensu lato, due to the presence of three preapical setae on the ad, d, and pd surfaces of the hind femur, and placed the species with only preapical ad and pd of the hind femur as *Coenosia* sensu stricto. This description was preserved by Snyder (1957) but later modified by Couri and Albuquerque (1979), who reincorporated the presence of the three setae ad, d, and pd of the hind tibia as a diagnostic character of the genus *Neodexiopsis*. The presence of three preapical setae on the hind femur was a synapomorphy observed by Couri and Pont (2000) in a clade made up by three Neotropical genera (*Cordiluroides* Albuquerque, *Haroldopsis* Albuquerque, and *Neodexiopsis*). However, the number of these setae may vary in some species of *Neodexiopsis*. Recently, in a re-examination of *N. rufipes*, results showed that the number of preapical setae of the hind femur may be different in males (two setae) and females (three setae) (Patitucci and Couri 2018). In the present study, we analyzed the presence/absence of these three setae independently in males and females (characters 65, 66, 67, 115, and 116), and these were not recovered as synapomorphies for node 46, or for nodes 45 and 51 within this clade. However, the absence of the preapical dorsal seta of the hind femur in males was recovered as an exclusive synapomorphy for its sister clade (node 58), which groups all the remaining species of *Coenosia* and the above mentioned *Neodexiopsis* excluded from this clade (node 46, Fig. 5). Three species of *Neodexiopsis* formed a monophyletic group (node 45, Fig. 5), supported by five non-exclusive apomorphies (Table S2) and its sister group was formed by three *Coenosia* species and *N. rufipes*, also supported by three non-exclusive apomorphies (node 51, Fig. 5). At node 45, *N. paulistensis* was placed as the sister taxon of the species of the *Neodexiopsis ovata* group (*N. genic-*

*ulata* and *N. neoaustralis*). This clade was supported by four non-exclusive apomorphies and three synapomorphies (39-1, 43-1, and 85-2). The presence of a prominent lobe on the anal angle of the wing (39-1) (Fig. 1D) and a glossy area between tergites 3 and 4 (43-1) (Fig. 1E) are morphological structures previously used by Snyder (1958) to define *N. ovata* group. The third synapomorphy (85-2), i.e., apical margin of the cercus with a bulge (Fig. 3C), is present in other species of the *ovata* group not included in this work (*Neodexiopsis ovata* Stein in Hockett 1934a: Fig. 5; and *Neodexiopsis parvula* Albuquerque in Albuquerque 1958: Fig. 9). On the other hand, node 51 included two *Coenosia* species (*C. curviventris* and *C. longipede*), whose male terminalia are highly similar to the male terminalia of *Neodexiopsis* species (Patitucci et al. 2021). A more detailed study including more *Neodexiopsis* species is necessary to better define the limits of this genus.

***Coenosia* grade (node 58).** This group was supported by three synapomorphies. One of them (34-1) was associated with a reduction in the number of setulae between katapisternal setae (Fig. 1C), with a reversal in *C. nigerrima*. A reduction in the number of setulae between katapisternal setae was also observed by Couri and Pont (2000) as a synapomorphy of the tribe Coenosiini. The two remaining synapomorphies were the absence of the preapical dorsal seta in the hind femur of males (66-1) and females (119-1). This character, which is observed in males and females, is not a very helpful diagnostic character, since it sometimes cannot be correctly differentiated from the respective rows of setae (e.g., anterodorsal preapical seta vs. row of anterodorsal seta); it may be ambiguous (presence, absence or reduction) when numerous specimens are studied (e.g.: *C. metalleg*) (Patitucci et al. 2021) or it may vary between males (two setae) and females (three setae) as in *N. rufipes* (Patitucci and Couri 2018).

***Coenosia chaetosa* group (clade 62).** In a recently study, we proposed this species group, with *C. chaetosa*, *C. inaequalis*, *C. mallochi*, *C. metalleg*, and *C. setiventris* based on several structures of males terminalia, among other characters (Patitucci et al. 2021). However, only three of these five species (*C. chaetosa*, *C. inaequalis* and *C. mallochi*) were recovered in the present analysis as a natural group. Clade 62 is supported by two characters of the male terminalia, considered as part of the diagnosis of this species-group in Patitucci et al. (2021): surstylus longer than broad (91-2) (Fig. 3F), and distal tip of surstylus curved towards cercus (94-1). However, both characters were non-informative and expressed in other terminals as *R. rufoapicata* and in several *Coenosia* species (e.g.: *C. metalleg* + *C. aurifera* group). In this phylogenetic analysis the absence of pd setae on the hind tibia used by Malloch (1934) to differentiated the *Coenosia* species from *Austrocoenosia* species resulted in a non-exclusive apomorphic character at clade 47 (*Coenosia* + *Neodexiopsis*). The number and position of the setae in the middle third of the hind tibia, have been used by different authors to

characterize and group species within *Coenosia* (Malloch 1934; Hockett 1934a, 1934b; Hennig 1961). Particularly, the presence of a pd setae on the hind tibia was used to originally characterize *Neodexiopsis* (Malloch 1920) and *Austrocoenosia* species (Malloch 1934). Snyder (1957) dismissed the character as he considered that the presence of pd setae responded to sexual dimorphism in males of some species of *Neodexiopsis*. Couri and Pont (2000) also found that the absence of pd setae in the hind tibia was a non-exclusive apomorphy for *Coenosia*.

**Clade 53.** Clade 53 included all species treated by Malloch (1934) as *Austrocoenosia*, *C. metalleg* and two new species presented in this study. All these species are distributed in the Andean region, principally in the Central Chilean and Subantarctic subregions (Morrone 2015), and were supported by four non-exclusive apomorphies of females. The species at this node were grouped in two clades: node 65 grouped four species: *C. metalleg*, *C. tarsata*, *C. delneneo* **sp. nov.**, and *C. aurifera* (originally included in *Austrocoenosia* by Malloch (1934)), and node 52 recovered all species designated by Malloch (1934) within the genus *Austrocoenosia*, and the new species *C. patagonica* **sp. nov.** Clade 65 was supported by six non-exclusive apomorphies (8-1, 81-3, 89-1, 91-1, 94-1, and 102-1), only two of which, absence of the frontal triangle in the frons (8-1) and presence of hairs in the acrophallus (102-1), can be compared with previous information available in the literature. The absence of the frontal triangle in the frons (8-1) is a character state present in all the species of this group, shared with *C. bimorpha* from the Australasian region and *C. argentifrons* (Fig. 13B) from the Andean region. These last two species have a silver coloration on the frons; consequently, the frontal triangle could be present but not visible to the naked eye. Some Coenosiinae have silver color frons presumably involved in emitting visual signals (flashes of light) to females or males or other species (Frantsevich and Gorb 2006; Werner and Pont 2006). The second character, presence of hairs in the acrophallus (102-1) (Fig. 3H), which is also present in *R. rufoapicata*, was observed for the first time in the description of *C. metalleg* (Patitucci et al. 2021). These hairs can be detected with a stereoscopic microscope under maximum magnification or with SEM and could be sensory structures.

***Coenosia aurifera* group (clade 69).** *Coenosia metalleg* was recovered as the sister taxon of clade 69 (*Coenosia aurifera* group), which was supported by five non-exclusive apomorphies (50-2, 51-1, 78-0, 123-1, and 129-0) and three synapomorphies (52-1, 90-1, and 130-1). Tergite 6 and epandrium visible on dorsal view (Fig. 2C), were character states shared only with *C. forcipiungula* and *C. zhongdianensis* from the Asian meridional region. Xue and Zhang (2011) described the abdomens of these last two species as cylindrical or long cone-shaped. We found no records in the literature on this conformation of the abdomen in other species of *Coenosia*. In addition, the abdomen of the species of the *C. aurifera* group presents a globose epandrium (52-1), which is unique within

the genus. This group was defined by two other synapomorphies. One of these synapomorphies was the presence of dorsal spine-like setae on the cercus (90-1) (Figs 6I, 8H, and 10H), which were analyzed with SEM. These spines were coeoloconic sencilla (basiconic pegs or cones that are positioned in shallow pits) and could be related to chemo-sensitive functions (Shields 2010). The other synapomorphy of this clade was the presence of four tergites on segment 6 in the female ovipositor (130-1) (Fig. 4F).

The extension of the female ovipositor and the reduction in the number of tergites area are changes that have occurred independently in different groups of Muscidae, and, according to Hennig (1965), are probably linked with changes in oviposition behavior. This author (op. cit.) also concluded that a long ovipositor along with the reduction in the number of plates (shaped like long rods) in the segments could be an apomorphic characteristic for *Coenosia*, but clarified that these structures are unknown in several species of *Coenosia*, particularly in those of the Neotropical region. It is important to highlight that the species of the *C. aurifera* group present gray coloration with light yellow and/or golden tones, and were collected in open environments outside of forested areas. In addition, in the original description of *C. aurifera*, Malloch (1934) mentioned various and notorious differences in external appearance (coloration, shape of the last segment of the abdomen in males) that could segregate this species from the others *Austrocoenosia* species. Many of these characteristics are shared by the other two species grouped with *C. aurifera* (*C. tarsata* and *C. delneneo* **sp. nov.**).

***Coenosia argentifrons* group (node 52).** *Austrocoenosia* species under Malloch's original concept (1934) were recovered as a monophyletic clade supported by four non-exclusive apomorphies (54-1, 76-0, 77-0, and 85-1) and two synapomorphies (87-1 and 131-4). The four non-exclusive apomorphies presented several reversals at different levels of this study and were not informative. The presence of a row of setae in the basal half on the anteroventral surface of the fore femur (54-1) was observed in diverse terminals as *R. rufoapicata*, some *Neodexiopsis* species, and *Coenosia* species from different regions. This structure is associated with predation behavior (Mateus 2012). Sternite 5 much broader than long (76-0) was also a non-informative character. This structure was observed in *Coenosia* species from the Afrotropical and Nearctic regions. Similarly, characters 77-0 and 85-1 (both structures associated with the cercus), were non-informative and observed in several species of *Neodexiopsis* and *Coenosia* from different regions. On the other hand, the two synapomorphies found constitute new elements at the subfamily level. The presence of keels on the cercus in male genitalia (87-1) (Fig. 3B), previously identified in *C. argentifrons* by Couri and Nuñez (2001), constitutes a diagnostic element of the *C. argentifrons* group, since this structure has not been observed in any other Coenosiinae. In a recent study, we proposed the cercus with keels could form the "fourth morphological pattern" and that this structure could be considered as a central element to

classify or group species within *Coenosia* (Patitucci et al. 2021). Similarly, females present erythrocyte-shaped spermathecae (131-4) (Fig. 4K), which differ from the three forms observed for Muscidae (Couri 1998). It is unknown whether the variation in sperm shape influences the number, size, or storage type of sperm, or whether it differentially affects sperm attraction, competition, or selection (Pascini and Martins 2017). Our data set supported the monophyly of all the species previously ascribed to *Austrocoenosia* under Malloch's original concept (1934) (with the exception of *C. aurifera*), conforming a clade inside the genus *Coenosia*. Undoubtedly, the singularities observed could be correlated with the fact that this group is endemic to the Andean region.

Our present study did not aim to resolve the complex intrinsic relationships within *Coenosia*; however, our results suggest that the structures of male and female genitalia can provide more robust results to clarify these relationships, and also provide a reinterpretation of the different groups of species in the different biogeographic regions of the world.

These comments are also valid to be able to understand and analyse in future investigations, the relationships within Coenosiini, and in particular the phylogenetic position of the species included in *Neodexiopsis*.

It would be important that, in addition to the external morphological characters, especially from leg chaetotaxy which had been considered of importance in previous studies (Couri and Pont 2000), future studies should incorporate the structures of female and male terminalia as well as additional molecular data and also data from immature stages, which will certainly contribute to the understanding of the relationships within this clade.

## 5.1. Summary of taxonomic changes proposed in this article

### *Coenosia* Meigen, 1826

*Austrocoenosia* as a junior synonymy of *Coenosia* (**syn. rest.**).

*Coenosia* species: *Coenosia brevicornis* (**new comb.**), *Coenosia dubia* (**comb. rest.**); *Coenosia hucketti*, Pont (**nom. nov.**) and *Coenosia nigerrima* (**comb. rest.**).

Unplaced species of *Coenosia* s. lat.

*Coenosia spumicola*.

## 6. Competing interests

The authors have declared that no competing interests exist.

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## Supplementary Material 1

### Table S1

**Authors:** Patitucci LD, Mulieri PR, Couri MS, Domínguez MC (2023)

**Data type:** .docx

**Explanation note:** Data matrix, polymorphic entries: a = (0,1). Inapplicable data= “-” and missing data= “?”.

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**Link:** <https://doi.org/asp.81.e104969.suppl1>

## Supplementary Material 2

### Table S2

**Authors:** Patitucci LD, Mulieri PR, Couri MS, Domínguez MC (2023)

**Data type:** .docx

**Explanation note:** List of changes. Exclusive synapomorphies in bold.

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**Link:** <https://doi.org/asp.81.e104969.suppl2>

## Supplementary Material 3

### Table S3

**Authors:** Patitucci LD, Mulieri PR, Couri MS, Domínguez MC (2023)

**Data type:** .xls

**Explanation note:** Table of localities.

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