



## Monograph

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# A revision of the South American species of the cleptoparasitic bee genus *Triepeolus* Robertson, 1901 (Hymenoptera: Apidae)

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**Abstract.** The cleptoparasitic bee genus *Triepeolus* Robertson, 1901 (Hymenoptera: Apidae) is revised for species occurring in South America. A total of nine species are confirmed from the continent, of which *T. tuberculifer* Onuferko, Rightmyer & Roig-Alsina sp. nov. is newly described. Four new synonymies are proposed: *T. aguilari* Moure, 1955 syn. nov. and *T. megadelphus* Cockerell, 1914 syn. nov. under *T. buchwaldi* (Friese, 1908); *T. bilineatus* Cockerell, 1949 syn. nov. under *T. flavipennis* (Friese, 1916); and *Epeolus merus* Brèthes, 1909 syn. nov. under *T. nemoralis* (Holmberg, 1886). Males of *T. alvarengai* Moure, 1955 and *T. rufotegularis* (Ashmead, 1900) and females of *T. atoconganus* Moure, 1955 and *T. cecilyae* Packer, 2016 are described for the first time. Lectotypes are designated for the following (all originally described under *Epeolus* Latreille, 1802 but now recognized as *Triepeolus*): *E. buchwaldi*, *E. flavipennis*, *E. osiriformis* Schrottky, 1910 and its junior synonym *E. luteipes* Friese, 1916, and *E. rufotegularis*. Diagnoses and complete descriptions/redescriptions are provided for all species, along with a fully illustrated dichotomous identification key (with Portuguese and Spanish versions available as supplementary material) to distinguish them based on external morphological features. Additionally, known collection records and information about the ecology of the treated species are presented.

**Keywords.** Epeolini, identification key, Neotropical, *simplex* species group, *verbesinae* species group.

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## Introduction

*Triepeolus* Robertson, 1901 is a large genus of cleptoparasitic bees distributed in the Holarctic and Neotropical regions, with 151 species recognized as valid before the present study (Rightmyer 2006, 2008; Rightmyer *et al.* 2014; Packer 2016; Gibbs *et al.* 2017). It is the most species-rich genus in the tribe Epeolini (Rightmyer 2004, 2008), which includes seven other genera: *Doeringiella* Holmberg, 1886, *Epeolus* Latreille, 1802, *Odyneropsis* Schrottky, 1902, *Pseudepeolus* Holmberg, 1886, *Rhinepeolus* Moure, 1955, *Rhogepeolus* Moure, 1955, and *Thalestria* Smith, 1854. Although South America is the continent with the greatest generic richness of epeolines and the only one where all eight genera are represented (half of which occur nowhere else), the South American *Triepeolus* fauna is depauperate compared with that of North America—the center of diversity of the genus (Rightmyer 2004).

Moure (1955) included a review of the South American species of *Triepeolus*, wherein three species were newly described. Rightmyer (2008) provided a key to the species of the genus in South America and the Caribbean; however, this treatment was incomplete for South American *Triepeolus*. Although the key excluded names deemed redundant by the author, they were not formally established as junior synonyms in the article. Additionally, the key included a newly identified but undescribed South American species. The known South American species of *Triepeolus* are divided between two large and taxonomically difficult species groups (comprised of species resembling *T. simplex* Robertson, 1903 and *T. verbesinae* (Cockerell, 1897), respectively), both of which were excluded from Rightmyer's (2008) revision and intended to be the focus of a separate taxonomic study. Another new and previously unknown species of *Triepeolus* from South America (based on a single, male specimen from Chile) has since been described by Packer (2016), although not in the context of a taxonomic revision.

In the present study, the species of *Triepeolus* known to occur in South America are formally revised, with up-to-date taxon concepts presented for all species. Additionally, information on the ecology of the treated species (if available) and their ranges is presented.

## Material and methods

Species were delineated based on discrete morphological features. A lack of DNA sequence data for species of *Triepeolus* represented in South America (other than two DNA barcodes available for *T. flavipennis* (Friese, 1916) and one for *T. rufotegularis* (Ashmead, 1900)) precluded the use of an integrative systematics approach.

Specimens from 23 entomological collections were studied (see Supp. file 1 for the complete list). The primary types of all species of *Triepeolus* known from South America and their junior synonyms were examined by at least one of the authors of this revision and imaged (see Supp. file 2) except for the holotype of *Doeringiella nemoralis* Holmberg, 1886 (orig. comb.), which has been destroyed. A few secondary type and non-type museum specimens were studied exclusively from images as noted in the 'Material examined' sections under the treated species. Otherwise, the lists of vouchered material are based on specimens personally examined by TO, MR, GARM, and/or ARA. Observations based on images of live specimens submitted to iNaturalist (<https://www.inaturalist.org/>) are also presented but listed separately under 'Non-preserved material', as in Onuferko & Sheffield (2022). Identifications of all iNaturalist specimens cited here were made or verified by TO.

**Abbreviated names of institutions/collections where studied specimens are deposited**

Names of curators and/or collection managers are in parentheses.

AMNH	=	American Museum of Natural History, New York, NY, USA (J.G. Rozen, Jr. and C. Smith)
ANSP	=	Academy of Natural Sciences of Drexel University, Philadelphia, PA, USA (J.D. Weintraub)
CAS	=	California Academy of Sciences, San Francisco, CA, USA (C. Grinter and R. Zuparko)
CNC	=	Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa, ON, Canada (J. Fernández-Triana on behalf of S. Cardinal)
DZUP	=	Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, PR, Brazil (G.A.R. Melo)
EMEC	=	University of California, Essig Museum of Entomology, Berkeley, CA, USA (P. Oboyski)
FAUBA	=	Entomology Collection of the Facultad de Agronomía, Universidad de Buenos Aires, Autonomous City of Buenos Aires, Argentina (J.P. Torretta)
FSCA	=	Florida State Collection of Arthropods, Gainesville, FL, USA (C. Whitehill)
ICN	=	Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, DC, Colombia (F. Fernández)
IFML	=	Instituto de Entomología de la Fundación Miguel Lillo, San Miguel de Tucumán, Tucumán, Argentina (E.C. Pérez)
INHS	=	Illinois Natural History Survey, Champaign, IL, USA (T. McElrath)
KUNHM	=	University of Kansas, Biodiversity Institute and Natural History Museum, Lawrence, KS, USA (R. Osborn)
LACM	=	Natural History Museum of Los Angeles County, Los Angeles, CA, USA (B.V. Brown and G. Kung)
MACN	=	Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Autonomous City of Buenos Aires, Argentina (A. Roig-Alsina and P. Mulieri)
MUSA	=	Museo de Historia Natural de la Universidad Nacional de San Agustín de Arequipa, Arequipa, Peru (J. Cerdeña)
MZUSP	=	Museu de Zoologia da Universidade de São Paulo, São Paulo, SP, Brazil (G. Camacho and C.R.F. Brandão)
NHMUK	=	Natural History Museum, London, United Kingdom (J. Monks)
PCYU	=	Packer Collection at York University, Toronto, ON, Canada (L. Packer)
UCMC	=	University of Colorado Museum of Natural History Entomology Collection, Boulder, CO, USA (V. Scott)
UNMSM	=	Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru (M. Alvarado)
USNM	=	U.S. National Entomological Collection, National Museum of Natural History, Washington, D.C., USA (S.G. Brady and E. Okonski)
USP-RP	=	Universidade de São Paulo em Ribeirão Preto, Ribeirão Preto, SP, Brazil (E.A.B. Almeida)
ZMB	=	Museum für Naturkunde, Berlin, Germany (B. Blaimer and S. Krause)

Specimens were observed under a standard dissecting microscope and measured using a calibrated ocular micrometer within the eyepiece. Images were taken (mostly by TO, GARM, and ARA at their respective institutions) using different camera systems (with different light settings) and focus-stacking software. Photographs of specimens deposited in the ZMB were taken previously by GARM during his stay in the museum in 2015 and 2016; for this publication, new photographs were taken and provided

by the ZMB digitization team and collections staff, respectively. Consequently, differences in the coloration of illustrated specimens may appear more pronounced than they are and should be interpreted cautiously. Images were minimally edited (to enhance brightness/contrast and adjust the color), resized, and cropped in PaintShop Pro (Jasc Software, Inc.), and labeled figure plates were compiled in Adobe Photoshop 2020 (Adobe Inc.).

The terminology for morphological features used here is largely consistent with that of Rightmyer (2008), which generally follows Michener (2007), but with some modifications as follows. As in Prentice (1998), ‘frontal area’, ‘genal area’, and ‘vertexal area’ are used instead of ‘frons’, ‘gena’, and ‘vertex’, respectively, since these parts of the head are not clearly delineated externally (see Mir Sharifi *et al.* 2019 for a recent example of the use of these terms in bee taxonomy). Herein, ‘length’ (except in reference to setae (hairs)) and ‘width’ do not refer to the longer and shorter sides of a particular shape (as in geometry) but rather measurements made along the longitudinal and lateral axial planes, respectively. Terms introduced for *Triepeolus* by Rightmyer (2008) and subsequently used in taxonomic studies of other cleptoparasitic bees (e.g., Onuferko 2019) are also explained here for clarity. In most species of *Triepeolus*, the mesoscutum has a pair of subparallel lines of pale tomentum originating in its anterior half, which are termed ‘paramedian bands’. The region of dark, short, appressed setae flanked or surrounded by bands of pale setae on the first metasomal tergum is called the ‘discal patch’. The first metasomal tergum has a ‘basal band’ of pale tomentum, which may be separated medially into a pair of anterolateral patches, and at least the second to fourth metasomal terga have ‘apical transverse bands’ of pale tomentum, which may be narrowed or interrupted medially. The mesoscutellum in *Triepeolus* has a pair of weak to strong rounded convexities and is thus described as ‘bigibbous’ to varying degrees, following Moure (1955).

### Abbreviated terms

d	=	diameters of punctures
F	=	flagellomere
i	=	interspaces between punctures
ITW	=	intertegular width
MOD	=	median ocellar diameter
PP	=	posterior probability
S	=	metasomal sternum
T	=	metasomal tergum

The name-bearing types (holotypes and lectotypes) of the treated species served as the basis for the descriptions/redescriptions, with references to other examined specimens added as needed to fill in information gaps. In the case of *T. nemoralis*, the holotype of *E. merus* Brèthes, 1909 (herein regarded as a junior synonym of *T. nemoralis*) served as the basis for the redescription, since the type of the former has been lost. Since *Triepeolus* is largely sexually monomorphic, a single description that applies to both sexes is provided for each species, with female- and male-specific features described under separate headings (as in Rightmyer 2008). Exact measurements of size (in mm) are given for each primary type that bears the accepted name for the species in question (except in the case of *T. nemoralis* as described above). Measurements of anatomical features were taken at their longest and/or widest extents, except ITW, which represents the shortest distance between the tegulae of a specimen. Body length was measured from the apex of protrusion of the supraclypeal area to the last visible tergum or sternum and does not include the terminalia, which are extended in some specimens.

A morphological diagnosis is provided to identify *Triepeolus* among all other bee genera in South America. Separate diagnoses are also provided for each of the treated species. Additionally, a single fully illustrated dichotomous identification key is presented to enable the identification of both sexes



of the species of *Triepeolus* occurring in South America. Since Portuguese and Spanish are by far the most widely spoken languages in South America, versions of the key in both languages are presented in Supp. file 3.

Species distribution maps were produced in RStudio (ver. 2022.07.0+548) based on known locality records, with the GPS coordinates associated with each observation taken either directly from the collection or image labels or, if not known, approximated from the named locality. The function ‘getData’ in the package raster (Hijmans 2022) installed in R ver. 4.2.1 (R Core Team 2022) was used to download spatial data for the Global Administrative Boundaries (source = <https://gadm.org/>) used to construct projected maps onto which the occurrence records were plotted. The Robinson projection was selected for the maps and specified using the function ‘CRS’ in the package maptools (Bivand & Lewin-Koh 2022) installed in R.

Available information on host and floral records was collated for the treated species. The World Flora Online (WFO) (<http://www.worldfloraonline.org/>) was consulted to ensure that the plant names presented herein are up to date.

## Results

### *Taxonomy*

Class Insecta Linnaeus, 1758  
 Order Hymenoptera Linnaeus, 1758  
 Superfamily Apoidea Latreille, 1802  
 Family Apidae Latreille, 1802  
 Tribe Epeolini Robertson, 1903

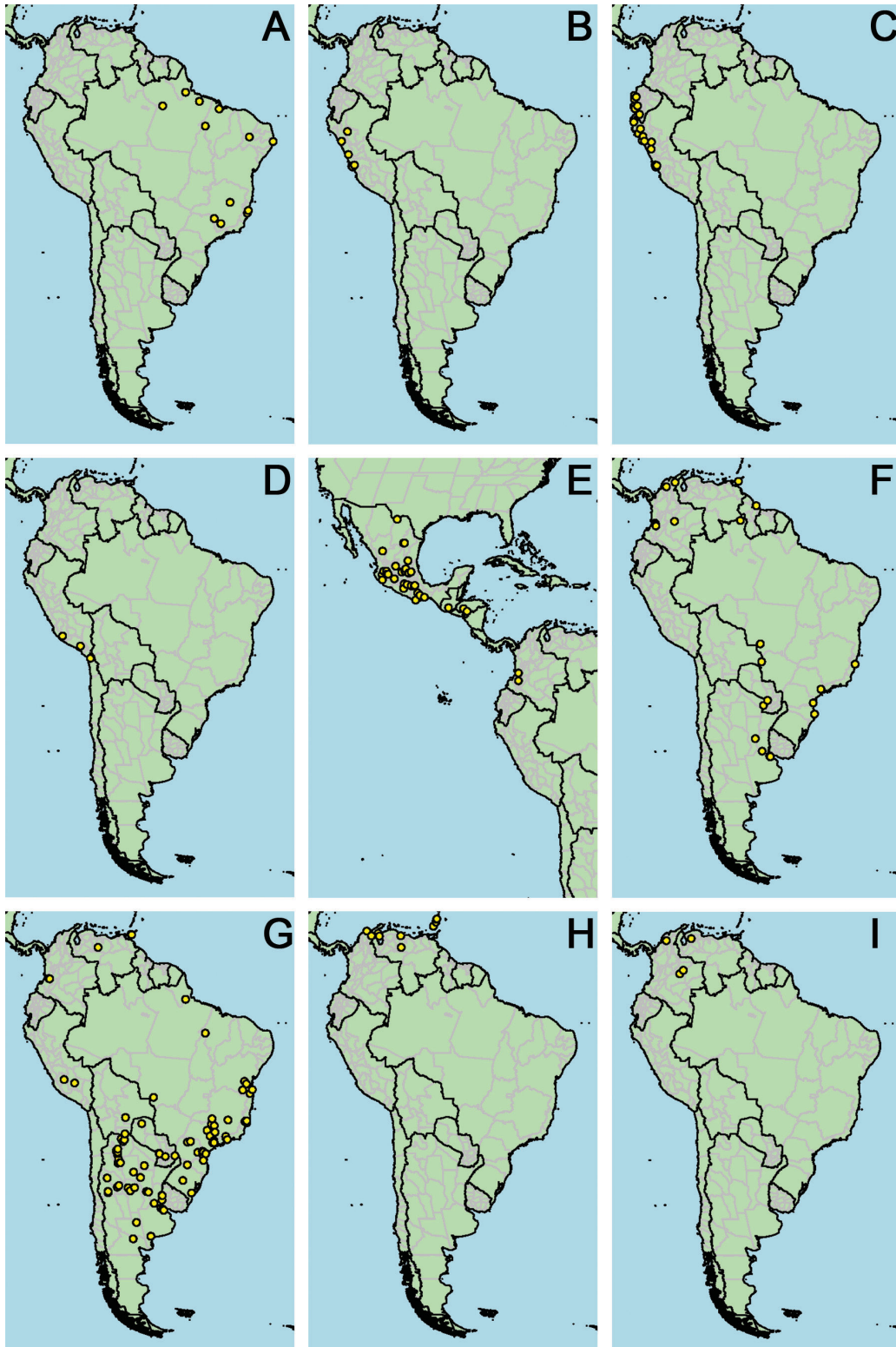
Genus *Triepeolus* Robertson, 1901

### Diagnosis for *Triepeolus* in South America

Species of *Triepeolus* are non-metallic epeoliform bees that closely resemble various other cleptoparasitic bees, especially the related genera *Doeringiella*, *Epeolus*, *Pseudepeolus*, *Rhinepeolus*, and *Rhogepeolus*. Although no single anatomical feature is diagnostic for *Triepeolus*, several features in combination separate the genus from all others in South America as follows. The front coxae are quadrate (as opposed to somewhat triangular), with the trochanters widely separated at their bases, and the axillae are produced to lobes or spines and thus do not continue the contour of the mesoscutellum (as in all Epeolini); the mandibles are simple; the scapes are normal (i.e., not flattened, dramatically swollen, or each forming a laterally directed subbasal angle); the eyes are convergent below; the mesoscutum (except sometimes in *T. nemoralis*) and T1–T4 in all South American (and most other) species of *Triepeolus* have well-defined bands of pale (white/off-white to yellow) tomentum; the mesoscutellum does not have a median longitudinal strip of pale, short, appressed setae and is to some degree bigibbous but not denticulate or tuberculate; and the fore wings of all South American (and most other) species of *Triepeolus* each have three submarginal cells. In the species of *Triepeolus* occurring in South America (as in some but not all congeners elsewhere), the pseudopygidial area of the female is known to be either triangular (with the apical margin of T5 concave) or distinctly circular (with the apical margin of T5 broadly convex).

### Distribution in South America

*Triepeolus* is found throughout most of South America but is notably absent from much of Chile and not known to occur in southern Patagonia. The genus is expected to occur in all 12 of the continent’s countries as well as French Guiana but has not yet been confirmed from the latter, Suriname, or Uruguay (see Fig. 1).



**Fig. 1.** Occurrence records (yellow circles) of species of *Triepeolus* Robertson, 1901 represented in South America. **A.** *T. alvarengai* Moure, 1955. **B.** *T. atoconganus* Moure, 1955. **C.** *T. buchwaldi* (Frieese, 1908). **D.** *T. cecilyae* Packer, 2016. **E.** *T. flavipennis* (Frieese, 1916). **F.** *T. nemoralis* (Holmberg, 1886). **G.** *T. osiriformis* (Schrottky, 1910). **H.** *T. rufotegularis* (Ashmead, 1900). **I.** *T. tuberculifer* Onuferko, Rightmyer & Roig-Alsina sp. nov.

### Included species

*Triepeolus alvarengai* Moure, 1955

*Triepeolus atoconganus* Moure, 1955

*Triepeolus buchwaldi* (Friese, 1908)

*Triepeolus cecilyae* Packer, 2016

*Triepeolus flavipennis* (Friese, 1916)

*Triepeolus nemoralis* (Holmberg, 1886)

*Triepeolus osiriformis* (Schrottky, 1910)

*Triepeolus rufotegularis* (Ashmead, 1900)

*Triepeolus tuberculifer* Onuferko, Rightmyer & Roig-Alsina sp. nov.

### *Triepeolus alvarengai* Moure, 1955

Figs 1A, 2, 3A

*Triepeolus alvarengai* Moure, 1955: 126 (♀).

### Diagnosis

The following morphological features in combination tell *T. alvarengai* apart from all other South American *Triepeolus*: the (medially narrowed or interrupted) T1 basal band is arched, continuous with (and indistinguishable from) the lateral longitudinal bands, and mesally concave on each side, such that the discal patch is semicircular (Figs 2B, 3A); the mesoscutum has well-defined paramedian bands (Figs 2B, 3A); and T2–T4 have complete apical transverse bands of yellow tomentum (Figs 2B, 3A). Specimens in which T1 has only a basal band or pair of anterolateral patches of pale tomentum (as in Fig. 2B) (as opposed to both basal and apical transverse bands, as in Fig. 3A) may be confused with *T. nemoralis*, but in *T. nemoralis* the mesoscutum has a large anteromedial ovate patch of yellow tomentum, which may be sparser medially such that the patch is suggestive of ill-defined paramedian bands. Males of *T. alvarengai* without an apical transverse band on T1 also closely resemble those of *T. flavipennis*, but in *T. flavipennis* the pair of anterolateral patches of pale tomentum on T1 are mesally convex, such that the discal patch forms a trapezoid or triangle with concave anterolateral sides. Females of *T. alvarengai* and *T. flavipennis* are more readily distinguished by the pseudopygidial area, which in the former is triangular, with the apical margin of T5 concave, and in the latter is distinctly circular, with the apical margin of T5 broadly convex.

### Etymology

The specific epithet (declined in the genitive case) honors L.C. Alvarenga, who collected the holotype (Moure 1955).

### Material examined

#### Primary type material

BRAZIL • ♀, holotype; Minas Gerais, Varginha; Feb. 1954; L.C. Alvarenga leg.; DZUP.

#### Secondary type material

BRAZIL • 1 ♀, paratype; Pará, Juruti (“Lago Grande de Villa Franca”); P. Lecointe leg.; MZUSP (still at DZUP, but to be returned).

#### Non-type material

BRAZIL • 1 ♂; Amapá, Macapá; “10.11.1900”; Ducke leg.; ZMB ed1bbe/M.G.R. Database No. 11694 • 1 ♀, 1 ♂; same collection data as for preceding; 10 Nov. 1900; Ducke leg.; DZUP • 1 ♀; Ceará, Barbalha; May 1969; M. Alvarenga leg.; AMNH • 1 ♀; Espírito Santo, Aracruz; 22–30 Dec. 1981; C. Elias leg.;



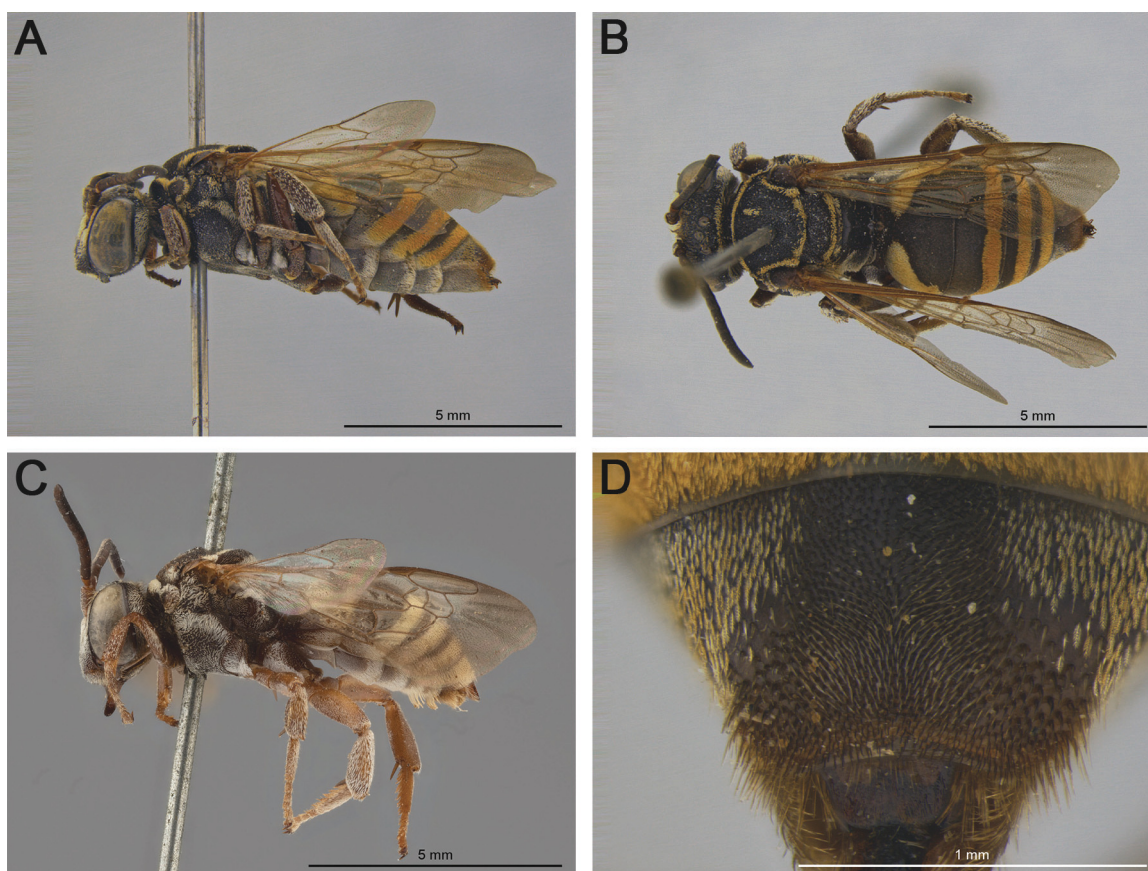
DZUP • 1 ♀; Espírito Santo, Linhares; May 1978; C. Elias leg.; DZUP • 9 ♀♀, 2 ♂♂; Maranhão, Imperatriz; 20 Feb. 1962; F.M. Oliveira leg.; DZUP • 1 ♀, 2 ♂♂; Maranhão, São Bento; 27 Feb. 1984; Mazucato leg.; USP-RP • 1 ♂; Minas Gerais, Couto Magalhães; Jul. 1959; M. Alvarenga leg.; DZUP • 1 ♂; Minas Gerais, Passos; Jun. 1961; C. Elias leg.; DZUP • 1 ♀; Pará, Belém; 30 Mar. 1965; S. Laroca leg.; MACN • 1 ♀; Pernambuco, Recife; 23 Nov. 1955; Michener and Moure leg.; DZUP.

## Redescription

MEASUREMENTS OF HOLOTYPE. Body length 9.7 mm; ITW 1.8 mm; head length 2.2 mm; head width 3.1 mm; fore wing length 7.6 mm.

### Both sexes

INTEGUMENT COLORATION. Dark brown to black except as follows. Mandible with middle portion reddish brown. Antenna (except for orange along outer and apical margins of F1 and orange spot basally on F2) dark brown in holotype; scape orange in part and pedicel and F1 extensively orange in some non-type specimens. Tegula dark brown in holotype; orange in some non-type specimens. Fore wing membrane subhyaline, apically dusky. Hind wing membrane dusky subhyaline to hyaline. Legs dark brown in holotype; trochanters to tarsi extensively orange in some non-type specimens. Pygidial plate reddish brown.

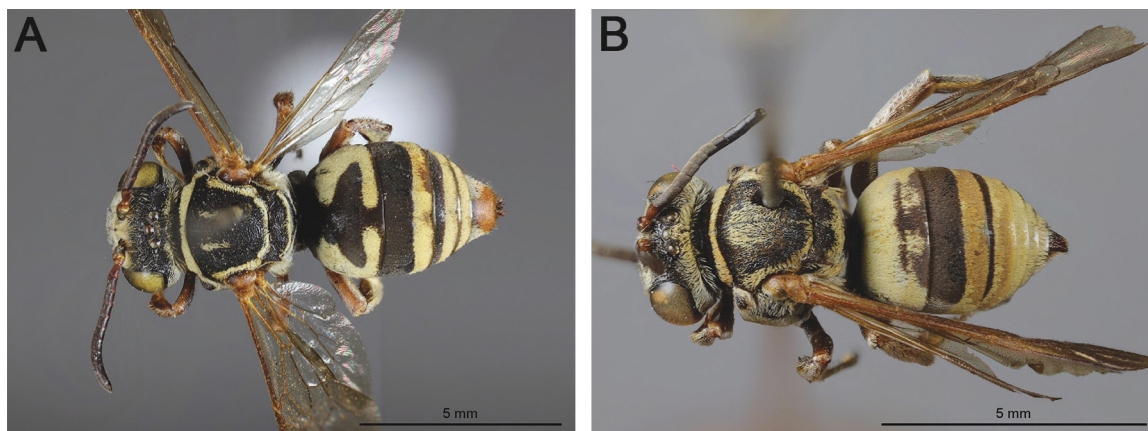


**Fig. 2.** *Triepeolus alvarengai* Moure, 1955. **A–B, D.** Holotype, ♀ (DZUP). **A.** Habitus, lateral view. **B.** Habitus, dorsal view. **C.** Male (ZMB ed1bbe/M.G.R. Database No. 11694), habitus, lateral view (image is copyright of the Museum für Naturkunde and reproduced here with permission). **D.** Pseudopygidial area, dorsal view.

**PUBESCENCE.** Face with tomentum densest around antennal socket. Tomentum slightly sparser on clypeus; upper paraocular and frontal areas and vertexal area mostly exposed. Pronotal collar with tomentum uniformly bright yellow. Mesoscutum with well-defined paramedian band of bright yellow tomentum, well separated from anterior margin; pale tomentum otherwise mostly restricted to lateral and posterior margins. Mesopleuron with off-white to pale-yellow, appressed, branched setae; densely setose just below scrobal groove (upper half otherwise sparsely setose); ventrolateral half nearly bare, except along margins. Metanotum with tomentum uninterrupted, pale yellow laterally and partially dark brown/gray and partially pale yellow medially (uniformly pale yellow in some non-type specimens). Propodeal triangle mostly glabrous, with (pale) setae restricted to small lateral patches. T1 with basal transverse band of bright yellow tomentum separated medially into pair of anterolateral patches, continuous with (and indistinguishable from) lateral longitudinal band, forming arch around semicircular discal patch; anterolateral patch with short, medially directed posterolateral extension in holotype; with medially interrupted apical transverse band in some non-type specimens. T2–T4 with complete apical transverse bands of bright yellow-orange tomentum without well-defined anterolateral extensions, although T2–T4 with faint lateral longitudinal bands of diffuse off-white setae. S2–S3 with apical transverse bands of white tomentum.

**SURFACE SCULPTURE.** Labrum and clypeus with punctures equally dense and nearly contiguous (most  $i < 1d$ ). Vertexal area somewhat sparsely punctate (some  $i > 2d$ ), especially around ocelli. Mesoscutum, mesoscutellum, and axilla with punctures more or less equally dense (most  $i \leq 1d$ ); interspaces well defined, shining. Mesopleuron with punctures in upper half not much denser (most  $i < 1d$ ) than in ventrolateral half (most  $i \leq 1d$ ); interspaces shining; punctures similar in size throughout. Discs of metasomal terga with punctures very fine, dense ( $i \approx 1d$ ), and evenly distributed; interspaces shining somewhat.

**STRUCTURE.** Labrum with pair of small subapical denticles. Pronotal collar short (medial length  $\sim \frac{1}{2}$  MOD). Mesoscutellum moderately bigibbous. Axilla extending beyond midlength of mesoscutellum but not as far back as its posterior margin; tip distinctly pointed and hooked (i.e., concave along medial margin), but mesally unattached to mesoscutellum for less than  $\frac{2}{3}$  medial length of axilla; lateral margin somewhat sinuate.



**Fig. 3.** *Triepeolus* spp., habitus, dorsal view. **A.** *T. alvarengai* Moure, 1955 female specimen (MACN) in which T1 has both basal and apical transverse bands. **B.** *T. nemoralis* (Holmberg, 1886) male specimen (DZUP) in which much of T1 is covered in pale-yellow tomentum.



### Female

T5 with concave apical margin and large patch of pale-yellow tomentum on each side lateral to pseudopygidial area. Pseudopygidial area with underlying integument dark brown in holotype (extensively orange in some non-type specimens), forming rounded triangle with concave sides, with brown spinelike setae laterally. Pygidial plate apically truncate. S4 with apical transverse band of white tomentum. S5 straight in lateral view, with apical fimbria of coppery bristle-like setae; S5 otherwise covered in off-white tomentum.

### Male

T5–T6 with complete apical transverse bands of bright yellow tomentum. Pygidial plate relatively flat and apically rounded. S4–S5 each with apical/subapical fringe of dense, long ( $> 1$  MOD), curved, coppery setae, contrasting with apical transverse bands of white tomentum of preceding sterna.

### Distribution

Eastern and northern Brazil (Fig. 1A).

### Ecology

#### Host records

Unknown.

#### Floral records

Unknown.

### Remarks

*Triepeolus alvarengai* exhibits unusual but continuous variation in the patterns of pale pubescence on T1, which may have only a medially interrupted basal band with a short, medially directed posterolateral extension on each side or both basal and apical transverse bands, with the latter varying in the extent to which it is separated medially. The description of the male of *T. alvarengai* is published here for the first time.

### *Triepeolus atoconganus* Moure, 1955

Figs 1B, 4A, 5

*Triepeolus atoconganus* Moure, 1955: 128 (♂).

*Triepeolus atoconganus* – Urban 2003: 28 (♂) (lectotype designation).

### Diagnosis

The following morphological features in combination tell *T. atoconganus* apart from all other South American *Triepeolus*: the frontal area, dorsum of the mesosoma (at least anterolaterally), and upper halves of the mesopleura have dense, long ( $\geq \frac{1}{2}$  MOD), erect/suberect, minutely branched setae (Fig. 4A); the ventrolateral halves of the mesopleura have sparse, erect, simple setae among the short ( $< \frac{1}{4}$  MOD), appressed, branched setae; and T1–T4 have medially widely interrupted transverse bands (Fig. 5B). *Triepeolus atoconganus* and *T. cecilyae* are the only South American species in the genus with long ( $\geq \frac{1}{2}$  MOD), erect/suberect setae on the upper face and much of the mesosoma, but in *T. cecilyae* these are longer for the most part (with many exceeding 1 MOD in length) and more abundant, covering much of both the upper and ventrolateral halves of the mesopleura. Additionally, in *T. cecilyae* at least the T3–T4 apical transverse bands of the female and T1–T4 apical transverse bands of the male are narrowed or narrowly interrupted medially.

## Etymology

The specific epithet refers to the type locality—Atocongo (near Lima), Peru. The Latin adjectival suffix ‘-anus’ means ‘of’ or ‘pertaining to’.

## Material examined

### Primary type material

PERU • ♂, lectotype; Lima, Atocongo; Aug. 1948; W.K. Weyrauch leg.; DZUP.

### Secondary type material

PERU • 8 ♂♂, paralectotypes; Lima, Atocongo; Aug. 1948; W.K. Weyrauch leg.; DZUP • 1 ♂, paralectotype; same collection data as for preceding; Aug. 1948; W.K. Weyrauch leg.; UNMSM MHN 1.350/M.G.R. Database No. 3526.

### Non-type material

PERU • 1 ♀; Amazonas, Rodríguez de Mendoza; 15 May 1982; M. Cooper leg.; NHMUK NHMUK013620580 • 1 ♂; same collection data as for preceding; 23 May 1984; M. Cooper leg.; NHMUK NHMUK013620577 • 1 ♂; same collection data as for preceding; 25 May 1984; M. Cooper leg.; NHMUK NHMUK013620573 • 1 ♂; Áncash, 7 km SW of Raquia; 14 May 1996; J.G. Rozen and A. Ugarte leg.; AMNH M.G.R. Database No. 3670 • 1 ♀; La Libertad, Samne (near Trujillo); 12–19 Jul. 1975; C. Porter and L. Stange leg.; IFML • 1 ♀; Lima, Atocongo; W.K. Weyrauch leg.; UNMSM MHN 1350/M.G.R. Database No. 1333 • 1 ♂; same collection data as for preceding; KUNHM M.G.R. Database No. 1449 • 1 ♂; same collection data as for preceding; Jul. 1948; W.K. Weyrauch leg.; UNMSM MHN 1350 • 2 ♀♀ (supposedly paralectotypes, but the designations are suspect as Moure 1955 only described the male); same collection data as for preceding; Aug. 1948; W.K. Weyrauch leg.; IFML WKW 3318, WKW 3319 • 1 ♀; same collection data as for preceding; 11 Sep. 1948; Blancas leg.; UNMSM MHN 1350/M.G.R. Database No. 3527 • 1 ♀; same collection data as for preceding; 11 Sep. 1948; W.K. Weyrauch leg.; UNMSM MHN 1350 • 1 ♀; same collection data as for preceding; 28 Sep. 1952; W.K. Weyrauch leg.; IFML • 1 ♂; same collection data as for preceding; 30 Aug. 1958; W.K. Weyrauch leg.; IFML • 1 ♂; Lima, La Tablada; 24 Oct. 1958; W.K. Weyrauch leg.; IFML • 1 ♂; Lima, Lima; Mar. 1949; P. Aguilar leg.; UNMSM M.G.R. Database No. 3525 • 1 ♀; Lima, San Bartolomé; 5 Jan. 1975; R. García leg.; UNMSM M.G.R. Database No. 1443 • 2 ♂♂; same collection data as for preceding; 20 Mar. 1977; R. García leg.; UNMSM • 2 ♂♂; same collection data as for preceding; 1 Apr. 1977; R. García leg.; UNMSM • 1 ♀, 9 ♂♂; Lima, Tornamesa; R. García leg.; UNMSM.

## Redescription

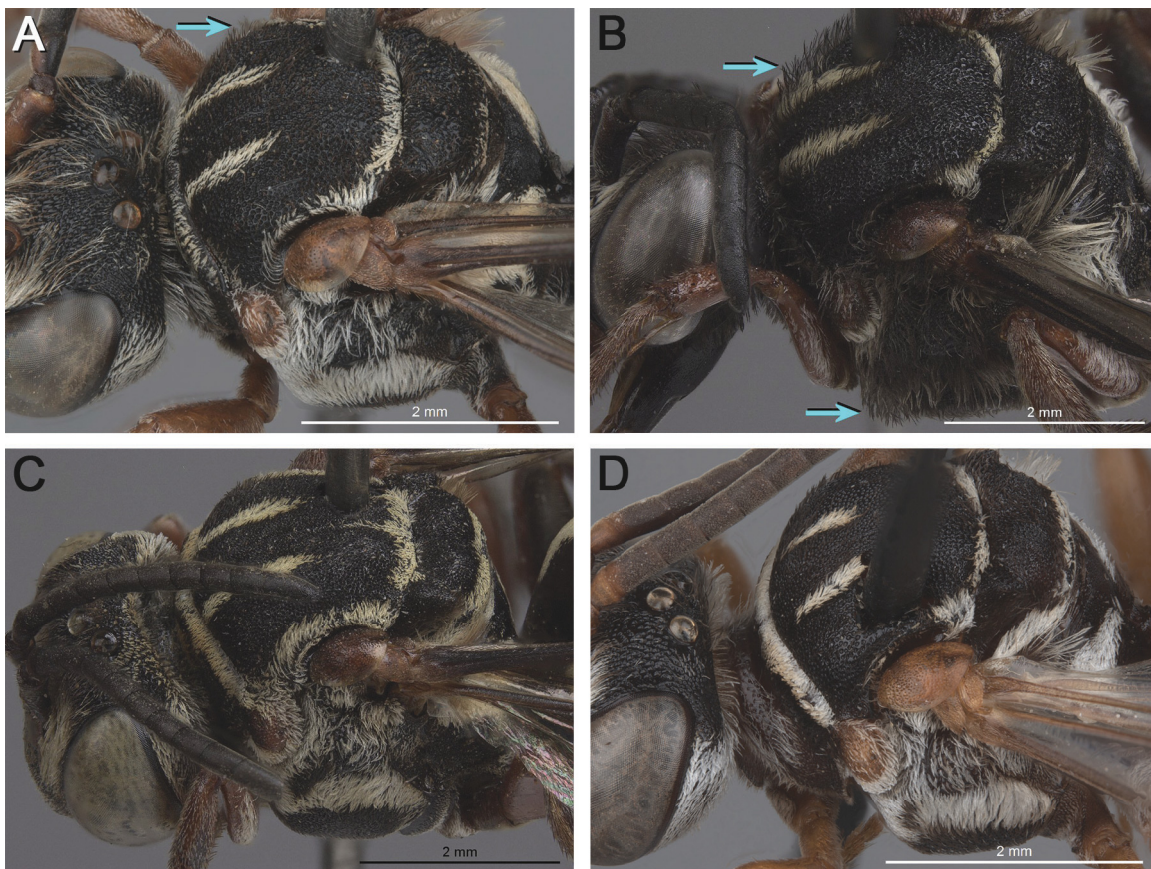
MEASUREMENTS OF LECTOTYPE. Body length 11.0 mm; ITW 2.4 mm; head length 2.6 mm; head width 3.7 mm; fore wing length 10.2 mm.

### Both sexes

INTEGUMENT COLORATION. Dark brown to black except as follows. Mandible with basal two-thirds, pronotal lobe, tegula, coxae to some extent, trochanters to tibiae (excluding brown meso- and metatibial spurs) partially to entirely, and tarsi entirely orange. Antenna entirely dark brown in lectotype; scape, pedicel, and F1 to some extent orange in multiple non-type specimens. Fore wing membrane dusky subhyaline throughout, slightly darker beyond venation. Hind wing membrane dusky subhyaline to hyaline. Pygidial plate to some extent reddish brown in lectotype and some non-type specimens.

PUBESCENCE. Face with tomentum densest around antennal socket. Tomentum slightly sparser on clypeus; upper paraocular and frontal areas and vertexal area mostly exposed. Labrum, clypeus, face around antennal socket, genal and vertexal areas, most of pronotum (including pronotal collar), mesoscutum (at least anterolaterally), and upper half of mesopleuron with off-white to dark brown/gray, erect, minutely

branched setae (reaching more than  $\frac{1}{2}$  MOD in length). Mesoscutum with well-defined paramedian band of off-white to pale-yellow, erect, minutely branched setae (tapering slightly toward but not attaining anterior margin in lectotype; attaining anterior margin in some non-type specimens); with off-white to pale-yellow, appressed, branched setae mostly restricted to posterior margin. Mesopleuron with off-white to pale-yellow, appressed, branched setae around pronotal lobe; upper half densely setose; ventrolateral half sparsely setose. Mesopleuron with sparse, erect, simple setae (reaching about  $\frac{1}{2}$  MOD in length) in addition to appressed and erect/suberect, minutely branched setae. Metanotum with tomentum uninterrupted, pale yellow laterally and partially to entirely black medially. Propodeal triangle mostly glabrous, with (off-white to dark brown/gray) setae restricted to small lateral patches. Metasomal terga with bands of off-white to pale-yellow tomentum, those of T3–T6 stained dark brown/black in lectotype (presumably due to poor preservation). T1 with basal transverse band widely interrupted medially, arched, and continuous with (and indistinguishable from) lateral longitudinal band; apical transverse band separated into pair of rounded lobes medially; discal patch triangular (semicircular in some non-type specimens). T2–T4 with medially widely interrupted apical transverse bands, that of T2 with pair of basomedially convergent anterolateral extensions (described from non-type specimens). S2–S3 with apical transverse bands of white tomentum (reduced to posterolateral patches in lectotype and some non-type specimens).



**Fig. 4.** Head and mesosoma of female, oblique view. **A.** *Triepeolus atoconganus* Moure, 1955 (NHMUK NHMUK013620580). **B.** *T. cecilyae* Packer, 2016 (PCYU). **C.** *T. buchwaldi* (Friese, 1908) (AMNH M.G.R. Database No. 3707). **D.** *T. rufotegularis* (Ashmead, 1900) (USNM M.G.R. Database No. 1332). Blue arrows indicate dense, long ( $\geq \frac{1}{2}$  MOD), erect/suberect, minutely branched setae.

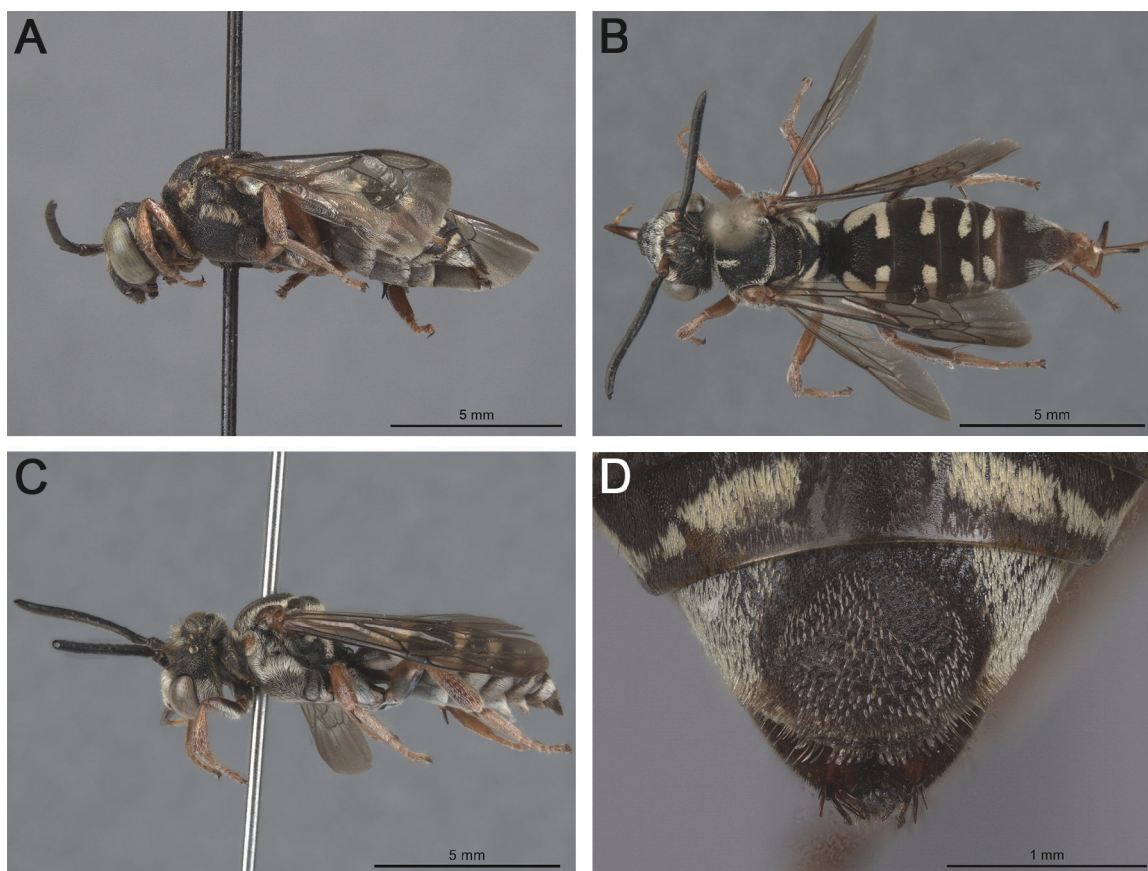


**SURFACE SCULPTURE.** Labrum, clypeus, mesoscutum, mesoscutellum, axilla, and mesopleuron with punctures more or less equally dense and nearly contiguous (most  $i < 1d$ ). Vertexal area somewhat sparsely punctate (some  $i > 2d$ ) anteriorly and around ocelli, otherwise densely (most  $i < 1d$ ) rugose-punctate. Mesopleuron with punctures similar in size throughout. Discs of metasomal terga with punctures very fine, dense ( $i \approx 1d$ ), and evenly distributed; interspaces shining somewhat.

**STRUCTURE.** Labrum with pair of small subapical denticles, each preceded by longitudinal carina. Pronotal collar short (medial length  $\sim \frac{1}{2}$  MOD). Mesoscutellum moderately bigibbous. Axilla extending little if at all beyond midlength of mesoscutellum; tip visible but somewhat blunt, mesally unattached to mesoscutellum for less than  $\frac{1}{3}$  medial length of axilla; lateral margin relatively straight.

### Female

T5 with broadly convex apical margin and large patch of off-white tomentum on each side lateral to pseudopygidial area. Pseudopygidial area circular, with setae glossy, predominantly grayish brown, and sparser centrally; apical margin with row of dense, appressed and suberect coppery to silvery setae. Pygidial plate apically truncate. S4 with apical transverse band of white tomentum. S5 mostly straight in lateral view (slightly downturned apically), covered in mostly brown tomentum and with apical fimbria of brown bristle-like setae.



**Fig. 5.** *Triepeolus atoconganus* Moure, 1955. **A, D.** Female (UNMSM MHN 1350/M.G.R. Database No. 1333). **A.** Habitus, lateral view. **B.** Female (NHMUK NHMUK013620580), habitus, dorsal view. **C.** Male (NHMUK NHMUK013620577), habitus, lateral view. **D.** Pseudopygidial area, dorsal view.

### Male

T5–T6 with medially interrupted apical transverse bands of off-white to pale-yellow tomentum (described from non-type specimens). Pygidial plate apically rounded and slightly downturned, with basal transverse ridge ill-defined and lateral margin somewhat sinuate. S4–S5 each with apical/subapical fringe of dense, long ( $>1$  MOD), curved setae; brown and contrasting strongly with posterolateral patches of white tomentum of preceding sterna in lectotype; coppery to silvery and not contrasting strongly with bands of preceding sterna in some non-type specimens.

### Distribution

Presently only known from western Peru and interandean valleys (Fig. 1B).

### Ecology

#### Host records

Unknown.

#### Floral records

Labels of examined voucher specimens indicate that this species has been collected from *Encelia canescens* Lam. (Asteraceae) and *Nolana* L.f. (Solanaceae).

### Remarks

The description of the female of *T. atoconganus* is published here for the first time.

### *Triepeolus buchwaldi* (Frieze, 1908)

Figs 1C, 4C, 6

*Epeolus buchwaldi* Frieze, 1908: 87 (♀, ♂), lectotype presently designated.

*Triepeolus megadelphus* Cockerell, 1914: 314 (♂), syn. nov.

*Triepeolus aguilaris* Moure, 1955: 130 (♂), syn. nov.

*Triepeolus buchwaldi* – Cockerell 1913: 372.

Non ?*Epeolus xanthurus* Cockerell, 1917 – Moure & Melo 2007: 590 (incorrectly tentatively synonymized with *T. buchwaldi*).

### Diagnosis

The following morphological features in combination tell *T. buchwaldi* apart from all other South American *Triepeolus*: the mesoscutum does not have long ( $\geq \frac{1}{2}$  MOD), erect setae (Fig. 4C); the T1 basal band is arched and continuous with (and indistinguishable from) the lateral longitudinal bands, such that the discal patch is semicircular or triangular (Fig. 6B); T1–T4 have medially interrupted bands of pale-yellow tomentum (Fig. 6B); and the T2 apical transverse bands have lobe-like anterolateral extensions (Fig. 6A–C). *Triepeolus buchwaldi* is very similar in overall appearance to *T. atoconganus* and *T. cecilyae*, but in the latter two species the dorsum of the mesosoma (at least anterolaterally) and mesopleura (at least in the upper half) have dense, long ( $\geq \frac{1}{2}$  MOD), erect/suberect, minutely branched setae.

### Etymology

The specific epithet (declined in the genitive case) honors G.V. Buchwald, who collected the lectotype (Frieze 1908).



## Material examined

### Primary type material

ECUADOR • ♂, lectotype of *E. buchwaldi*; Guayas, Guayaquil; 1901; G.V. Buchwald leg.; ZMB 8e2500 • ♂, holotype of *T. megadelphus*; Guayas, Guayaquil; May–Jun. 1913; C.T. Brues leg.; AMNH AMNH\_IZC 00323951.

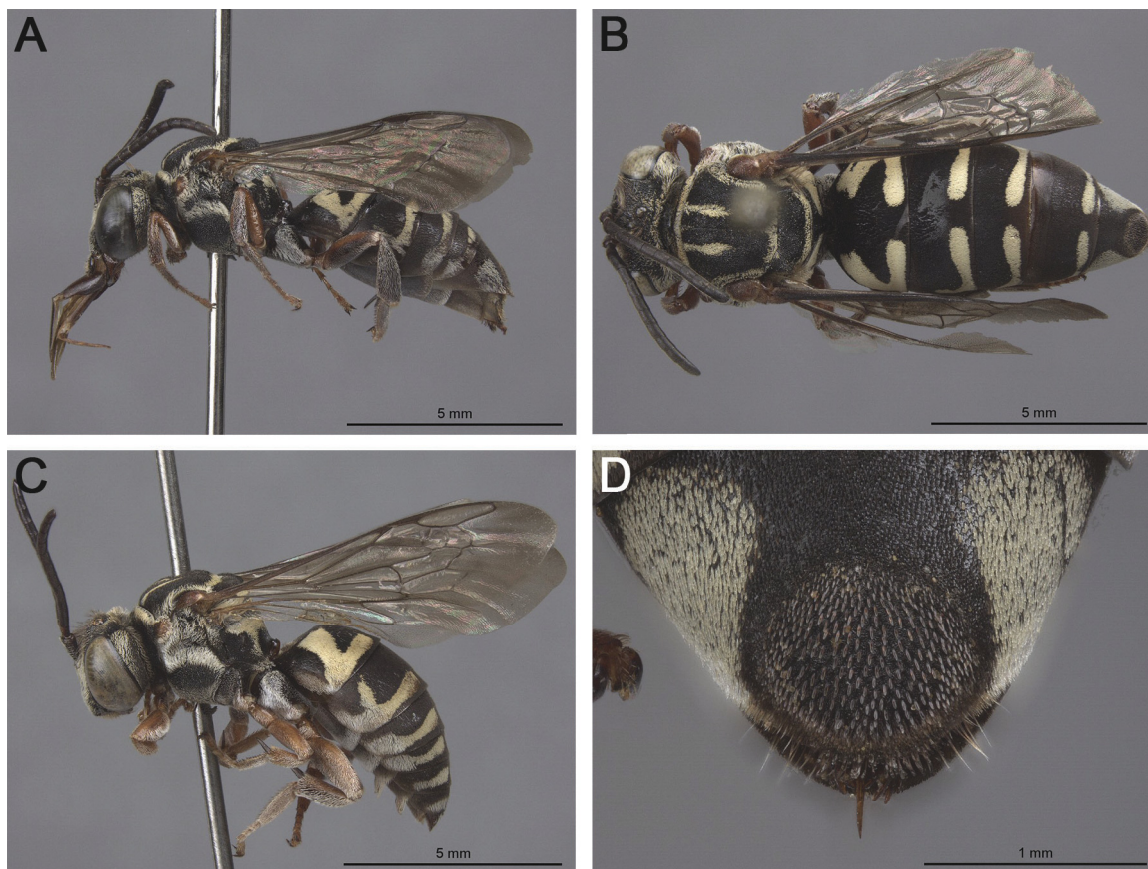
PERU • ♂, holotype of *T. aguilar*; Lima, Lima; Jan. 1949; P. Aguilar leg.; DZUP.

### Secondary type material

ECUADOR • 1 ♀, paralectotype of *E. buchwaldi*; Guayas, Guayaquil; Apr. 1901; Buchwald leg.; AMNH No. 25147 • 2 ♀♀, paralectotypes of *E. buchwaldi*; same collection data as for preceding; Apr. 1901; Buchwald leg.; ZMB.

### Non-type material

ECUADOR • 1 ♂; El Oro, 19 km NE of Piñas (Hotel Machay); 2 Jul. 1989; L. Stange and R. Miller leg.; FSCA M.G.R. Database No. 3490 • 1 ♀; same collection data as for preceding; 5 Jul. 1989; L. Stange and R. Miller leg.; FSCA M.G.R. Database No. 1327 • 1 ♂; Guayas, Guayaquil; 1930; F. Campos leg.; DZUP • 1 ♀; Guayas, Playas; 26 Feb. 1972; M. Deyrup leg.; AMNH • 3 ♀♀; same collection data as for preceding; 3 Apr. 1987; M. Cooper leg.; NHMUK NHMUK013620574, NHMUK013620578, NHMUK013620585 • 1 ♂; Loja, Loja (14 km W of Catamayo); 9 Jul. 1989; L. Stange and R. Miller



**Fig. 6.** *Triepeolus buchwaldi* (Friese, 1908). **A.** Female (AMNH M.G.R. Database No. 1328), habitus, lateral view. **B, D.** Female (AMNH M.G.R. Database No. 3707). **B.** Habitus, dorsal view. **C.** Male (INHS 387483), habitus, lateral view. **D.** Pseudopygidial area, dorsal view.

leg.; FSCA M.G.R. Database No. 3491 • 1 ♀; Manabí, Canoa; 10 Jan. 1981; A. Roig leg.; MACN • 2 ♂♂; Manabí, Chone; May 1976; M. Fritz leg.; MACN • 1 ♀; Manabí, Portoviejo; 30 Apr. 1969; P. Alcivar leg.; USNM M.G.R. Database No. 5936 • 16 ♀♀; same collection data as for preceding; 30 Apr. 1969; P. Alcivar leg.; USNM • 1 ♂; Santa Elena, El Azúcar (near Santa Elena); 12 Apr. 1977; M.E. Irwin leg.; INHS 387483.

PERU • 1 ♀; Áncash, 1 km NE of Carhuaz; 15 May 1996; J.G. Rozen and A. Ugarte leg.; AMNH M.G.R. Database No. 2264 • 6 ♀♀; Cajamarca, 14 km E of Tembladera; 7.2017° S, 79.0386° W; 22 Mar. 1999; J.G. Rozen and A. Ugarte leg.; AMNH M.G.R. Database Nos. 2245, 2247, 2255, 2257, 2261, 2263 • 1 ♀; same collection data as for preceding; 22 Mar. 1999; J.G. Rozen and A. Ugarte leg.; AMNH AMNH\_IZC 00292365/M.G.R. Database No. 2260 • 14 ♀♀; same collection data as for preceding; 24 Mar. 1999; J.G. Rozen and A. Ugarte leg.; AMNH M.G.R. Database Nos. 2246, 2248, 2249, 2250, 2251, 2252, 2253, 2254, 2256, 2258, 2259, 2262, 3707, 3708 • 1 ♂; La Libertad, Cartavio; 20 Mar. 1987; E.G. Sayth leg.; LACM M.G.R. Database No. 3653 • 1 ♂; La Libertad, Chillia; 15 Mar. 1953; Weyrauch leg.; IFML • 1 ♀, 6 ♂♂; La Libertad, Simbal; 4 Jul. 1974; L. Stange and C. Porter leg.; IFML • 1 ♀; Lambayeque, 32 km ENE of Olmos; 21 May 1996; J.G. Rozen and A. Ugarte leg.; AMNH M.G.R. Database No. 1328 • 1 ♀; Lambayeque, Lambayeque; 5 Mar. 1981; M.E. Irwin leg.; INHS 7774/M.G.R. Database No. 3706 • 1 ♀, 1 ♂; Lima, Chosica; 20 Feb. 1928; R.C. Shanon leg.; USNM • 1 ♂; same collection data as for preceding; 7 Apr. 1970; R. García leg.; DZUP • 1 ♀; Lima, Lima; 3 Feb. 1949; P. Aguilar leg.; UNMSM • 1 ♂ (erroneously labeled as the holotype but actually a non-type specimen); same collection data as for preceding; 3 Feb. 1949; P. Aguilar leg.; UNMSM M.G.R. Database No. 3488 • 1 ♂; Lima, Miraflores (Lima); 3 Feb. 1949; P.A.F. leg.; IFML FC 234 • 1 ♂; Lima, Río Chillón; 14 Mar. 1953; Weyrauch leg.; IFML • 1 ♂; Lima, Río Lurín; 22 Nov. 1952; Weyrauch leg.; IFML • 1 ♂; Lima, Valle del Chillón; 6 Mar. 1966; R. García leg.; UNMSM M.G.R. Database No. 3489 • 1 ♂; Piura, Querecotillo; 23 Jul. 1982; R.B. Miller and L. Stange leg.; FSCA.

### Non-preserved material

PERU • 1 ♀; Lambayeque, Lambayeque; 31 Jan. 2023; M. Campos obs.; iNaturalist record #152688525.

### Redescription

MEASUREMENTS OF LECTOTYPE. Body length 8.8 mm; ITW 1.7 mm; head length 2.0 mm; head width 2.8 mm; fore wing length 7.3 mm.

### Both sexes

INTEGUMENT COLORATION. Dark brown to black except as follows. Mandible with apical third golden yellow (entirely dark brown/black in some non-type specimens). Mandible with basal two-thirds, scape and pedicel to some extent, F1 extensively, pronotal lobe, tegula, coxae to some extent, trochanters to tarsi (excluding brown meso- and metatibial spurs) partially to entirely, metasomal terga laterally, and metasomal sterna to some extent orange. Fore wing membrane subhyaline, apically dusky. Hind wing membrane dusky subhyaline to hyaline. Pygidial plate to some extent reddish brown.

PUBESCENCE. Face with tomentum densest around antennal socket. Tomentum slightly sparser on clypeus; upper paraocular and frontal areas and vertexal area mostly exposed. Pronotal collar with tomentum uniformly pale yellow. Mesoscutum with well-defined paramedian band of pale-yellow tomentum, tapering slightly toward and attaining anterior margin; pale tomentum otherwise mostly restricted to lateral and posterior margins. Mesopleuron with off-white, appressed, branched setae; upper half densely setose, except behind pronotal lobe, with setae slightly sparser on hypoepimeral area; ventrolateral half sparsely setose. Metanotum with tomentum uninterrupted, uniformly pale yellow. Propodeal triangle mostly glabrous, with (pale) setae restricted to small lateral patches. Metasomal terga with bands of off-white to pale-yellow tomentum. T1 with basal transverse band widely interrupted medially, arched, and

continuous with (and indistinguishable from) lateral longitudinal band; apical transverse band separated into pair of rounded lobes medially; discal patch triangular (semicircular in some non-type specimens). T2–T4 with medially interrupted apical transverse bands, that of T2 with pair of basomedially convergent anterolateral extensions. S2–S3 with apical transverse bands of white tomentum.

**SURFACE SCULPTURE.** Labrum and clypeus with punctures equally dense (most  $i < 1d$ ); interspaces well defined, shining. Vertexal area densely punctate (most  $i < 1d$ ). Mesoscutum, mesoscutellum, and axilla with punctures more or less equally dense and nearly contiguous (most  $i < 1d$ ). Mesopleuron with punctures in upper half not much denser (most  $i < 1d$ ) than in ventrolateral half (most  $i \leq 1d$ ); interspaces shining; punctures similar in size throughout. Discs of metasomal terga with punctures very fine, dense ( $i \approx 1d$ ), and evenly distributed; interspaces shining somewhat.

**STRUCTURE.** Labrum with pair of small subapical denticles, each preceded by discrete longitudinal ridge. Pronotal collar rather short (medial length  $\sim \frac{2}{3}$  MOD). Mesoscutellum moderately bigibbous. Axilla extending little if at all beyond midlength of mesoscutellum; tip visible but somewhat blunt, mesally unattached to mesoscutellum for less than  $\frac{1}{3}$  medial length of axilla; lateral margin relatively straight.

#### **Female**

T5 with broadly convex apical margin and large patch of off-white to pale-yellow tomentum on each side lateral to pseudopygidial area. Pseudopygidial area circular, with setae glossy, predominantly grayish brown, and sparser centrally; apical margin with row of dense, appressed and suberect coppery to silvery setae. Pygidial plate apically truncate. S4 with apical transverse band of white tomentum. S5 straight in lateral view, covered in brown tomentum and with apical fimbria of brown bristle-like setae.

#### **Male**

T5–T6 with medially interrupted apical transverse bands of off-white to pale-yellow tomentum. Pygidial plate relatively flat and apically rounded. S4–S5 each with apical/subapical fringe of dense, long ( $> 1$  MOD), curved, coppery to silvery setae, not contrasting strongly with bands of preceding sterna.

#### **Distribution**

Ecuador and Peru, west of the Andes (Fig. 1C).

#### **Ecology**

##### **Host records**

One (female) specimen of *T. buchwaldi* at the AMNH (M.G.R. Database No. 2260) is pinned with a specimen identified by C.D. Michener as *Florilegus purpurascens* Cockerell, 1914 (Hymenoptera: Apidae: Eucerini), both of which were apparently taken from the same nest 14 km E of Tembladera in Cajamarca, Peru.

##### **Floral records**

Rightmyer (2006) reported this species on *Bidens* L. (Asteraceae) and *Gossypium hirsutum* L. (Malvaceae). Images on iNaturalist show this species visiting *Ludwigia* L. (Onagraceae). The label of one examined voucher specimen says “soybean var. trial bloom”.

#### **Remarks**

In his treatment of South American *Triepeolus*, Moure (1955) indicated that he was not familiar with *T. megadelphus*. However, Moure subsequently examined the holotype, in 1957—the year indicated on his determination label (Fig. S9F in Supp. file 2)—and identified the specimen as *T. buchwaldi* but did not publish the synonymy. The authors of the present study agree with Moure’s designation, as the

specimen does not exhibit any morphological features to suggest that it belongs to a separate species, so *T. megadelphus* is herein synonymized under *T. buchwaldi*.

Moure (1955) described *T. aguilari* based on a male specimen from Lima, Peru, claiming it to be similar to *T. ancoratus* Cockerell, 1916 from the southwestern United States. The types of both species are markedly different despite both belonging to the *T. verbessinae* species group, with the latter (USNM 534611) exhibiting a transversely oblong (as opposed to triangular) discal patch on T1 and complete (as opposed to medially interrupted) transverse bands on T1–T4. The metasomal tergal bands in *T. buchwaldi* are typically more widely interrupted medially in the female than male, and the patterns of pubescence exhibited by the holotype of *T. aguilari* do not differ markedly from those exhibited by the studied male type of *E. buchwaldi*—in both specimens, the metasomal tergal bands are only narrowly interrupted medially. Hence, the authors of the present study do not consider these to be distinct species, and *T. aguilari* is herein synonymized under *T. buchwaldi*.

Since Friese (1908) did not explicitly designate a holotype, one of the two studied syntypes—the male, which bears a red label that says “Type”—is herein designated as the lectotype of *E. buchwaldi*. The female, which is from the type locality and was identified as *E. buchwaldi* by Friese but is not labeled as a type, is recognized as a paralectotype.

Moure & Melo (2007) tentatively synonymized *Epeolus xanthurus* Cockerell, 1917 with *T. buchwaldi* and erroneously indicated the AMNH as the repository for the holotype of the former (the specimen is actually deposited in the USNM). *Epeolus xanthurus* is now correctly placed in *Epeolus* as a junior synonym of *E. luteipennis* Friese, 1916 (Onuferko 2019).

### ***Triepeolus cecilyae* Packer, 2016**

Figs 1D, 4B, 7–9

*Triepeolus cecilyae* Packer, 2016: 2 (♂), figs 1–6.

#### **Diagnosis**

The following morphological features in combination tell *T. cecilyae* apart from all other South American *Triepeolus*: the frontal area, dorsum of the mesosoma, and both the upper and ventrolateral halves of the mesopleura have dense, long (clearly  $> \frac{1}{2}$  MOD), erect/suberect, minutely branched setae (Fig. 4B) and the T3–T4 apical transverse bands are narrowed or narrowly interrupted medially (Figs 7B, 8). *Triepeolus cecilyae* and *T. atoconganus* are the only South American species in the genus with long ( $\geq \frac{1}{2}$  MOD), erect/suberect setae on the upper face and much of the mesosoma, but in *T. atoconganus* these are shorter for the most part (with few exceeding 1 MOD in length) and less abundant, covering much of the upper but not ventrolateral halves of the mesopleura. Additionally, in *T. atoconganus* the T1–T4 transverse bands are all widely interrupted medially.

#### **Etymology**

The specific epithet (declined in the genitive case) honors Cecily Bradshaw, a friend of the taxonomic authority and advocate for (and supporter of) bee research (Packer 2016).

#### **Material examined**

##### **Primary type material**

CHILE • ♂, holotype; Region I [sic, actually Arica y Parinacota Region], 30 km W of Zapahuira; 24 Apr. 2001; R.E. Owen leg.; PCYU.



### Non-type material

PERU • 1 ♂; Arequipa, Characato; 16.4669° S, 71.4753° W; 15 May 2022; Y.A. Calizaya leg.; PCYU • 1 ♀ (studied from image); same collection data as for preceding; 17 Jan. 2023; Y.A. Calizaya leg.; MUSA • 1 ♀ (studied from image); same collection data as for preceding; 17 Jan. 2023; Y.A. Calizaya leg.; PCYU • 1 ♀; Ica, 51.1 km E of Nazca; 14.8104° S, 74.6660° W; 2 May 2011; Ohl, Krause, and Breitkreuz leg.; PCYU • 1 ♂; same collection data as for preceding; 2 May 2011; Ohl, Krause, and Breitkreuz leg.; ZMB • 1 ♀; same collection data as for preceding; 3 May 2011; Ohl, Krause, and Breitkreuz leg.; ZMB • 1 ♂; same collection data as for preceding; 3 May 2011; Ohl, Krause, and Breitkreuz leg.; UNMSM.

### Redescription

MEASUREMENTS OF HOLOTYPE. Body length 10.6 mm; ITW 2.1 mm; head length 2.5 mm; head width 3.5 mm; fore wing length 9.0 mm.

### Both sexes

INTEGUMENT COLORATION. Dark brown to black except as follows. Mandible with apical third golden yellow (entirely dark brown/black in some non-type specimens) and basal two-thirds reddish brown. Labrum with small orange spot basolaterally. F1 orange in part. F2 with orange spot basally in some non-type specimens. Pronotal lobe, tegula, anterior metasomal terga laterally, and S1 to some extent reddish brown. Fore wing membrane dusky subhyaline throughout except around third submarginal crossvein and second recurrent vein, where subhyaline. Hind wing membrane dusky subhyaline to hyaline. Coxae to some extent and trochanters to tarsi entirely reddish orange (meso- and metatibiae, including spurs, and metafemur to varying degrees dark brown/black in non-type specimens).

PUBESCENCE. Face with tomentum densest around antennal socket. Clypeus, upper paraocular and frontal areas, and vertexal area mostly exposed. Labrum, face around antennal socket, most of pronotum (including pronotal collar), and mesopleuron along posterior margin above base of mesocoxa (and just below pronotal lobe and scrobal groove in non-type specimens) with off-white, erect, minutely branched setae (clearly reaching more than  $\frac{1}{2}$  MOD in length). Clypeus, genal and vertexal areas, most of mesoscutum, mesoscutellum, axilla, most of mesopleuron, metapleuron, and propodeum laterally with dark brown/gray, erect, minutely branched setae (clearly reaching more than  $\frac{1}{2}$  MOD in length). Mesoscutum with well-defined paramedian band of pale-yellow, erect, minutely branched setae (tapering slightly toward but not attaining anterior margin in holotype; attaining anterior margin in some non-type specimens); with pale-yellow, appressed, branched setae restricted to posterior margin. Mesopleuron densely setose throughout, with off-white, appressed, branched setae around pronotal lobe. Metanotum with tomentum uninterrupted, dark brown/gray except for small patch of off-white tomentum laterally. Propodeal triangle mostly glabrous, with (dark brown/gray) setae restricted to small lateral patches. T1 with basal transverse band of off-white to pale-yellow tomentum widely interrupted medially, arched, and continuous with (and indistinguishable from) lateral longitudinal band; apical transverse band of pale-yellow tomentum separated into pair of rounded lobes medially; discal patch semicircular (triangular in some non-type specimens). T2–T4 with medially narrowed or narrowly interrupted apical transverse bands of pale-yellow tomentum, that of T2 with pair of faint lateral longitudinal bands of diffuse pale-yellow setae in holotype (with pair of well-defined basomedially convergent anterolateral extensions in some non-type specimens). S2–S3 with apical transverse bands of white tomentum, that of S2 interrupted medially (complete but narrowed medially in one non-type specimen).

SURFACE SCULPTURE. Labrum and clypeus with punctures equally dense (most  $i < 1d$ ); interspaces well defined, shining. Vertexal area densely rugose-punctate (most  $i < 1d$ ). Mesoscutum, mesoscutellum, and axilla with punctures more or less equally dense and nearly contiguous (most  $i < 1d$ ). Mesopleuron with punctures in upper half not much denser (most  $i < 1d$ ) than in ventrolateral half (most  $i \leq 1d$ ); interspaces



shining; punctures similar in size throughout. Discs of metasomal terga with punctures very fine, dense ( $i \approx 1d$ ), and evenly distributed; interspaces dull due to tessellate surface microsculpture.

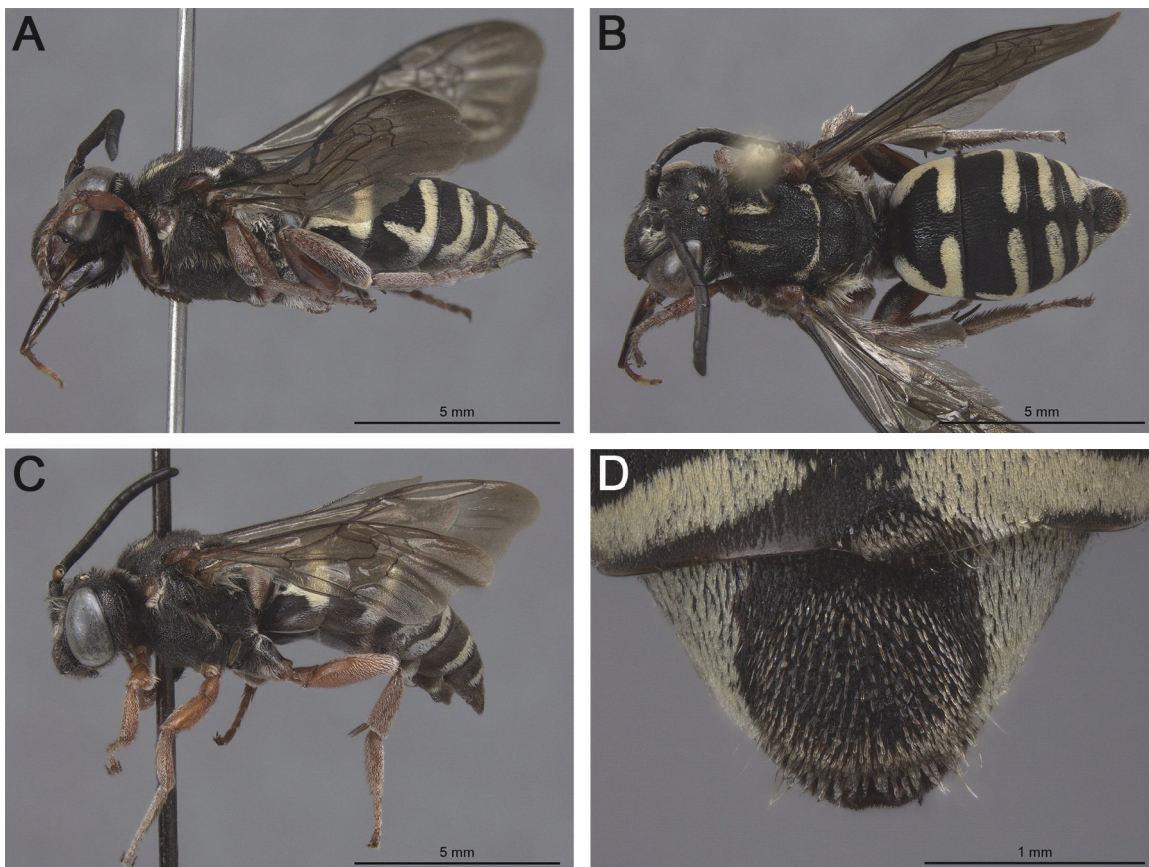
**STRUCTURE.** Labrum with pair of small subapical denticles, each preceded by longitudinal carina. Pronotal collar rather short (medial length  $\sim \frac{2}{3}$  MOD). Mesoscutellum moderately bigibbous. Axilla not extending beyond midlength of mesoscutellum; tip visible but somewhat blunt, mesally unattached to mesoscutellum for less than  $\frac{1}{3}$  medial length of axilla; lateral margin relatively straight.

#### Female

T5 with broadly convex apical margin and large patch of pale-yellow tomentum on each side lateral to pseudopygidial area. Pseudopygidial area circular, with setae glossy, predominantly grayish brown, and sparser centrally; apical margin with row of dense, appressed and suberect coppery to silvery setae. Pygidial plate apically truncate. S4 with apical transverse band of white tomentum. S5 slightly downturned apically, with apical fimbria of brown bristle-like setae and dark brown tomentum laterally, posteriorly, and in apicomedial triangular area; S5 otherwise covered in off-white to pale brown tomentum.

#### Male

T5–T6 with complete or medially narrowly interrupted apical transverse bands of pale-yellow tomentum. Pygidial plate apically rounded and slightly downturned, with basal transverse ridge ill-defined and lateral margin somewhat sinuate. S4–S5 each with apical/subapical fringe of dense, long ( $> 1$  MOD),



**Fig. 7.** *Triepeolus cecilyae* Packer, 2016. **A–B, D.** Female (PCYU). **A.** Habitus, lateral view. **B.** Habitus, dorsal view. **C.** Holotype, ♂ (PCYU), habitus, lateral view. **D.** Pseudopygidial area, dorsal view.

curved setae; coppery to silvery laterally, brown and contrasting strongly with bands of preceding sterna medially.

### Distribution

Arid regions of southern Peru and northern Chile (Fig. 1D).

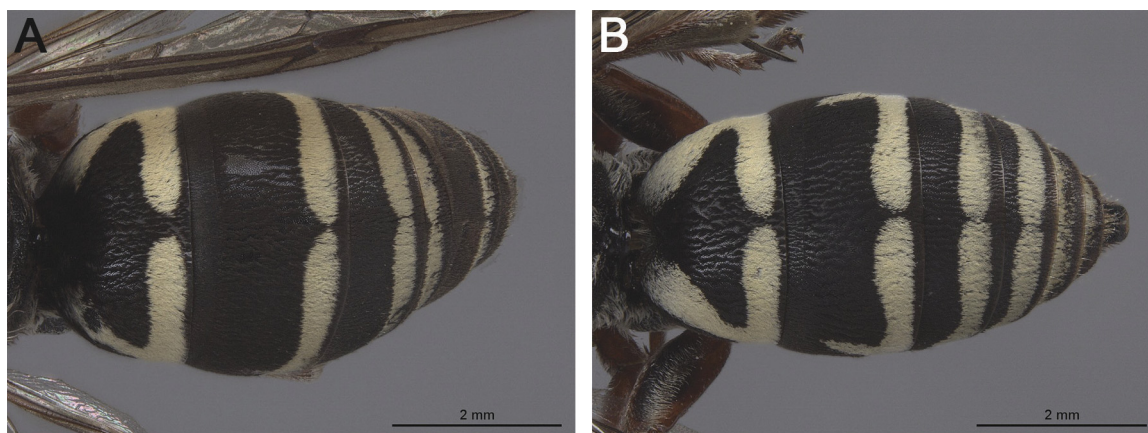
### Ecology

#### Host records

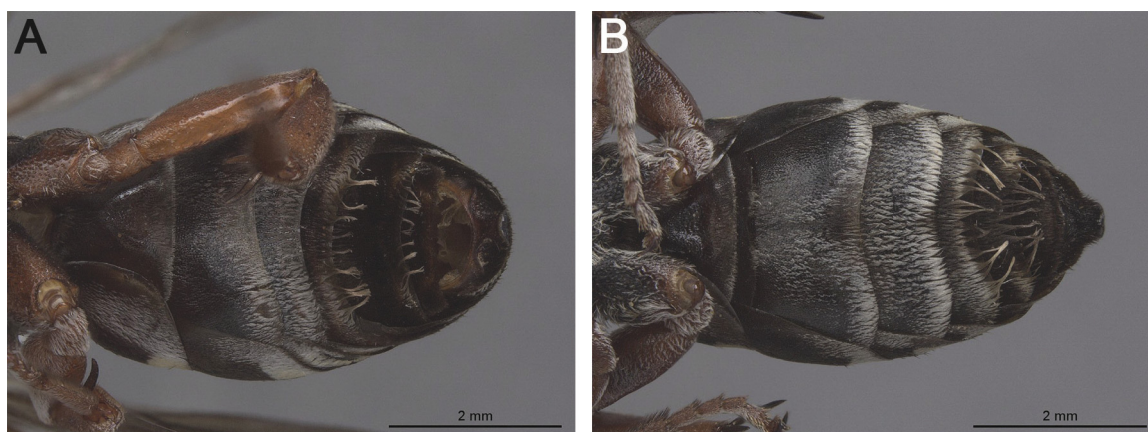
Packer (2016) suggested that *Mirnapis inca* Urban, 1998 (Hymenoptera: Apidae: Eucerini) might be the host of *T. cecilyae* based on its size and occurrence in the area where the holotype of the latter was collected.

#### Floral records

This species has been collected from *Grindelia tarapacana* Phil. (Asteraceae).



**Fig. 8.** *Triepeolus cecilyae* Packer, 2016, metasoma of male, dorsal view. **A.** Holotype (PCYU). **B.** Non-type specimen from southern Peru (ZMB).



**Fig. 9.** *Triepeolus cecilyae* Packer, 2016, metasoma of male, ventral view. **A.** Holotype (PCYU). **B.** Non-type specimen from southern Peru (ZMB).



## Remarks

*Triepeolus cecilyae* was described from a single, male specimen collected in northern Chile (Packer 2016). Its status as a new species was based in part on morphological comparisons to four specimens from Peru (two females and two males, all from the same locality and collected within a two-day period) tentatively identified by the author as *T. atoconganus* (L. Packer, personal communication, 2023). These specimens and the holotype of *T. cecilyae* were personally examined by TO, and all appear to be conspecific. One of the diagnostic features of *T. cecilyae* identified by Packer (2016) is that the T3 apical transverse band is complete (as opposed to interrupted medially). Additionally, in *T. cecilyae* S3 was described as “uniformly covered in pale hairs”. In the two male specimens from Peru, the bands on the metasomal terga and sterna were partly stained dark brown/black (presumably due to poor preservation) when received and initially examined by TO. Their original coloration was restored by applying small pieces of tissue paper dampened with 70% ethanol to the dorsal and ventral surfaces of the metasoma for several minutes. This treatment revealed that the T3–T6 apical transverse bands are complete in one of the two males from Peru (Fig. 8B) and the T3–T4 bands are only narrowly interrupted medially in the other. Additionally, in both specimens the metasomal sterna, including S3, were revealed to be extensively covered in white tomentum, as in the holotype of *T. cecilyae* (Fig. 9). Although the T1–T4 apical transverse bands are all interrupted medially in the two females (Fig. 7B), they are more narrowly interrupted than in what is understood to be the female of *T. atoconganus* (Fig. 5B). Three additional specimens (two females and one male) have since been discovered (also in Peru but closer to the type locality in Chile), and in the two females some of the metasomal tergal bands are complete albeit narrowed medially whereas the rest are narrowly interrupted medially. Another feature of *T. cecilyae* originally considered to be diagnostic is that the legs are entirely reddish orange from the trochanters to tarsi, but among the now seven known non-type specimens from Peru there is continuous variation in the degree of dark brown/black coloration on the meso- and metatibiae and metafemora, which range from almost entirely reddish orange to mostly dark brown/black.

The eight known specimens are far more similar to one another morphologically than to any studied representatives (including the lectotype) of *T. atoconganus*, agreeing with the present diagnosis for *T. cecilyae*. Most notably, in these specimens the mesosoma is more extensively and obviously “hairy” than that of *T. atoconganus* and the T3–T4 apical transverse bands are at most only narrowly (as opposed to widely) interrupted medially. Further suggesting conspecificity is that all known collection localities (in Chile and Peru) are in the Atacama Desert and outlying arid areas along the Pacific coast. Based on known records, adults of *T. cecilyae* are active in summer and autumn (January to May).

Given the discovery of these additional exemplars of *T. cecilyae*, a re-description of this species is warranted. The female of *T. cecilyae* is described here for the first time.

### *Triepeolus flavipennis* (Fries, 1916)

Figs 1E, 10, 13A

*Epeolus flavipennis* Fries, 1916: 337 (♂), lectotype presently designated.

*Triepeolus bilineatus* Cockerell, 1949: 460 (♀, ♂), syn. nov.

*Triepeolus flavipennis* – Moure & Melo 2007: 586 (in Fries’s original paper, the name is spelled both “*flavipennis*” (p. 337) and “*flavipennis*” (p. 349 in reprint; p. 372 in bound volume); as first revisers, Moure & Melo established ‘*flavipennis*’ as the valid original spelling, with ‘*flavipennis*’ recognized as a misprint; see also Rasmussen & Ascher 2008).

## Diagnosis

The following morphological features in combination tell *T. flavipennis* apart from all other South American *Triepeolus*: T1 has a medially interrupted basal band or pair of anterolateral patches of pale tomentum, which on each side (or each of which) is mesally convex, such that the discal patch forms a trapezoid or triangle with concave anterolateral sides (Fig. 10B), and the T2 apical transverse band does not have lobe-like anterolateral extensions. *Triepeolus flavipennis* is the only species in the *T. verbesinae* species group—containing species in which the pseudopygidial area of the female is distinctly circular (Fig. 10D)—that (usually) does not have an apical transverse band on T1. More commonly in this species, the T1 anterolateral patches of pale tomentum each have a short, medially directed posterolateral extension (Fig. 10B).

## Etymology

Although Friese (1916) did not explain the etymology of his *Epeolus flavipennis*, the specific epithet was presumably inspired by its yellow-orange wings, which do not reliably distinguish this species from similar-looking congeners.

## Material examined

### Primary type material

COLOMBIA • ♂, lectotype of *E. flavipennis*; Cauca, Popayán; 1900; Lehmann leg.; ZMB 323e41.

HONDURAS • ♀, holotype of *T. bilineatus*; Francisco Morazán, Zamorano; 20 Jan. 1947; A. Rivera leg.; USNM 534618.

### Secondary type material

COLOMBIA • 1 ♂, paralectotype of *E. flavipennis*; Cauca, Popayán; 1900; Lehmann leg.; ZMB 505a65.

HONDURAS • 1 ♂, allotype of *T. bilineatus*; Francisco Morazán, Zamorano; 20 Jan. 1947; USNM Allotype NO. 58538 USNM; 165/M.G.R. Database No. 5611.

### Non-type material

COLOMBIA • 1 ♀; Valle del Cauca, Lobo Guerrero; 23 Sep. 1976; Bell, Breed, and Michener leg.; KUNHM • 3 ♂♂; same collection data as for preceding; 23 Sep. 1977; Bell, Breed, and Michener leg.; KUNHM • 1 ♂; same collection data as for preceding; 20 Oct. 1977; C. García leg.; DZUP.

GUATEMALA • 1 ♀; Guatemala, Ciudad San Cristóbal; Jan.; AMNH Ac. 4875/M.G.R. Database No. 1550.

HONDURAS • 1 ♂; Comayagua, El Taladro; 15 Jun. 1979; J.A. Chemsak, A. and M. Michelbacher, and W.W. Middlekauff leg.; EMEC M.G.R. Database No. 1454 • 1 ♂; Francisco Morazán, Zamorano; J. Williams leg.; USNM M.G.R. Database No. 5933 • 1 ♂; same collection data as for preceding; 20 Jan. 1947; USNM M.G.R. Database No. 5932.

MEXICO • 1 ♀, paralectotype of *E. mexicanus*; F. Sumichrast leg.; ANSP 2229-8 • 1 ♂; Colima, 10 mi W of Colima; 1 Aug. 1954; M. Cazier, W. Gertsch, and Bradts leg.; AMNH M.G.R. Database No. 2243 • 1 ♀; Durango, 5 mi W of Durango; 14 Jun. 1964; J.F. McAlpine leg.; CNC 753863 • 2 ♀♀; same collection data as for preceding; 23 Jul. 1964; J.F. McAlpine leg.; CNC 808413, 808414 • 1 ♂; same collection data as for preceding; 23 Jul. 1964; J.F. McAlpine leg.; CNC 808385 • 1 ♂; same collection data as for preceding; 29 Jul. 1964; J.F. McAlpine leg.; CNC 808394 • 2 ♀♀; Guerrero, 17 mi N of Chilpancingo; 7 Aug. 1962; KU Mex Expedition leg.; KUNHM M.G.R. Database Nos. 5176, 5177 • 1 ♀; Guerrero, 3.9 km NE of Taxco (mi. 73588.7); 16 Sep. 1976; C.D. George and R.R. Snelling leg.;

USNM No. 73588 A/M.G.R. Database No. 5610 • 2 ♀♀; Guerrero, Mezcala; 29 Jun. 1951; H.E. Evans leg.; KUNHM M.G.R. Database Nos. 5174, 5175 • 1 ♂; Hidalgo, 4 km N of Metzquititlán; 11 Nov. 1991; Noguera leg.; KUNHM M.G.R. Database No. 7120 • 1 ♀; Hidalgo, 9 mi NW of Actopan; 1 Sep. 1962; KU Mex Expedition leg.; KUNHM M.G.R. Database No. 5180 • 1 ♂; same collection data as for preceding; 1 Sep. 1962; KU Mex Expedition leg.; KUNHM M.G.R. Database No. 5181 • 1 ♀; Jalisco, 10 mi W of Tizapán; 18 Jul. 1953; KU Mex Expedition leg.; KUNHM M.G.R. Database No. 1549 • 1 ♀; Jalisco, 15.5 mi NE of Lagos de Moreno; 26 Jul. 1962; KU Mex Expedition leg.; KUNHM M.G.R. Database No. 1330 • 3 ♂♂; Jalisco, Guadalajara; Crawford leg.; USNM M.G.R. Database Nos. 5929, 5930, 5931 • 1 ♀; same collection data as for preceding; “IX.18”; McClendon leg.; ANSP • 1 ♀; Jalisco, Villa de Guadalupe; 26 Jul. 1951; H.E. Evans leg.; KUNHM M.G.R. Database No. 5173 • 1 ♂; Michoacán, Palo Alto; 12 Jul. 1970; R.E. Beer and party leg.; KUNHM M.G.R. Database No. 5183 • 1 ♀; Michoacán, Río del Marqués (3 km E of Cuatro Caminos on Hwy 120); 17 Jul. 1989; A. Roig-Alsina and R. Brooks leg.; KUNHM #061/M.G.R. Database No. 5172 • 1 ♀; Morelos, Sierra de Huautla (2.5 km N and 4 km W of the Center for Environmental Education and Research Sierra de Huautla); 18.4500° N, 99.0333° W; 5 Sep. 1996; R. Brooks leg.; KUNHM MEX1B96 013/M.G.R. Database No. 5171 • 1 ♀; same collection data as for preceding; 5 Sep. 1996; R. Brooks leg.; KUNHM MEX1B96 014/M.G.R. Database No. 5170 • 1 ♂; same collection data as for preceding; 5 Sep. 1996; R. Brooks leg.; KUNHM MEX1B96 012/M.G.R. Database No. 5185 • 1 ♂; Oaxaca, 17 km W of Tehuantepec; 8 Sep. 1965; D.H. Janzen leg.; USNM M.G.R. Database No. 5928 • 2 ♂♂; Oaxaca, 6 km S of San Sebastián Frontera; 18.2129° N, 97.6490° W; 5 Oct. 2007; L. Packer leg.; PCYU • 1 ♂; Oaxaca, El Camarón; 7 Jul. 1953; KU Mex Expedition leg.; KUNHM M.G.R. Database No. 1331 • 1 ♀; Oaxaca, El Camarón; 7 Jul. 1952; KU Mex Expedition leg.; KUNHM M.G.R. Database No. 5178 • 1 ♀; Oaxaca, San Sebastián Frontera; 25 Sep. 2008; L. Packer leg.; PCYU CCDB-00601 H01 • 1 ♀; Puebla, 6 km SW of Zapotitlán Salinas; 3 Nov. 1991; T. Griswold leg.; KUNHM SM0326486/M.G.R. Database No. 7119 • 1 ♀; Puebla, 8 mi SE of Tehuiztzingo; 29 Jun. 1961; KU Mex Expedition leg.; KUNHM M.G.R. Database No. 5182 • 1 ♂; Puebla, SW of Plan de San Miguel, Hwy 125 (km 53.4); 18.2125° N, 97.5450° W; 13 Sep. 1996; R. Brooks leg.; KUNHM MEX1B96 056/M.G.R. Database No. 5184 • 1 ♀; Puebla, SW of Zapotitlán; 24 Sep. 2008; L. Packer leg.; PCYU CCDB-00601 H02 • 1 ♀; Querétaro, Peña Blanca; 12 Aug. 1979; R. Murillo leg.; USNM M.G.R. Database No. 5926 • 1 ♀; Querétaro, Peña Blanca; 27 May 1979; R. Murillo leg.; USNM M.G.R. Database No. 5927 • 1 ♀; San Luis Potosí, 6.5 mi E of Ciudad del Maíz; 23 Jul. 1962; KU Mex Expedition leg.; KUNHM M.G.R. Database No. 5179.

USA • 1 ♂; Texas, The Basin, Big Bend National Park; 13–14 Jul. 1948; M.A. Cazier leg.; AMNH M.G.R. Database No. 2244.

### Non-preserved material

MEXICO • 1 unsexed specimen; Coahuila, Arteaga; 25.3451° N, 100.7944° W; 30 Jun. 2020; L. Jimenez Hernandez obs.; iNaturalist record #53088456 • 1 ♂; Coahuila, Saltillo; 25.3363° N, 100.9900° W; 3 Aug. 2019; L. Jimenez Hernandez obs.; iNaturalist record #30154605 • 1 ♂; Jalisco, Teuchitlán; 28 May 2023; J.A. Álvarez Ruiz obs.; iNaturalist record #165064942 • 1 ♀; Oaxaca, Monte Albán, Santa Cruz Xoxocotlán; 23 Jul. 2022; J. Kemner obs.; iNaturalist record #142220347 • 1 ♀; Oaxaca, San Pedro Totolapa; 28 Jun. 2022; J. Kemner obs.; iNaturalist record #140242303 • 1 ♂; Querétaro, Cadereyta de Montes; 20.6872° N, 99.8048° W; 30 Jun. 2017; H. Ugalde obs.; iNaturalist record #6902218 • 1 ♂; Querétaro, Cadereyta de Montes; 20.6860° N, 99.8035° W; 24 Aug. 2023; J.B. Hernández Díaz obs.; iNaturalist record #180022886 • 1 ♀; Querétaro, Fraccionamiento Vista Real, Corregidora; 20.5219° N, 100.3881° W; 31 May 2022; C. Govaerts obs.; iNaturalist record #119663290 • 1 ♀; Querétaro, Fraccionamiento Vista Real, Corregidora; 20.5219° N, 100.3882° W; 6 Oct. 2021; C. Govaerts obs.; iNaturalist record #97401415 • 1 ♀; Querétaro, Fraccionamiento Vista Real, Corregidora; 20.5221° N, 100.3880° W; 7 Nov. 2019; C. Govaerts obs.; iNaturalist record #35428605 • 1 ♀; Querétaro, Fraccionamiento Vista Real, Corregidora; 20.5226° N, 100.3884° W; 31 Oct. 2019; C. Govaerts obs.;



iNaturalist record #35147139 • 1 ♂; Querétaro, Fraccionamiento Vista Real, Corregidora; 20.5227° N, 100.3882° W; 28 Aug. 2020; C. Govaerts obs.; iNaturalist record #57873580 • 1 ♀; Querétaro, Santiago de Querétaro; 10 Jul. 2020; F. Fleck obs.; iNaturalist record #52755779.

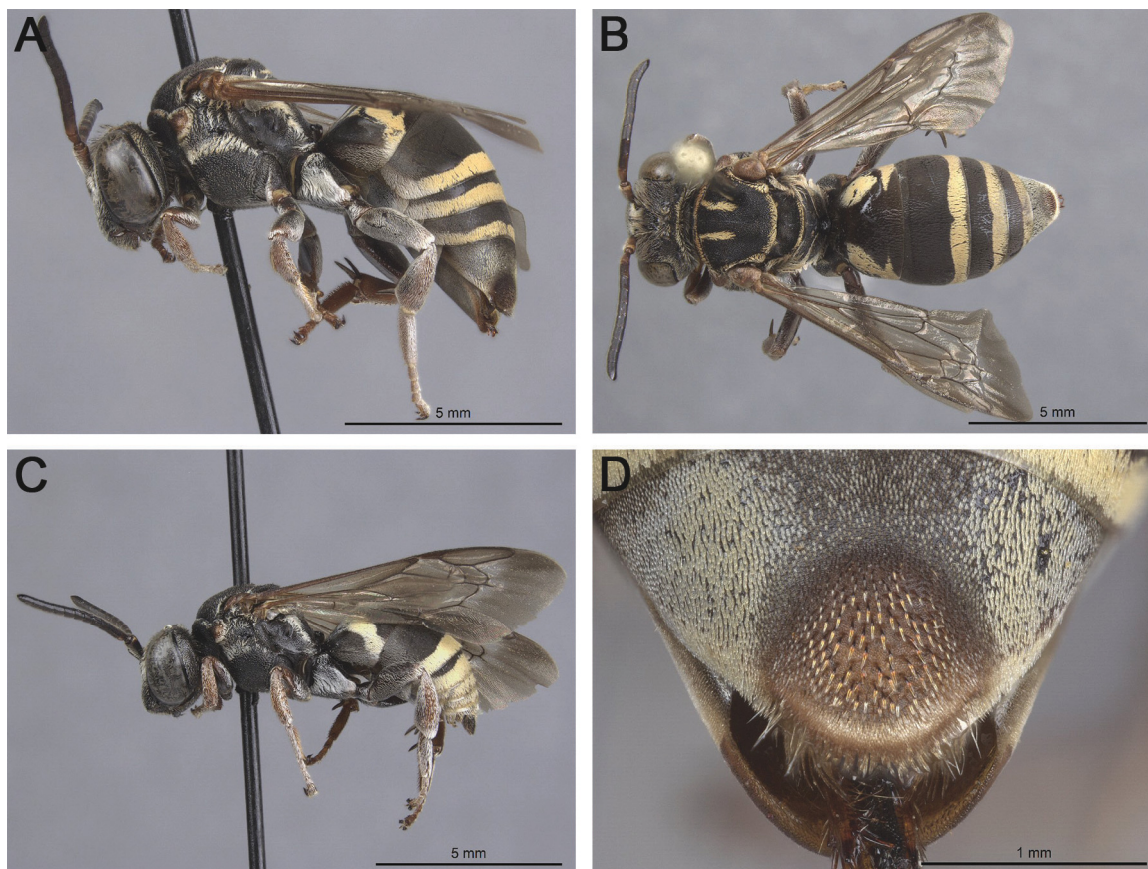
### Redescription

MEASUREMENTS OF LECTOTYPE. Body length 8.2 mm; ITW 1.7 mm; head length 2.0 mm; head width 2.8 mm; fore wing length 7.5 mm.

#### Both sexes

INTEGUMENT COLORATION. Dark brown to black except as follows. Mandible with apical two-fifths golden yellow (entirely dark brown/black in some non-type specimens). Mandible with middle fifth (middle three-fifths in holotype of *T. bilineatus*), labrum to some extent (except basomedially), scape and pedicel to some extent, F1 extensively, pronotal lobe, tegula, coxae to some extent, trochanters to tarsi (excluding brown meso- and metatibial spurs) partially to entirely, metasomal terga laterally, and metasomal sterna to some extent orange. F2 with orange spot basally. Fore wing membrane dusky subhyaline throughout. Hind wing membrane dusky subhyaline to hyaline. Pygidial plate to some extent reddish brown.

PUBESCENCE. Face with tomentum densest around antennal socket. Tomentum slightly sparser on clypeus; upper paraocular and frontal areas and vertexal area mostly exposed. Pronotal collar with tomentum



**Fig. 10.** *Triepeolus flavipennis* (Friese, 1916). **A.** Female (CNC 753863), habitus, lateral view. **B.** Female (CNC 808414), habitus, dorsal view. **C.** Male (PCYU), habitus, lateral view. **D.** Female (CNC 808413) pseudopygidial area, dorsal view.

uniformly pale yellow. Mesoscutum with well-defined paramedian band of pale-yellow tomentum, tapering slightly toward and attaining anterior margin; pale tomentum otherwise mostly restricted to lateral and posterior margins. Mesopleuron with off-white, appressed, branched setae; upper half densely setose, except behind pronotal lobe, with setae slightly sparser on hypoepimeral area; ventrolateral half sparsely setose. Metanotum with tomentum uninterrupted, uniformly off-white. Propodeal triangle mostly glabrous, with (pale) setae restricted to small lateral patches. Metasomal terga with bands of bright to pale-yellow tomentum. T1 with basal band separated medially into pair of anterolateral patches, each continuous with (and indistinguishable from) lateral longitudinal band and mesally convex, such that discal patch forming trapezoid or triangle with concave anterolateral sides; anterolateral patch with short, medially directed posterolateral extension in lectotype of *E. flavipennis*; with medially interrupted apical transverse band in some non-type specimens. T2–T4 with medially narrowly interrupted apical transverse bands (in lectotype of *E. flavipennis*) or medially narrowed apical transverse bands (in paralectotype of *E. flavipennis*, holotype of *T. bilineatus*, and multiple non-type specimens); these bands without well-defined anterolateral extensions, although T2–T3 with faint lateral longitudinal bands of diffuse off-white setae in types of *E. flavipennis* and multiple non-type specimens. S2–S3 with apical transverse bands of white tomentum.

**SURFACE SCULPTURE.** Labrum and clypeus with punctures equally dense (most  $i < 1d$ ); interspaces well defined, shining. Vertexal area densely punctate (most  $i < 1d$ ). Mesoscutum, mesoscutellum, and axilla with punctures more or less equally dense and nearly contiguous (most  $i < 1d$ ). Mesopleuron with punctures in upper half not much denser (most  $i < 1d$ ) than in ventrolateral half (most  $i \leq 1d$ ); interspaces shining; punctures similar in size throughout. Discs of metasomal terga with punctures very fine, dense ( $i \approx 1d$ ), and evenly distributed; interspaces shining somewhat.

**STRUCTURE.** Labrum with pair of small subapical denticles, each preceded by discrete longitudinal ridge. Pronotal collar rather short (medial length  $\sim \frac{2}{3}$  MOD). Mesoscutellum weakly bigibbous. Axilla extending little if at all beyond midlength of mesoscutellum; tip visible but somewhat blunt, mesally unattached to mesoscutellum for less than  $\frac{1}{3}$  medial length of axilla; lateral margin relatively straight.

### Female

T5 with broadly convex apical margin and large patch of off-white to pale-yellow tomentum on each side lateral to pseudopygidial area or large, continuous patch (or band) of pale tomentum bordering and contacting pseudopygidial area. Pseudopygidial area circular, with basal crescent of dense, silvery setae; setae glossy, coppery, and sparser centrally; apical margin with row of dense, appressed and suberect coppery to silvery setae. Pygidial plate apically truncate. S4 with apical transverse band of white tomentum. S5 slightly downturned apically, with apical fimbria of coppery bristle-like setae; S5 otherwise covered in off-white tomentum.

### Male

T5–T6 with complete or medially narrowly interrupted apical transverse bands of pale-yellow tomentum. Pygidial plate apically rounded and slightly downturned, with basal transverse ridge ill-defined and lateral margin somewhat sinuate. S4–S5 each with apical/subapical fringe of dense, long ( $> 1$  MOD), curved, coppery to silvery setae, not contrasting strongly with bands of preceding sterna.

### Distribution

Texas (USA) to Colombia (Fig. 1E).

## Ecology

### Host records

Unknown. One vouchered male bears a label indicating that the specimen was collected in the presence of “*Anthocopa* on rock wall” near Metzquititlán in Hidalgo, Mexico, but an association between the two taxa seems very unlikely given that no osmiine bees have been confirmed as hosts of *Triepeolus* (Rightmyer 2006).

### Floral records

Rightmyer (2006) reported this species on *Aloysia gratissima* (Gillies & Hook.) Tronc. (Verbenaceae), *Cleome viscosa* L. (Cleomaceae), *Larrea tridentata* (Sessé & Moc. ex DC.) Coville (Zygophyllaceae), *Prosopis* L. (Fabaceae), and *Zanthoxylum* L. (Rutaceae). Images on iNaturalist show this species visiting *Heterotheca inuloides* Cass. (Asteraceae), *Lantana velutina* M.Martens & Galeotti (Verbenaceae), *Lysiloma divaricatum* (Jacq.) J.F.Macbr. (Fabaceae), and *Verbesina serrata* Cav. (Asteraceae). The label of one more recently examined voucher specimen further indicates that this species has been collected from *Bidens pilosa* L.

## Remarks

Rightmyer (2006) indicated that *T. bilineatus* and *T. flavipennis* are likely conspecific. In one of the two studied (male) types of *E. flavipennis*, the T2–T4 apical transverse bands of yellow tomentum are narrowly interrupted medially. In this species, the bands are more commonly complete, but specimens with medially narrowed and/or narrowly interrupted metasomal tergal bands have been observed from across the range of this species. In both the other type of *E. flavipennis* and (female) holotype of *T. bilineatus*, the T2–T4 apical transverse bands are complete, albeit somewhat narrowed medially. The authors of the present study do not consider these to be distinct species, and *T. bilineatus* is herein synonymized under *T. flavipennis*.

Since Friese (1916) did not explicitly designate a holotype, one of the two studied male syntypes (that which bears a red label that says “Type”) is herein designated as the lectotype of *E. flavipennis*. The other male, which bears an orange label that says “Typus”, is recognized as a paralectotype.

In South America, this species is presently only known from a couple of localities along the Pacific coast of Colombia. *Triepeolus flavipennis* has not yet been confirmed from the Isthmus of Panama and consequently shows a disjunct distribution (Fig. 1E); however, its presence there is expected based on its occurrence in northern South America and the Northern Triangle of Central America.

### *Triepeolus nemoralis* (Holmberg, 1886)

Figs 1F, 3B, 11, 13B

*Doeringiella nemoralis* Holmberg, 1886: 280 (♀).

*Epeolus merus* Brèthes, 1909: 250 (♂), syn. nov.

*Epeolus merus* – Schrottky 1913: 265 (in regional checklist).

*Triepeolus nemoralis* – Roig-Alsina 1989: 578.

## Diagnosis

The following morphological features in combination tell *T. nemoralis* apart from all other South American *Triepeolus*: the T1 basal band is arched, continuous with (and indistinguishable from) the lateral longitudinal bands, and mesally concave on each side, such that the discal patch is semicircular (Fig. 11B); the mesoscutum has a large anteromedial ovate patch of yellow tomentum (Fig. 3B), which

may be sparser medially such that the patch is suggestive of ill-defined paramedian bands (Fig. 11B); and T2–T4 have complete apical transverse bands of yellow tomentum (Figs 3B, 11B). *Triepeolus nemoralis* most closely resembles specimens of *T. alvarengai* without an apical transverse band on T1 and *T. mexicanus* (Cresson, 1878), the latter of which is known only from North and Central America, but in *T. alvarengai* the mesoscutum has well-defined paramedian bands and in *T. mexicanus* pale tomentum on the mesoscutum is restricted to the lateral and posterior margins. Males of *T. nemoralis* also closely resemble those of *T. flavipennis*, but in *T. flavipennis* the mesoscutum has well-defined paramedian bands and the pair of anterolateral patches of pale tomentum on T1 are mesally convex, such that the discal patch forms a trapezoid or triangle with concave anterolateral sides. This species is also very similar in overall appearance to *Epeolus luteipennis*, and in both species the mesoscutum has a large anteromedial patch of yellow tomentum as opposed to well-defined paramedian bands, but both sexes of *T. nemoralis* are easily told apart from any similar-looking *Epeolus* by their simple mandibles; in *E. luteipennis* and all other South American *Epeolus*, the mandibles each have a distinct preapical tooth.

### Etymology

Although Holmberg (1886) did not explain the etymology of his *Doeringiella nemoralis*, the specific epithet seemingly alludes to the habitat (grove or woodland) in which the type of this species was collected.

### Material examined

#### Primary type material

ARGENTINA • ♀, holotype of *D. nemoralis*; Formosa, Formosa; Mar. 1885; E.L. Holmberg leg.; MACN (not examined, destroyed).

PARAGUAY • ♂, holotype of *E. merus*; Cordillera, San Bernardino (Chaco, Alto Paraguay according to the original description); K. Fiebrig leg.; MACN 10136.

#### Non-type material

ARGENTINA • 1 ♀; Autonomous City of Buenos Aires; 1918; A. Frers leg.; MACN • 1 ♀; Autonomous City of Buenos Aires, Jardín Botánico Carlos Thays (Palermo); 20 Jan. 2020; R.A. González Vaquero and Z. Cairey leg.; FAUBA 327 • 1 ♀ (studied from images); same collection data as for preceding; 3 Feb. 2020; R.A. González Vaquero and Z. Cairey leg.; FAUBA 416 • 1 ♂ (studied from images); same collection data as for preceding; 27 Feb. 2020; R.A. González Vaquero and Z. Cairey leg.; FAUBA 596 • 1 ♀; Buenos Aires, San Isidro; 20 Feb. 1950; MACN • 2 ♀♀; Buenos Aires, San Pedro, Vuelta de Obligado; 33.6817° S, 59.8100° W; 13 Dec. 2012; C. and A. Roig leg.; MACN • 1 ♂; Santa Fe, Santa Fe; 27 Feb. 1930; Bridarolli leg.; MACN.

BOLIVIA • 2 ♀♀, 1 ♂; Santa Cruz, Pedra Branca; Apr.; ANSP.

BRAZIL • 1 ♂; Espírito Santo, Linhares; Jan. 1962; C. Elias leg.; DZUP • 1 ♀; Mato Grosso, Cáceres; 12 Mar. 1985; C. Elias leg.; DZUP • 1 ♀, 3 ♂♂; Paraná, Matinhos; 25.7667° S, 48.5833° W; 3 Mar. 2002; G.A.R. Melo and J.S. Moure leg.; DZUP • 1 ♂; Roraima, Surumu; Nov. 1966; M. Alvarenga leg.; DZUP • 1 ♀; Santa Catarina, Florianópolis; 2 Mar. 2001; E.P. Feja leg.; DZUP • 1 ♀; São Paulo, Barueri; Mar. 1958; K. Lenko leg.; DZUP • 1 ♂; same collection data as for preceding; Apr. 1958; K. Lenko leg.; DZUP.

COLOMBIA • 1 ♀; Bolívar, Zambrano; 7 Jun. 1994; IFML • 1 ♂; Cesar, Valledupar; 11 Jul. 1968; B. Malkin leg.; AMNH • 1 ♂ (studied from images); Meta, Vereda La Balsa, Puerto López; 27 Jul. 1983; A. Becerra leg.; ICN 101501 • 2 ♂♂; Valle del Cauca, Cali; 11 Feb. 1935; H.F. Schwarz leg.; AMNH • 1 ♀; Valle del Cauca, Hormiguero, Cali; 14 Jan. 1935; H.F. Schwarz leg.; AMNH • 1 ♂; Valle del Cauca,



Lobo Guerrero; 20 Oct. 1977; C. García leg.; DZUP • 2 ♂♂; Valle del Cauca, Near Lobo Guerrero; 6 Oct. 1976; M. Breed leg.; KUNHM.

GUYANA: 1 ♂; 1908; J. Rodway leg.; NHMUK • 2 ♂♂; Demerara-Mahaica, Pln. Cane Grove; 20 Jul. 1946; H.C. James leg.; NHMUK.

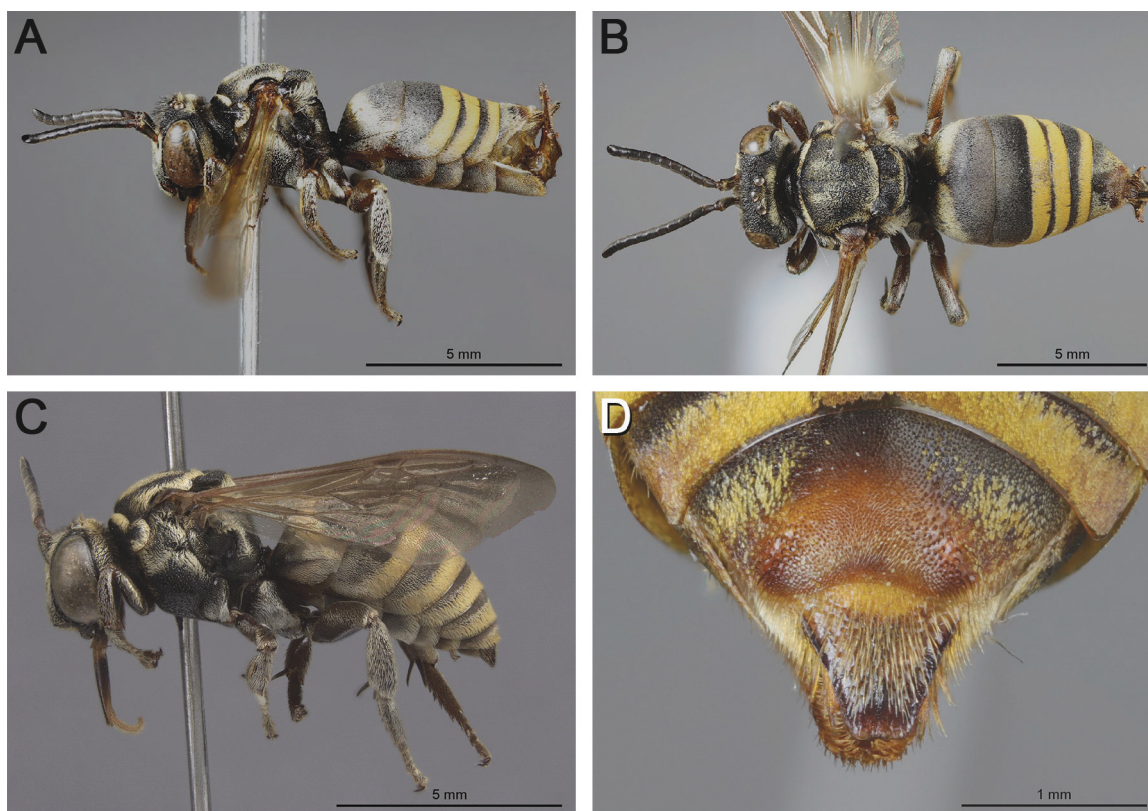
TRINIDAD AND TOBAGO • 1 ♂; Tunapuna-Piarco, Curepe (Trinidad); 20 Apr. 1961; N. Gopaul leg.; CNC 1801912.

### Redescription

MEASUREMENTS OF HOLOTYPE OF *E. MERUS*. Body length 10.7 mm; ITW 2.3 mm; head length 2.5 mm; head width 3.4 mm; fore wing length 9.4 mm.

#### Both sexes

INTEGUMENT COLORATION. Dark brown to black except as follows. Mandible with middle quarter in basal half reddish brown (basal half entirely reddish brown in some non-type specimens). Scape to some extent, pedicel and F1 extensively, and tegula orange. F2 with orange spot basally. Antenna entirely dark brown in some non-type specimens. Fore wing membrane dusky subhyaline throughout. Hind wing membrane dusky subhyaline to hyaline. Legs to some extent reddish brown in holotype of *E. merus*; dark brown to black in some non-type specimens. Pygidial plate reddish brown.



**Fig. 11.** *Triepeolus nemoralis* (Holmberg, 1886). **A–B.** Female (FAUBA 327). **A.** Habitus, lateral view. **B.** Habitus, dorsal view. **C.** Male (CNC 1801912), habitus, lateral view. **D.** Female (MACN) pseudopygidial area, dorsal view.

**PUBESCENCE.** Face with tomentum densest around antennal socket. Tomentum slightly sparser on clypeus; upper paraocular and frontal areas and vertexal area mostly exposed. Pronotal collar with tomentum pale yellow laterally and black medially (uniformly bright yellow in some non-type specimens). Mesoscutum with large anteromedial ovate patch of pale-yellow tomentum, slightly separated from anterior margin (setae rather diffuse and patch thus ill-defined in holotype of *E. merus*; well-defined in some non-type specimens); pale tomentum otherwise mostly restricted to lateral and posterior margins. Mesopleuron with off-white, appressed, branched setae; densely setose just below scrobal groove (upper half otherwise sparsely setose); ventrolateral half nearly bare, except along margins. Metanotum with tomentum uninterrupted, uniformly off-white (black medially in some non-type specimens). Propodeal triangle mostly glabrous, with (pale) setae restricted to small lateral patches. T1 with basal transverse band of pale-yellow tomentum complete (separated medially into pair of anterolateral patches in some non-type specimens), continuous with (and indistinguishable from) lateral longitudinal band, forming arch around semicircular discal patch. T2–T4 with complete apical transverse bands of bright yellow tomentum without well-defined anterolateral extensions, although T2–T3 with faint lateral longitudinal bands of diffuse off-white setae in some non-type specimens. S2–S3 with apical transverse bands of white tomentum.

**SURFACE SCULPTURE.** Labrum and clypeus with punctures equally dense and nearly contiguous (most  $i < 1d$ ). Vertexal area densely rugose-punctate (most  $i < 1d$ ). Mesoscutum, mesoscutellum, and axilla with punctures more or less equally dense ( $i \leq 1d$ ); interspaces well defined, shining. Mesopleuron with punctures in upper half denser (most  $i \leq 1d$ ) than in ventrolateral half ( $i \leq 3d$ ), where punctures irregularly distributed; interspaces shining where punctures not contiguous; punctures similar in size throughout. Discs of metasomal terga with punctures very fine, dense ( $i \approx 1d$ ), and evenly distributed; interspaces somewhat dull due to tessellate surface microsculpture.

**STRUCTURE.** Labrum with pair of small subapical denticles. Pronotal collar rather short (medial length  $\sim \frac{2}{3}$  MOD). Mesoscutellum moderately bigibbous. Axilla extending beyond midlength of mesoscutellum but not as far back as its posterior margin; tip distinctly pointed and hooked (i.e., concave along medial margin), but mesally unattached to mesoscutellum for less than  $\frac{2}{3}$  medial length of axilla; lateral margin somewhat sinuate.

### **Female**

Mesoscutum with ill-defined paramedian band among diffuse pale-yellow setae in some non-type specimens. T5 with concave apical margin and large patch of pale-yellow tomentum on each side lateral to pseudopygidial area. Pseudopygidial area with underlying integument extensively orange, forming rounded triangle with concave sides, with orange spinelike setae laterally. Pygidial plate apically truncate. S4 with apical transverse band of white tomentum. S5 straight in lateral view, with apical fimbria of coppery bristle-like setae; S5 otherwise covered in off-white tomentum.

### **Male**

T5–T6 with complete apical transverse bands of bright yellow tomentum. Pygidial plate relatively flat and apically rounded. S4–S5 each with apical/subapical fringe of dense, long ( $> 1$  MOD), curved, coppery setae, contrasting with apical transverse bands of white tomentum of preceding sterna.

### **Distribution**

Northern and eastern South America (Fig. 1F).

### **Ecology**

#### **Host records**

Unknown.

### Floral records

This species has been collected from the flowers of *Grindelia pulchella* Dunal (Asteraceae), *Verbena gracilescens* (Cham.) Herter (Verbenaceae), and *V. intermedia* Gillies & Hook. (R.A. González-Vaquero, personal communication, 2022). The label of one examined voucher specimen further indicates that this species has been collected from *Ludwigia adscendens* (L.) H.Hara.

### Remarks

The type of *D. nemoralis* is meant to be at the MACN but has been destroyed (Moure & Melo 2007). In a revision of *Doeringiella*, Roig-Alsina (1989) indicated that “*D. nemoralis* should be called *Triepeolus nemoralis* (Holmberg) (new combination)” based on its description. The ill-defined spots (of pale tomentum) on the mesoscutum, (single) medially narrowed yellow band on T1, complete golden bands on T2–T4, and orange-squamous T5 (in reference to the pseudopygidial area and underlying integument coloration) describe a single species of *Triepeolus* in South America (in the *T. simplex* species group).

This species was later described under the name *Epeolus merus* (by Brèthes 1909) from a male specimen, supposedly from Alto Paraguay in the Paraguayan Chaco (or Western Region), but this does not correspond with the locality given on the collection label (i.e., San Bernardino, Paraguay) (Fig. S10D in Supp. file 2). Although male, the holotype of *E. merus* closely matches the original description of *D. nemoralis* (based on the female) and both are regarded as belonging to the same species, so *E. merus* is herein established as a junior synonym of *D. nemoralis* (= *T. nemoralis*).

### *Triepeolus osiriformis* (Schrottky, 1910)

Figs 1G, 12, 13C, 15A

*Epeolus osiriformis* Schrottky, 1910: 208 (♀, ♂), lectotype presently designated.

*Epeolus luteipes* Friese, 1916: 336 (♀, ♂), lectotype presently designated.

*Epeolus paraensis* Friese, 1925: 36 (♀).

*Triepeolus osiriformis* – Rightmyer 2008: 72 (stat. rev.).

Non *Triepeolus nobilis* (Friese, 1908) – Moure 1955: 125 (incorrectly synonymized with *E. osiriformis*, *E. luteipes*, and ? *E. paraensis*). — Rightmyer 2004: 6, 13, 19, 32–33, 39, 42, figs 19b, 92, 126 (misidentification).

### Diagnosis

*Triepeolus osiriformis* can be told apart from all other South American *Triepeolus* by the reddish brown (as opposed to black) axillae and mesoscutellum (Figs 12A–C, 13C). Additionally, much of the head, rest of the mesosoma, and metasoma are also reddish brown in *T. osiriformis* (Figs 12A–C, 15A). In this respect and in terms of the patterns of pubescence on the metasoma, *T. osiriformis* superficially resembles *Rhinepeolus rufiventris* (Friese, 1908), from which it is easily told apart by the presence of well-defined paramedian bands (as opposed to a median longitudinal strip of pale, short, appressed setae) on the mesoscutum as well as its mutic (i.e., non- as opposed to distinctly bituberculate) mesoscutellum.

### Etymology

The specific epithet was inspired by the elongate (male) metasoma, which in the original description was said to be “affecting the shape of [the bee genus] *Osiris*” (Schrottky 1910). The Latin adjectival suffix ‘-formis’ means ‘having the form of’.

## Material examined

### Primary type material

BRAZIL • ♀, holotype of *E. paraensis*; Amapá (previously Pará), Macapá; 28 May 1900; Ducke leg.; ZMB 4070a7.

PARAGUAY • ♂, lectotype of *E. osiriformis*; Alto Paraná, Puerto Bertoni; 22 Apr. 1909; MZUSP 102.272 • ♀, *E. luteipes* lectotype; Guairá, Villarrica; 1900; Burgdorf leg.; ZMB 235ffd.

### Secondary type material

BRAZIL • 1 ♀, paralectotype of *E. luteipes*; São Paulo, Jundiaí; 1899; Schrottky leg.; ZMB • 1 ♂, paralectotype of *E. luteipes*; Amapá, Macapá; 19 May 1900; Ducke leg.; ZMB.

COSTA RICA • 1 ♂, paralectotype of *E. luteipes*; San José; Schmidt leg.; ZMB (likely a mislabeled specimen as in the case of the type material of Friese's *Anthidium albitarse* and *Melipona torrida*; see respectively González & Griswold 2011 and Melo 2013).

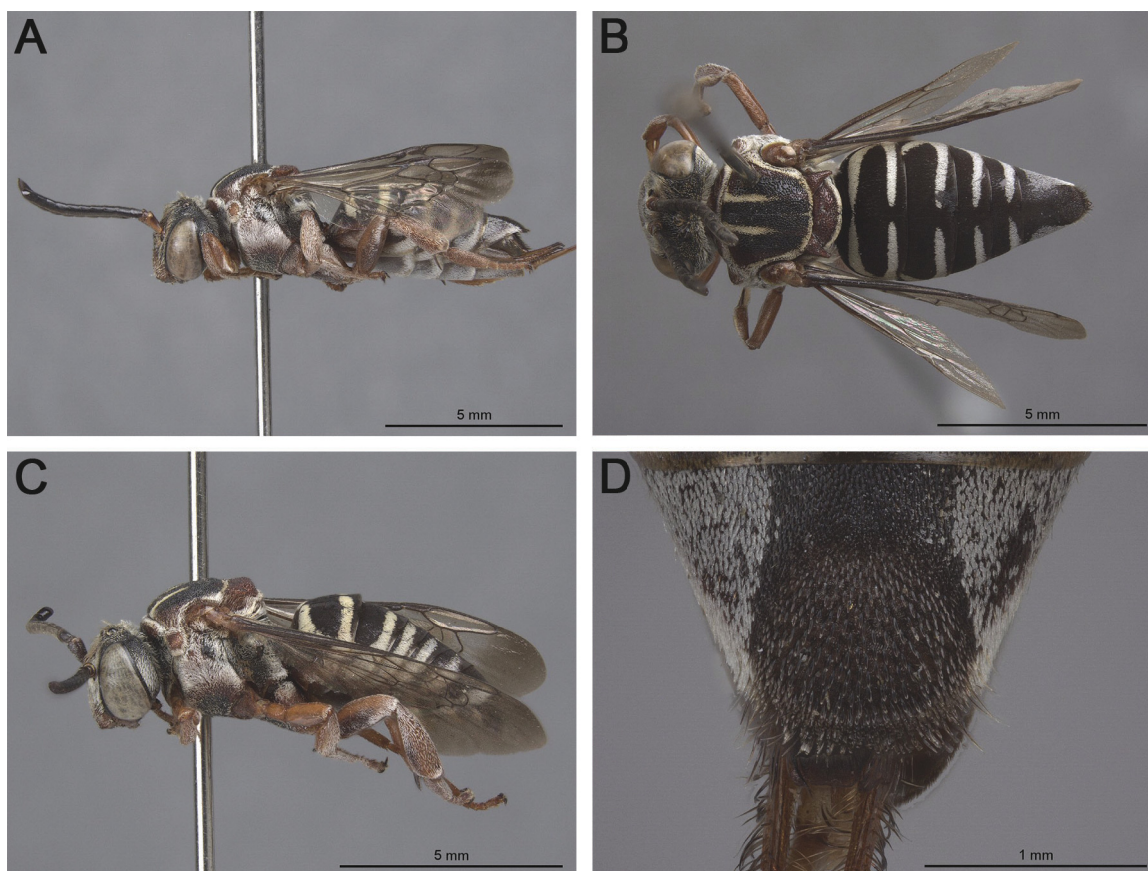
### Non-type material

ARGENTINA • 2 ♀♀, 1 ♂; Autonomous City of Buenos Aires, Reserva Ecológica Costanera Sur; 23 Jan. 2017; L. Compagnucci leg.; MACN • 1 ♀; Buenos Aires, Otamendi; Feb. 1993; P. Hazeldine leg.; MACN • 1 ♀; Buenos Aires, Punta Chica; May 1951; J. Foerster leg.; KUNHM M.G.R. Database No. 3873 • 1 ♀, 1 ♂; Buenos Aires, Refugio Ribera Norte (San Isidro); 21 Jan. 2005; A. Roig leg.; MACN • 1 ♂; Chaco, San Bernardo; Di Iorio leg.; MACN • 1 ♂; Córdoba, Dolores; 20–30 Nov. 1997; C. Porter leg.; FSCA • 2 ♀♀; Córdoba, Córdoba; E. Giacomelli leg.; MACN • 1 ♂; Córdoba, Dolores (ca. La Cumbre); 14 Mar.–7 Apr. 1996; C. Porter leg.; FSCA • 1 ♂; Córdoba, La Cumbre; 26 Feb. 1966; Willink and Stange leg.; IFML • 1 ♀; Córdoba, La Puerta; 4 Mar. 1971; M.A. Fritz leg.; DZUP • 1 ♀, 1 ♂; Entre Ríos, Colón; Zelich leg.; MACN • 2 ♂♂; Entre Ríos, Liebig; Apr. 1974; Zelich leg.; MACN • 1 ♀; La Pampa, Santa Rosa; 19 Mar. 2005; J.J. Martínez leg.; MACN • 1 ♂; La Rioja, Iliar; Feb. 1934; M. Gómez leg.; KUNHM M.G.R. Database No. 3885 • 1 ♂; La Rioja, Malanzán; Feb. 1923; M. Gómez leg.; MACN • 1 ♂; La Rioja, Villa Unión; 12 Dec. 1971; Porter and Stange leg.; IFML • 2 ♀♀; Río Negro, Luis Beltrán; Jan. 1988; U. Fritz leg.; MACN • 1 ♂; Salta, 40 km WNW of Hickmann; 12–14 Nov. 1989; J.G. Rozen and A. Roig leg.; AMNH M.G.R. Database No. 1329 • 1 ♂; Salta, Coronel Moldes; Dec. 1994; M. Fritz leg.; MACN • 1 ♂; Salta, El Alisal; Apr. 1994; M. Fritz leg.; MACN • 1 ♂; Salta, La Viña; Feb. 1995; M. Fritz leg.; MACN • 1 ♀; Salta, Pichanal; Dec. 1978; M. Fritz leg.; MACN • 1 ♀; Salta, Pocitos; Oct. 1949; A.F. Prosen leg.; KUNHM M.G.R. Database No. 3878 • 1 ♀; same collection data as for preceding; Nov. 1950; F.H. Walz leg.; KUNHM M.G.R. Database No. 3844 • 2 ♀♀; same collection data as for preceding; Dec. 1971; M.A. Fritz leg.; DZUP • 1 ♀; Salta, Reserva Campo Alegre; 5 Apr. 1921; G. Ellenrieder leg.; MACN • 1 ♂; Salta, Río Pescado; 10 May 1979; Terán and Willink leg.; IFML • 1 ♂; Salta, Rosario de Lerma; Nov. 1992; M. Fritz leg.; MACN • 1 ♀; Salta, Sumalao; Dec. 1990; M. Fritz leg.; MACN • 1 ♂; San Juan, Desamparados; 27 Dec. 1922; M. Gómez leg.; MACN • 1 ♂; San Juan, La Rinconada, Pocito; 31 Jan. 1937; DZUP • 1 ♂; San Juan, San Juan; Jan. 1946; DZUP • 1 ♀; Santa Fe, Santa Fe; 27 Feb. 1930; Bridarolli leg.; MACN • 3 ♂♂; Santa Fe, Tostado Ferrocarril Central Norte, El Orden; A.J. Giai leg.; KUNHM M.G.R. Database Nos. 3886, 3887, 3892 • 1 ♀; Santiago del Estero, Desvío 511, Matara; 24 Oct. 1928; M. Gómez leg.; MACN • 1 ♂; Tucumán, Horco Molle; 5 Jan. 1966; L. Stange leg.; IFML • 1 ♀; Tucumán, San Pedro de Colalao, Departamento Trancas; Feb. 1951; KUNHM M.G.R. Database No. 5090 • 1 ♂; same collection data as for preceding; Feb. 1951; KUNHM M.G.R. Database No. 3884 • 1 ♂; Tucumán, Tafi del Valle; Dec. 1945; K.J. Hayward leg.; IFML • 1 ♂; Tucumán, Trancas; 1 Feb. 1953; Arnau leg.; IFML • 1 ♀; Tucumán, Tucumán; M. Arnau leg.; KUNHM M.G.R. Database No. 3888 • 1 ♂; same collection data as for preceding; M. Arnau leg.; KUNHM M.G.R. Database No. 3882.



BOLIVIA • 1 ♀; Santa Cruz, Cordillera Aimirí; Feb. 1971; Fritz leg.; DZUP.

BRAZIL • 1 ♂; Amapá, Macapá; 19 May 1900; Ducke leg.; DZUP • 1 ♂; same collection data as for preceding; 22 May 1900; Ducke leg.; DZUP • 1 ♀; Bahia, Camacan; 25 Feb. 2003; A. Raw leg.; DZUP • 1 ♂; same collection data as for preceding; 21 Feb. 2004; A. Raw leg.; DZUP • 7 ♀♀, 2 ♂♂; Bahia, Ilhéus; 16 Jul. 1965; S. Laroca leg.; DZUP • 1 ♀; Bahia, Jequié; 10 Aug. 1964; C. Elias leg.; DZUP • 2 ♀♀; Bahia, Maracás; Jun. 1961; F.M. Oliveira leg.; DZUP • 47 ♀♀; same collection data as for preceding; Feb. 1963; F.M. Oliveira leg.; DZUP • 1 ♀, 7 ♂♂; same collection data as for preceding; 19 Nov. 1965; F.M. Oliveira leg.; DZUP • 1 ♀; Bahia, Vitória da Conquista; 10–20 Jun. 1961; F.M. Oliveira leg.; DZUP • 1 ♂; Espírito Santo, Cariacica; 10–15 Apr. 1967; C. Elias leg.; DZUP • 1 ♂; Espírito Santo, Fundão; 20 Jan. 1966; C. Elias leg.; DZUP • 1 ♀; Espírito Santo, Santa Maria de Jetibá; 11 Mar. 1966; C. Elias leg.; DZUP • 1 ♀; same collection data as for preceding; 21 Jan. 1967; C. Elias leg.; DZUP • 1 ♂; Espírito Santo, Santa Teresa; 6 Jul. 1964; C. Elias leg.; DZUP • 2 ♂♂; same collection data as for preceding; 27 Jan. 1966; C. Elias leg.; DZUP • 2 ♂♂; same collection data as for preceding; 4 Feb. 1966; C. Elias leg.; DZUP • 1 ♂; same collection data as for preceding; 12 May 1966; C. Elias leg.; DZUP • 1 ♂; same collection data as for preceding; 19 May 1966; C. Elias leg.; DZUP • 1 ♀; same collection data as for preceding; 28 Jan. 1967; C. Elias leg.; DZUP • 1 ♀; same collection data as for preceding; 18 Jun. 1967; C. Elias leg.; DZUP • 1 ♀, 1 ♂; Espírito Santo, Santo Antônio; 22 Apr. 1966; C. Elias leg.; DZUP • 2 ♀♀; Espírito Santo, São Domingos; 27 Mar. 1966; C. Elias leg.; DZUP • 3 ♂♂; Espírito



**Fig. 12.** *Triepeolus osiriformis* (Schrottky, 1910). **A, D.** Female (AMNH M.G.R. Database No. 3709). **A.** Habitus, lateral view. **B.** Female (AMNH M.G.R. Database No. 3121), habitus, dorsal view. **C.** Male (AMNH M.G.R. Database No. 1329), habitus, lateral view. **D.** Pseudopygidial area, dorsal view.

Santo, São Roque; 5 May 1966; C. Elias leg.; DZUP • 3 ♀♀; Maranhão, Imperatriz; 20 Feb. 1962; F.M. Oliveira leg.; DZUP • 1 ♂; Mato Grosso, Cáceres; 19 Mar. 1985; C. Elias leg.; DZUP • 1 ♀, 1 ♂; same collection data as for preceding; 4 Apr. 1985; C. Elias leg.; DZUP • 1 ♀; Minas Gerais, Araxá 5–11 Feb. 1965; C. Elias leg.; DZUP • 1 ♂; Minas Gerais, Ibiraci; 15 Oct. 1962; C. Elias leg.; DZUP • 1 ♂; Minas Gerais, Passos; 24 Oct. 1963; C. Elias leg.; DZUP • 5 ♀♀; Minas Gerais, Poços de Caldas; Nov. 1961; C. Elias leg.; DZUP • 2 ♂♂; Paraíba, Santa Luzia; 26 Mar. 1956; A.G.A. Silva leg.; DZUP • 1 ♀; Paraná, Antonina; 25.3200° S, 48.6500° W; 9 Dec. 2006; C. Maia leg.; DZUP DZUP 160965 • 3 ♀♀; Paraná, Cerro Azul; 24.9175° S, 49.2719° W; 14 Dec. 2002; G.A.R. Melo leg.; DZUP • 1 ♀; Paraná, Curitiba; Feb. 1949; P.J. Moure leg.; USNM • 1 ♀; same collection data as for preceding; Dec. 1951; J.S. Moure leg.; DZUP • 1 ♂; Paraná, Maringá; 7 Dec. 1965; V. Graf and L. Azevedo leg.; DZUP • 1 ♂; Paraná, Ponta Grossa; Mar. 1965; Moure, Mitchell, and Laroca leg.; DZUP • 1 ♀; Paraná, Rolândia; Apr. 1950; DZUP • 2 ♀♀; Paraná, Tunas do Paraná; 25.0333° S, 49.0833° W; 16 Jan. 2008; G. Weiss and C.M. Maia leg.; DZUP DZUP 168755, DZUP 168796 • 1 ♀; Rio de Janeiro, Angra dos Reis; Feb. 1944; Wygodzinsky leg.; DZUP • 1 ♂; Rio de Janeiro, Itatiaia; 20 Oct. 1942; I. Burchad leg.; DZUP • 1 ♀, 1 ♂; same collection data as for preceding; Apr. 1961; F.M. Oliveira leg.; DZUP • 1 ♂; Rio Grande do Sul, Pelotas; Biezanko leg.; DZUP • 1 ♀; Santa Catarina, Corupá; Feb. 1956; A. Maller leg.; DZUP • 1 ♂; Santa Catarina, Corupá (previously Hansa Humboldt); Jan. 1945; A. Maller leg.; KUNHM M.G.R. Database No. 3875 • 2 ♂♂; Santa Catarina, Nova Teutônia; 11 Nov. 1939; F. Plaumann leg.; AMNH M.G.R. Database Nos. 2350, 2352 • 7 ♂♂; same collection data as for preceding; 13 Nov. 1939; F. Plaumann leg.; AMNH M.G.R. Database Nos. 2343, 2344, 2345, 2346, 2347, 2349, 2351 • 1 ♂; same collection data as for preceding; 21 Nov. 1939; F. Plaumann leg.; AMNH M.G.R. Database No. 2348 • 2 ♂♂; same collection data as for preceding; Jan.–Mar. 1949; F. Plaumann leg.; DZUP • 1 ♂; same collection data as for preceding; Jan.–Mar. 1949; F. Plaumann leg.; KUNHM M.G.R. Database No. 3843 • 1 ♀; same collection data as for preceding; 25 Mar. 1951; F. Plaumann leg.; DZUP • 1 ♂; same collection data as for preceding; Oct. 1951; F. Plaumann leg.; DZUP • 2 ♂♂; same collection data as for preceding; Oct. 1951; L.E. Plaumann leg.; KUNHM M.G.R. Database Nos. 3866, 3869 • 1 ♀; same collection data as for preceding; Nov. 1951; F. Plaumann leg.; DZUP • 1 ♀; same collection data as for preceding; Nov. 1951; L.E. Plaumann leg.; DZUP • 6 ♀♀; same collection data as for preceding; Nov. 1951; L.E. Plaumann leg.; KUNHM M.G.R. Database Nos. 3857, 3858, 3863, 3874, 3890, 5582 • 25 ♂♂; same collection data as for preceding; Nov. 1951; L.E. Plaumann leg.; KUNHM M.G.R. Database Nos. 3845, 3846, 3847, 3848, 3849, 3850, 3851, 3852, 3853, 3854, 3855, 3856, 3859, 3860, 3861, 3862, 3864, 3865, 3867, 3870, 3871, 3872, 3879, 3880, 3891 • 1 ♀; same collection data as for preceding; 15 Feb. 1952; F. Plaumann leg.; KUNHM M.G.R. Database No. 3889 • 3 ♂♂; same collection data as for preceding; Nov. 1952; F. Plaumann leg.; KUNHM M.G.R. Database Nos. 3876, 3877, 5583 • 1 ♂; same collection data as for preceding; Dec. 1952; F. Plaumann leg.; KUNHM M.G.R. Database No. 3881 • 1 ♀; same collection data as for preceding; 5 Nov. 1954; F. Plaumann leg.; USNM M.G.R. Database No. 5852 • 1 ♂; same collection data as for preceding; 30 Mar. 195?; F. Plaumann leg.; KUNHM M.G.R. Database No. 3868 • 1 ♀; São Paulo, Barueri; Mar. 1957; K. Lenko leg.; DZUP • 1 ♂; São Paulo, Guataparã; Jan. 1943; M. Carrera leg.; DZUP • 2 ♂♂; São Paulo, Rio Claro; Nov. 1943; P. Flamenghi leg.; DZUP • 2 ♀♀; São Paulo, São José do Barreiro (Parque Nacional da Serra da Bocaina); Nov. 1968; M. Alvarenga leg.; AMNH M.G.R. Database Nos. 3122, 3709.

COLOMBIA • 1 ♂; Valle del Cauca, Cali; 20 Nov. 1935; H.F. Schwarz leg.; AMNH AMNH\_IZC 00292363/M.G.R. Database No. 3123 • 1 ♀; Valle del Cauca, Finca San Luis, Candelaria; 21–23 Apr. 1975; R.C. Wilkerson leg.; FSCA.

PARAGUAY • 1 ♀; Alto Paraguay, Cerro León; Oct. 1979; M. Fritz leg.; MACN • 1 ♂; Alto Paraná, Puerto Bertoni; 6 Nov. 1919; USNM M.G.R. Database No. 5853 • 1 ♀; Central, San Lorenzo; 29 Nov. 1949; KUNHM M.G.R. Database No. 3842 • 1 ♀; Distrito Capital, Asunción (Jardín Botánico); 1 Jan. 1990; M. Cooper leg.; NHMUK NHMUK013620572.

PERU • 2 ♀♀; Apurímac, 40 mi E of Abancay; 5 Mar. 1951; Ross and Michelbacher leg.; CAS.

TRINIDAD AND TOBAGO • 1 ♀; Diego Martin, Petit Valley (Trinidad); 23 Dec. 1974; T.E. Rogers leg.; FSCA • 1 ♀; Tunapuna–Piarco, Curepe (Trinidad); 22 Jul. 1964; F.D. Bennett leg.; AMNH AMNH\_IZC 00292362/M.G.R. Database No. 3121 • 1 ♂; same collection data as for preceding; 23. Dec. 1968; F.D. Bennett leg.; AMNH AMNH\_IZC 00292361/M.G.R. Database No. 3124 • 1 ♀; Tunapuna–Piarco, Saint Augustine (Trinidad); 17 Jan. 1941; D.J. Billes leg.; USNM.

VENEZUELA • 1 ♀; Guárico, Hato Masaguaral (44 km S of Calabozo); 20–28 May 1985; Menke and Carpenter leg.; USNM.

### Non-preserved material

ARGENTINA • 1 ♀; Autonomous City of Buenos Aires; 34.5981° S, 58.3618° W; 28 Mar. 2019; C. Chase obs.; iNaturalist record #24679119 • 1 unsexed specimen; same collection data as for preceding; 28 Mar. 2019; C. Chase obs.; iNaturalist record #24679123 • 1 ♂; Autonomous City of Buenos Aires, Jardín Botánico Carlos Thays (Palermo); 34.5834° S, 58.4170° W; 27 Feb. 2020; R.A. González Vaquero obs.; iNaturalist record #56507520 • 1 ♂; Autonomous City of Buenos Aires, Jardín Botánico Carlos Thays (Palermo); 34.5835° S, 58.4171° W; 13 Mar. 2020; R.A. González Vaquero obs.; iNaturalist record #56471474 • 1 ♀; Autonomous City of Buenos Aires, Puerto Madero; 3 Feb. 2023; G.F. Durán obs.; iNaturalist record #148424314 • 1 ♀; Buenos Aires, Camino de la Ribera Norte 480, B1641 Acassuso; 34.4700° S, 58.4962° W; 2 Feb. 2019; “RAP” obs.; iNaturalist record #20342311 • 1 ♂; Buenos Aires, Punta Alta; 38.8896° S, 62.0723° W; 11 Mar. 2021; “lor-en-zoo” obs.; iNaturalist record #71163087 • 1 ♂; Buenos Aires, Ramallo; 33.4740° S, 60.0008° W; 21 Mar. 2021; A. Rotondo obs.; iNaturalist record #71791624 • 1 ♀; Córdoba, Alta Córdoba; 31.3981° S, 64.1890° W; 17 Mar. 2023; A.A. Cocucci obs.; iNaturalist record #151426876 • 1 ♀; Córdoba, Córdoba; 31.4342° S, 64.1913° W; 4 Mar. 2021; A.A. Cocucci obs.; iNaturalist record #70571934 • 1 ♀; Entre Ríos, Gualeguaychú; 32.9473° S, 58.3494° W; 24 Mar. 2018; “mendezcla7” obs.; iNaturalist record #23023156 • 1 ♀; Santa Fe, Las Colonias; 11 Mar. 2023; G. Fernando Durán obs.; iNaturalist record #151516122 • 1 ♂; Santa Fe, San Jerónimo Norte; 7 Nov. 2021; G. Fernando Durán obs.; iNaturalist record #100888380 • 1 ♀; same collection data as for preceding; 5 Feb. 2023; G. Fernando Durán obs.; iNaturalist record #149660519 • 1 ♂; same collection data as for preceding; 12 Mar. 2023; G. Fernando Durán obs.; iNaturalist record #152194347.

BRAZIL • 1 ♀; Rio Grande do Sul; 29.7248° S, 53.6609° W; 5 Mar. 2023; F.T. Sautter obs.; iNaturalist record #150339218.

PERU • 1 ♀; Ayacucho, C.h Jose Ortiz Vergara, Ayacucho; 13.1425° S, 74.2267° W; 3 Jan. 2022; J. Rodríguez Janampa obs.; iNaturalist record #104306493.

### Redescription

MEASUREMENTS OF LECTOTYPE. Body length 10.5 mm; ITW 1.9 mm; head length 2.1 mm; head width 2.9 mm; fore wing length 7.3 mm.

### Both sexes

INTEGUMENT COLORATION. Dark brown to black except as follows. Mandible with apical third golden yellow in some non-type specimens. Mandible with basal two-thirds, labrum partially to entirely, scape and usually also pedicel and F1 to some extent (pedicel and F1 entirely dark brown/black in lectotype of *E. osiriformis* and some non-type specimens), tegula, coxae partially to entirely, trochanters to tarsi (excluding brown meso- and metatibial spurs) entirely, metasomal terga laterally, and metasomal sterna to some extent orange. Clypeus partially to entirely, pronotal collar (except laterally), pronotal lobe, mesoscutum along margins (and narrowly behind paramedian band in lectotype of *E. osiriformis*,



lectotype of *E. luteipes*, and some non-type specimens), mesoscutellum, axilla, metanotum, mesopleuron extensively (more so in upper half than in ventrolateral half), and propodeum to some extent (in lectotype of *E. luteipes* and some non-type specimens) reddish brown. Fore wing membrane subhyaline, apically dusky. Hind wing membrane dusky subhyaline to hyaline.

**PUBESCENCE.** Face with tomentum densest around antennal socket. Tomentum slightly sparser on clypeus; upper paraocular and frontal areas and vertexal area mostly exposed. Pronotal collar with tomentum uniformly off-white. Mesoscutum with well-defined paramedian band of pale-yellow tomentum, tapering slightly toward and attaining anterior margin; pale tomentum otherwise mostly restricted to lateral and posterior margins. Mesopleuron with off-white, appressed, branched setae; densely setose except for two sparsely setose circular patches (one beneath base of fore wing (hypoepimeral area) and slightly larger one in ventrolateral half of mesopleuron). Metanotum with tomentum sparser medially, off-white laterally and reddish brown medially (uniformly off-white in holotype of *E. paraensis* and some non-type specimens). Propodeal triangle mostly glabrous, with (off-white to dark brown/gray) setae restricted to small lateral patches. Metasomal terga with bands of white to pale-yellow tomentum. T1 with basal transverse band complete or narrowly interrupted medially, apical transverse band narrowed or interrupted medially, transverse bands subparallel, discal patch transversely oblong. T2–T4 with medially interrupted apical transverse bands, that of T2 with pair of basomedially convergent anterolateral extensions. S2–S3 with apical transverse bands of white tomentum.

**SURFACE SCULPTURE.** Labrum and clypeus with punctures equally dense and nearly contiguous (most  $i < 1d$ ). Vertexal area somewhat sparsely punctate (some  $i > 2d$ ), especially around ocelli. Mesoscutum densely punctate (most  $i \leq 1d$ ) but interspaces well defined, shining. Mesoscutellum and axilla more sparsely punctate (most  $i \geq 1d$ ); interspaces shining. Mesopleuron with punctures in upper half denser (most  $i < 1d$ ) than in ventrolateral half ( $i \leq 2d$ ); interspaces shining; punctures similar in size throughout. Discs of metasomal terga with punctures very fine, dense ( $i \approx 1d$ ), and evenly distributed; interspaces shining somewhat.

**STRUCTURE.** Labrum with pair of small subapical denticles, each preceded by discrete longitudinal ridge. Pronotal collar short (medial length  $\sim \frac{1}{2}$  MOD). Mesoscutellum weakly bigibbous, with lower posterior margin forming shelf-like ridge overhanging metanotum. Axilla extending beyond midlength of mesoscutellum but not as far back as its posterior margin; tip distinctly pointed and hooked (i.e., concave along medial margin), mesally unattached to mesoscutellum for  $\sim \frac{1}{3}$ – $\frac{1}{2}$  medial length of axilla; lateral margin somewhat sinuate.

### Female

T5 with broadly convex apical margin and large patch of white to off-white tomentum on each side lateral to pseudopygidial area. Pseudopygidial area circular, with setae glossy, predominantly grayish brown, and sparser centrally; apical margin with row of dense, appressed and suberect coppery to silvery setae. Pygidial plate apically truncate. S4 with apical transverse band of white tomentum. S5 straight in lateral view, with apical fimbria of coppery bristle-like setae; S5 otherwise covered in off-white tomentum.

### Male

T5–T6 with medially interrupted apical transverse bands of off-white tomentum. T7, including much of pygidial plate, with long ( $\geq \frac{1}{2}$  MOD), dark brown/black appressed and suberect setae. Pygidial plate apically rounded and strongly downturned, with basal transverse ridge rather ill-defined and lateral margin somewhat sinuate. S4–S5 each with apical/subapical fringe of dense, long ( $> 1$  MOD), curved, coppery to silvery setae, not contrasting strongly with bands of preceding sterna.

## Distribution

*Triepeolus osiriformis* is the most widely distributed member of its genus in South America, ranging across much of the continent; not known to occur in the arid or temperate regions along the Pacific coast or in southern Patagonia (Fig. 1G).

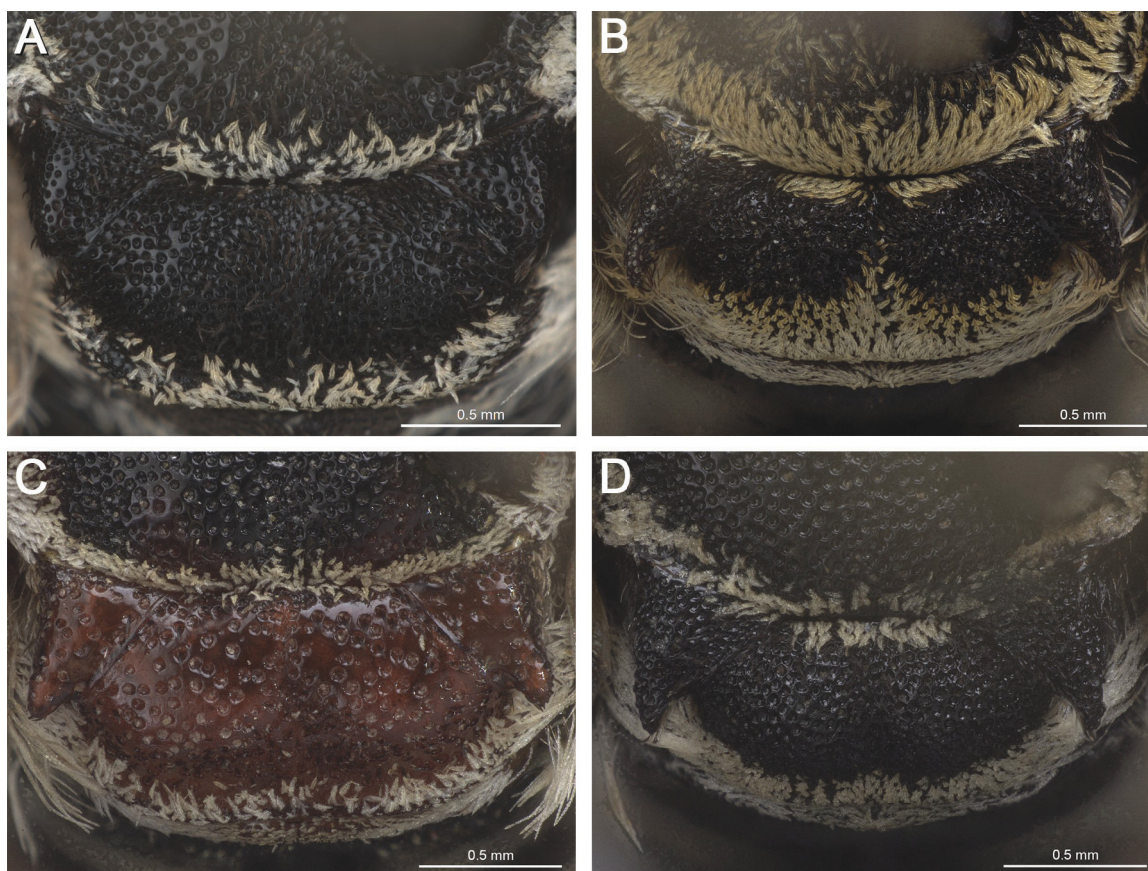
## Ecology

### Host records

Unknown.

### Floral records

Female and male type specimens of *E. osiriformis* were collected from the flowers of *Vernonia* Schreb. (Asteraceae) (Schrottky 1910). Additionally, this species has been collected from the flowers of *Acmella decumbens* (Sm.) R.K.Jansen (Asteraceae), *Verbena gracilescens*, and *V. intermedia* (R.A. González-Vaquero, personal communication, 2022). Images on iNaturalist show this species visiting *Ageratum conyzoides* (L.) L. (Asteraceae), *Aloysia gratissima*, *Baccharis* L. (Asteraceae), *Cirsium* Mill. (Asteraceae), *Coreopsis lanceolata* L. (Asteraceae), *Helianthus* L. (Asteraceae), *Pascalina glauca* Ortega (Asteraceae), and *Solidago chilensis* Meyen (Asteraceae). Labels of examined voucher specimens further indicate that this species has been collected from *Cuphea racemosa* (L.f.) Spreng. (Lythraceae) and *Wedelia triloba* (L.) Hitchc. (Asteraceae).



**Fig. 13.** Axillae and mesoscutellum of male, dorsal view. **A.** *Triepeolus flavipennis* (Friese, 1916) (PCYU). **B.** *T. nemoralis* (Holmberg, 1886) (CNC 1801912). **C.** *T. osiriformis* (Schrottky, 1910) (AMNH M.G.R. Database No. 1329). **D.** *T. tuberculifer* Onuferko, Rightmyer & Roig-Alsina sp. nov., allotype (FSCA M.G.R. Database No. 3704).

## Remarks

This species was previously known by the name *T. nobilis* (Friese, 1908). However, Rightmyer (2008) recognized the primary type of *Epeolus nobilis* (original combination) as conspecific with that of *T. intrepidus* (Smith, 1879), a species from Mexico and the southwestern United States, and established the former as a junior synonym of the latter. Although Friese (1908) described *E. nobilis* in a paper on bees of Argentina, *T. intrepidus* is not known to occur anywhere in South America. According to Friese (1908), the types of *E. nobilis* came from an old collection of Hermann Burmeister in Argentina. The (male) lectotype of *E. nobilis* and a conspecific female at the ZMB each bear a label that says ‘Argentini 1900’, but this information does not conform with the expected collection locality or date. Most likely, the specimens were erroneously presumed to have originated in Argentina having been sent to Germany from the Burmeister collection at the MACN in Buenos Aires, where there are still two specimens of *T. intrepidus* (one female and one male) that might belong to the same series. Interestingly, whereas the female lacks a collection label, the male bears a small, green, poorly handwritten label indicating the word Mexico. The lectotype of *E. nobilis* has a separate label indicating only the letter M, which appears to be original and likely stands for Mexico. As Burmeister died in 1892, the specimens could not have been collected by him in 1900, which may instead indicate the year the specimens were received by Friese. Presumably, Moure (1955) confused *T. nobilis* with *T. osiriformis* based on Friese’s (1908) description of the former having a red mesoscutellum and there being only one species of *Triepeolus* in South America in which the mesoscutellum is red.

*Epeolus osiriformis* Schrottky, 1910 was described from both sexes. The MZUSP has a male labeled as the type and referred to as such by Moure (1955). Rightmyer (2008) referred to this specimen as the holotype; however, since Schrottky (1910) did not explicitly designate a holotype, the specimen is herein designated as the lectotype of *E. osiriformis*.

Moure (1955) regarded *Epeolus luteipes* Friese, 1916 and *E. paraensis* Friese, 1925 as synonymous with *E.* (now *T.*) *osiriformis*. The authors of the present study examined the primary types of *E. osiriformis*, *E. luteipes*, and *E. paraensis* and agree with Moure’s treatment. *Epeolus luteipes* was described from both sexes. A female syntype at the ZMB, which bears an orange label that says “Typus”, is herein designated as the lectotype of *E. luteipes*.

## *Triepeolus rufotegularis* (Ashmead, 1900)

Figs 1H, 4D, 14

*Epeolus rufotegularis* Ashmead, 1900: 211 (♀), lectotype presently designated.

*Triepeolus rufotegularis* – Cockerell 1938: 280.

## Diagnosis

The following morphological features in combination tell *T. rufotegularis* apart from all other South American *Triepeolus*: the T1 discal patch is reniform, T1–T4 (in females) or T1–T6 (in males) have medially interrupted bands of white to off-white tomentum, and the T2 apical transverse bands do not have lobe-like anterolateral extensions (Fig. 14A–C). In terms of the patterns of pubescence on the mesosoma and metasoma, *T. rufotegularis* most closely resembles *T. verbessinae*, a North American species, but in *T. verbessinae* the T1 discal patch is triangular with concave sides, the metasomal tergal bands are pale yellow, the T2 apical transverse bands have lobe-like anterolateral extensions, and the female S5 is strongly (as opposed to slightly) downturned apically. Males of *T. rufotegularis* are also similar to those of *T. tuberculifer* sp. nov., but in *T. tuberculifer* sp. nov. the pro- and mesotrochanters are distinctly (as opposed to non-) tuberculate, the free portion of each axilla is more (as opposed to less)



than  $\frac{1}{3}$  as long as its entire medial length, and the T1 basal and apical transverse bands are subparallel, such that the discal patch is transversely oblong.

### Etymology

Although Ashmead (1900) did not explain the etymology of his *Epeolus rufotegularis*, the specific epithet was presumably inspired by its orange tegulae, which do not reliably distinguish this species from similar-looking congeners.

### Material examined

#### Primary type material

GRENADA • ♀, lectotype; Saint George, St. George's (Leeward side); H.H. Smith leg.; USNM 534865.

#### Secondary type material

SAINT VINCENT AND THE GRENADINES • 1 ♀ [sic, actually ♂], paralectotype (studied from images); Grenadines Parish, Canouan Island; H.H. Smith leg.; NHMUK NHMUK014022734.

#### Non-type material

COLOMBIA • 1 ♀; Cesar, Valledupar; 21–24 May 1963; B. Malkin leg.; AMNH • 1 ♀; Magdalena, 7 km E of Santa Marta; 30 Nov. 1974; M. Cooper leg.; KUNHM (Donald & Madge Baker Collection) M.G.R. Database No. 3705.

GRENADA • 2 ♀♀; Saint George, Grand Anse; 14 Jun. 1977; L. Kimo Tanaka leg.; CAS.

SAINT VINCENT AND THE GRENADINES • 1 ♀; Saint Vincent; “5.4.38”; USNM M.G.R. Database No. 1332 • 1 ♂; same collection data as for preceding; 4 May 1938; J. O. leg.; UCMC M.G.R. Database No. 1514 • 1 ♂; Saint Andrew Parish, Campden Park (Saint Vincent); 13.1651° N, 61.2438° W; 10 May 2017; R.R. Ferrari leg.; PCYU CCDB-34570 B08.

VENEZUELA • 1 ♂; Aragua, 2 km N of Ocumare de la Costa; 12 Jun. 1976; Menke and Carpenter leg.; USNM • 1 ♀; Guárico, Hato Masaguaral (44 km S of Calabozo); 11–19 May 1985; Menke and Carpenter leg.; USNM M.G.R. Database No. 6451 • 5 ♀♀; same collection data as for preceding; 20–28 May 1985; A.S. Menke and D. Vincent leg.; USNM • 1 ♀; Zulia, 14 km W of Campo Mara; 18 Jun. 1976; A.S. Menke and D. Vincent leg.; USNM • 1 ♀; Zulia, 6 km W of La Concepción; 18 Jun. 1976; A.S. Menke and D. Vincent leg.; USNM.

### Redescription

MEASUREMENTS OF LECTOTYPE. Body length 8.8 mm; ITW 1.9 mm; head length 2.3 mm; head width 3.2 mm; fore wing length 7.5 mm.

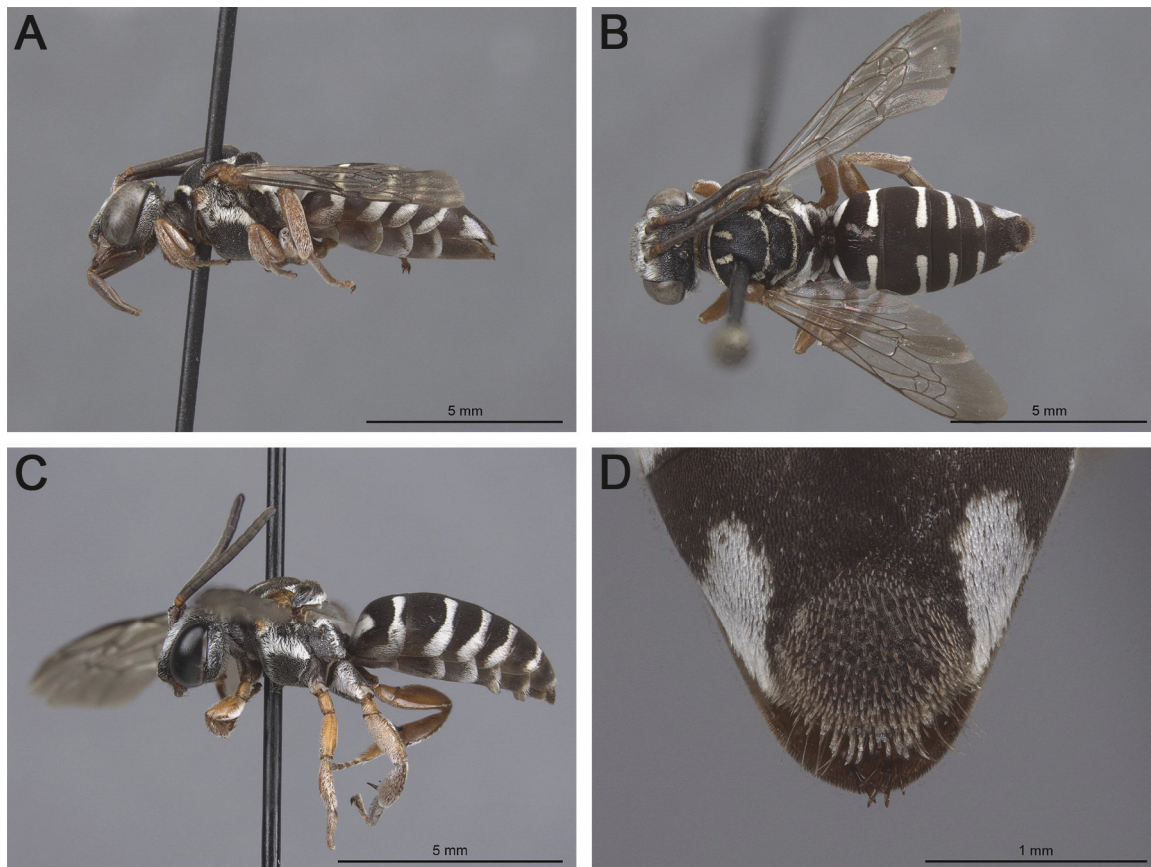
#### Both sexes

INTEGUMENT COLORATION. Dark brown to black except as follows. Mandible with apical third golden yellow. Mandible with basal two-thirds, scape, pedicel, F1, pronotal lobe, tegula, coxae to some extent, trochanters to tarsi (excluding brown meso- and metatibial spurs) entirely, metasomal terga laterally, and metasomal sterna to some extent orange. F2 with orange spot basally. Fore wing membrane subhyaline, apically dusky. Hind wing membrane dusky subhyaline to hyaline.

PUBESCENCE. Face with tomentum densest around antennal socket. Tomentum slightly sparser on clypeus; upper paraocular and frontal areas and vertexal area mostly exposed. Pronotal collar with tomentum off-white to pale yellow. Mesoscutum with well-defined paramedian band of pale-yellow tomentum (tapering toward and barely attaining anterior margin in lectotype; not attaining anterior

margin in paralectotype and some non-type specimens); pale tomentum otherwise mostly restricted to posterior margin. Mesopleuron with black, appressed, branched setae just anterior to hypoepimeral area and off-white, appressed, branched setae elsewhere; upper half densely setose, except behind pronotal lobe, with setae slightly sparser on hypoepimeral area; ventrolateral half sparsely setose. Metanotum with tomentum uninterrupted, uniformly dark brown/gray (with varying amount of off-white tomentum in non-type specimens). Propodeal triangle mostly glabrous, with (dark brown/gray) setae restricted to small lateral patches. Metasomal terga with bands of white to off-white tomentum. T1 with basal transverse band widely separated medially into pair of anterolateral patches (narrowly interrupted medially in non-type specimen), each convex along medial margin and separated from apical transverse band (joined to apical transverse band by lateral longitudinal band in some non-type specimens); apical transverse band separated into pair of rounded lobes medially; discal patch reniform. T2–T4 with medially widely interrupted apical transverse bands without anterolateral extensions. S2–S3 with apical transverse bands of white tomentum.

**SURFACE SCULPTURE.** Labrum and clypeus with punctures equally dense (most  $i < 1d$ ); interspaces well defined, shining. Vertexal area somewhat sparsely punctate (some  $i > 2d$ ), especially around ocelli. Mesoscutum, mesoscutellum, and axilla with punctures more or less equally dense ( $i \leq 1d$ ); interspaces well defined, shining. Mesopleuron with punctures in upper half not much denser (most  $i < 1d$ ) than in ventrolateral half (most  $i \leq 1d$ ); interspaces shining; punctures similar in size throughout. Discs of



**Fig. 14.** *Triepeolus rufotegularis* (Ashmead, 1900). **A–B, D.** Female (USNM M.G.R. Database No. 1332). **A.** Habitus, lateral view. **B.** Habitus, dorsal view. **C.** Male (PCYU CCDB-34570 B08), habitus, lateral view. **D.** Pseudopygidial area, dorsal view.

metasomal terga with punctures very fine, dense ( $i \approx 1d$ ), and evenly distributed; interspaces shining somewhat.

STRUCTURE. Labrum with pair of small subapical denticles, each preceded by discrete longitudinal ridge. Pronotal collar rather short (medial length  $\sim \frac{3}{5}$  MOD). Mesoscutellum weakly bigibbous. Axilla not extending beyond midlength of mesoscutellum; tip visible but somewhat blunt, mesally unattached to mesoscutellum for less than  $\frac{1}{3}$  medial length of axilla; lateral margin relatively straight.

### Female

T5 with broadly convex apical margin and large patch of white to off-white tomentum on each side lateral to pseudopygidial area. Pseudopygidial area circular, with setae glossy, predominantly grayish brown, and sparser centrally; apical margin with row of dense, appressed and suberect coppery to silvery setae. Pygidial plate orange in part and apically truncate (T6 entirely retracted in lectotype; described from non-type specimen). S4 with apical transverse band of white tomentum. S5 slightly downturned apically, with apical fimbria of coppery bristle-like setae; S5 otherwise covered in brown tomentum.

### Male

T5–T6 with medially interrupted apical transverse bands of off-white tomentum. Pygidial plate reddish brown and apically rounded and slightly downturned, with basal transverse ridge rather ill-defined and lateral margin sinuate. S4–S5 each with apical/subapical fringe of dense, long ( $> 1$  MOD), curved setae; coppery to silvery laterally (more so on S4 than S5), brown and contrasting strongly with bands of preceding sterna medially.

### Distribution

Northern South America to Saint Vincent in the Lesser Antilles (Fig. 1H).

### Ecology

#### Host records

Unknown.

#### Floral records

Unknown.

### Remarks

Although Ashmead (1900) described only the female of this species, a syntype of *E. rufotegularis* at the NHMUK, which bears a circular label that says “Type”, was incorrectly sexed and is a male. The description of the male of *T. rufotegularis* is published here for the first time. Since Ashmead (1900) did not explicitly designate a holotype among the eight specimens comprising the type series, a female syntype at the USNM, which bears a red label that says “Type”, is herein designated as the lectotype of *E. rufotegularis*.

*Triepeolus tuberculifer* Onuferko, Rightmyer & Roig-Alsina sp. nov.  
urn:lsid:zoobank.org:act:1504F420-5757-4BA3-B68A-89EF4254722A

Figs 1I, 13D, 15B, 16

*Triepeolus* n. sp. 2 – Rightmyer 2008: 30 (in key).



## Diagnosis

*Triepeolus tuberculifer* sp. nov. can be told apart from all other South American *Triepeolus* by the distinctly tuberculate pro- and mesotrochanters (Fig. 15B). Otherwise, the following morphological features in combination tell *T. tuberculifer* sp. nov. apart from all other South American *Triepeolus*: the axillae and mesoscutellum are black and densely punctate (most  $i < 1d$ ) (Fig. 13D) and the T1 basal and apical transverse bands are subparallel, such that the discal patch is transversely oblong (Fig. 16B). *Triepeolus tuberculifer* sp. nov. is the only species in the *T. simplex* species group—containing species in which the pseudopygidial area of the female is triangular, with the apical margin of T5 concave (Fig. 16D)—with medially interrupted apical transverse bands on T2–T4 (Fig. 16B). Males of *T. tuberculifer* sp. nov. most closely resemble those of *T. osiriformis* and *T. rufotegularis*, but in the latter two species the trochanters are not at all tuberculate, in *T. osiriformis* the axillae and mesoscutellum are reddish brown (as are much of the head, rest of the mesosoma, and metasoma) and sparsely punctate (most  $i \geq 1d$ ), and in *T. rufotegularis* the free portion of each axilla is less (as opposed to more) than  $\frac{1}{2}$  as long as its entire medial length and the T1 discal patch is reniform.

## Etymology

The specific epithet refers to the conspicuous tubercles on the pro- and mesotrochanters. The Latin adjectival suffix ‘-fer’ means ‘that which carries’.

## Material examined

### Primary type material

COLOMBIA • ♀; holotype; Bolívar, Monterrey Forestal, Zambrano; 17 Nov. 1993; G. Ulloa and F. Fernández leg.; ICN HY-1056.

### Secondary type material

COLOMBIA • 2 ♂♂, paratypes (studied from images); Casanare, Parque Ecotemático Wisirare, Orocué; 4.8887° N, 71.4381° W; 9 Nov. 2010; ICN 101499, 101500 • 1 ♀, paratype; Meta, Puerto Gaitán; 21 Mar. 1993; G. Ulloa and F. Fernández leg.; MACN.

VENEZUELA • 1 ♂, allotype; Lara, 18 km SW of Carora; 11 Jul. 1988; C. Porter and L. Stange leg.; FSCA M.G.R. Database No. 3704.

## Description

MEASUREMENTS OF HOLOTYPE. Body length 9.7 mm; ITW 2.0 mm; head length 2.3 mm; head width 3.2 mm; fore wing length 7.6 mm.

### Both sexes

INTEGUMENT COLORATION. Dark brown to black except as follows. Mandible with middle third, labrum with apical two-fifths (apical half in female paratype), scape and pedicel to some extent, F1 extensively, tegula, anterior metasomal terga and sterna laterally, and pygidial plate reddish brown. Fore wing membrane subhyaline, apically dusky. Hind wing membrane dusky subhyaline to hyaline. Coxae to some extent and trochanters to tarsi entirely orange.

PUBESCENCE. Face with tomentum densest around antennal socket. Tomentum slightly sparser on clypeus; upper paraocular and frontal areas and vertexal area mostly exposed. Pronotal collar with tomentum uniformly pale yellow. Mesoscutum with short but well-defined paramedian band of pale-yellow tomentum, well separated from anterior margin; pale tomentum otherwise mostly restricted to lateral and posterior margins. Mesopleuron with off-white, appressed, branched setae; upper half densely setose, except behind pronotal lobe, with setae slightly sparser on hypoepimeral area; ventrolateral half nearly bare, except along margins. Metanotum with tomentum uninterrupted, off-white laterally and pale yellow medially. Propodeal triangle mostly glabrous, laterally with punctures bearing very short dark brown setae. Metasomal terga with bands of off-white tomentum. T1 with basal and apical

transverse bands interrupted medially (former somewhat more widely than latter) and subparallel, discal patch transversely oblong. T2–T4 with medially interrupted apical transverse bands, that of T2 with pair of basomedially convergent anterolateral extensions. S2–S3 with apical transverse bands of white tomentum.

**SURFACE SCULPTURE.** Labrum and clypeus with punctures equally dense and nearly contiguous (most  $i < 1d$ ). Clypeus without glabrous midline in holotype and female paratype, but with incomplete and very short glabrous midline extending from upper margin down to  $< \frac{1}{3}$  length of clypeus in (male) allotype. Vertexal area somewhat sparsely punctate (some  $i > 2d$ ), especially around ocelli. Mesoscutum densely punctate (most  $i \leq 1d$ ) but interspaces well defined, shining. Mesoscutellum and axilla with punctures equally dense and nearly contiguous (most  $i < 1d$ ). Mesopleuron with punctures in upper half not much denser (most  $i < 1d$ ) than in ventrolateral half (most  $i \leq 1d$ ); interspaces shining; punctures similar in size throughout. Discs of metasomal terga with punctures very fine, dense ( $i \approx 1d$ ), and evenly distributed; interspaces dull due to tessellate surface microsculpture.

**STRUCTURE.** Labrum with pair of small subapical denticles. Pronotal collar short (medial length  $\sim \frac{1}{2}$  MOD). Mesoscutellum moderately bigibbous. Axilla not extending much beyond midlength of mesoscutellum (extending to  $\sim \frac{3}{5}$ – $\frac{2}{3}$  its length); tip distinctly pointed and hooked (i.e., concave along medial margin), mesally unattached to mesoscutellum for  $\sim \frac{1}{3}$ – $\frac{2}{5}$  medial length of axilla; lateral margin somewhat sinuate. Pro- and mesotrochanters distinctly tuberculate.

#### **Female**

T5 with concave apical margin and large patch of off-white tomentum on each side lateral to pseudopygidial area. Pseudopygidial area with underlying integument reddish brown in part; forming rounded triangle with concave sides; with brown erect/suberect setae basally and brown spinelike setae laterally. Pygidial plate apically truncate. S4 with apical transverse band of white tomentum. S5 straight in lateral view, with patch of off-white tomentum submedially (absent in paratype) and apical fimbria of coppery bristle-like setae; S5 otherwise covered in brown tomentum.

#### **Male**

T5–T6 with medially narrowed or narrowly interrupted apical transverse bands of off-white tomentum. Pygidial plate relatively flat and apically rounded. S4–S5 each with apical/subapical fringe of dense, long ( $> 1$  MOD), curved, coppery to silvery setae, not contrasting strongly with bands of preceding sterna.

#### **Distribution**

Northern South America (Fig. 11).

#### **Ecology**

##### **Host records**

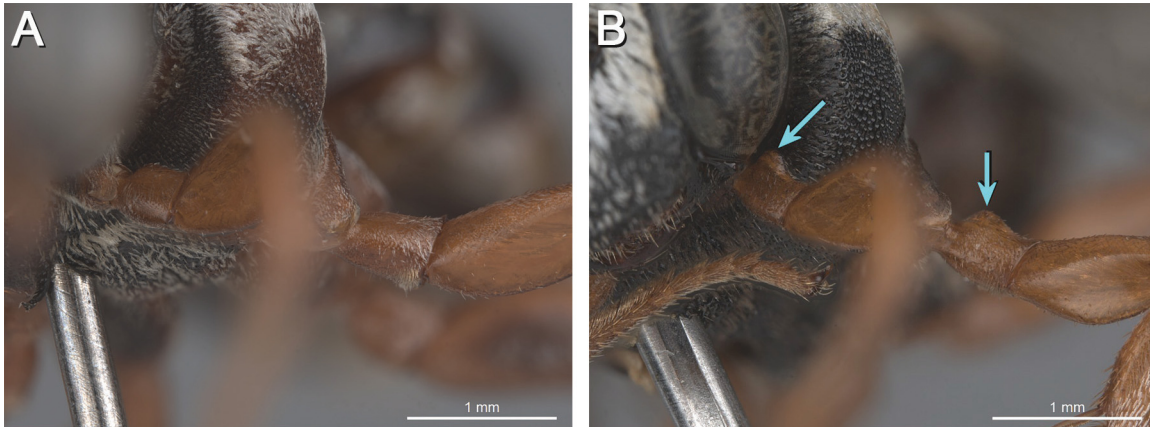
Unknown.

##### **Floral records**

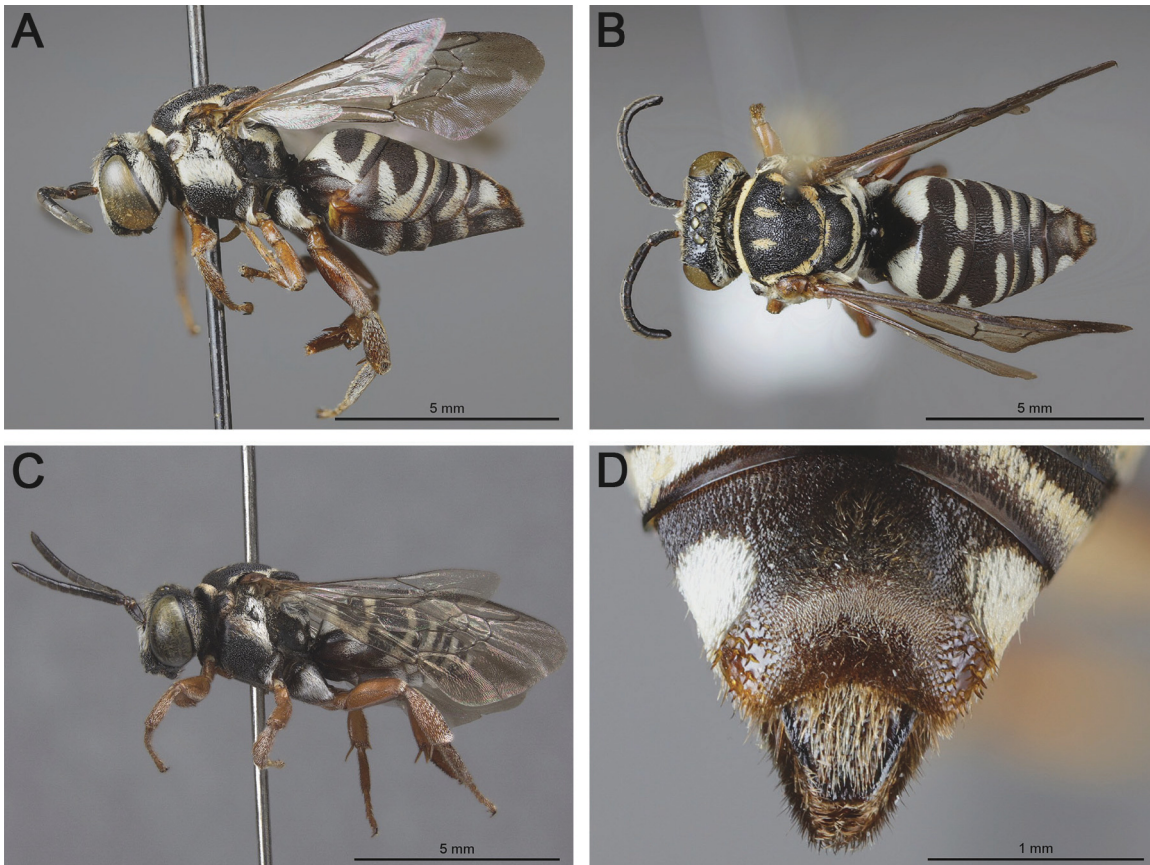
Unknown.

#### **Remarks**

This species was first documented in Rightmyer's (2006) dissertation, wherein it was referred to as "sp. 169". Rightmyer (2008) included the species in a key to *Triepeolus* from South America and the Caribbean but under the name *Triepeolus* n. sp. 2. Although Rightmyer (2006, 2008) treated the species, then based on a single, male specimen (herein designated as the allotype of *T. tuberculifer* sp. nov.), as a member of the *T. verbesinae* species group, the subsequent discovery of the female confirms its true placement in the *T. simplex* species group.



**Fig. 15.** Left pro- and mesotrochanters of male, frontal view. **A.** *Triepeolus osiriformis* (Schrottky, 1910) (FSCA). **B.** *T. tuberculifer* Onuferko, Rightmyer & Roig-Alsina sp. nov., allotype (FSCA M.G.R. Database No. 3704), showing distinct protuberances (blue arrows).



**Fig. 16.** *Triepeolus tuberculifer* Onuferko, Rightmyer & Roig-Alsina sp. nov. **A–B, D.** Holotype, ♀ (ICN HY-1056). **A.** Habitus, lateral view. **B.** Habitus, dorsal view. **C.** Allotype, ♂ (FSCA M.G.R. Database No. 3704), habitus, lateral view. **D.** Pseudopygidial area, dorsal view.



**Key to both sexes of the species of *Triepeolus* in South America**

1. T1 without apical transverse band (only basal band or pair of anterolateral patches of pale tomentum present, which may on each side (or each) have short, medially directed posterolateral extension) (Figs 2B, 10B, 11B); if T1 extensively covered in pale tomentum, then tomentum on apical impressed area not forming distinct transverse band (Fig. 3B) ..... 2
  - T1 with both basal and apical transverse bands (Figs 3A, 5B, 6B, 7B, 8, 12B, 14B, 16B) ..... 4
2. T1 with pair of anterolateral patches of yellow tomentum, each mesally convex, such that discal patch in dorsal view forming trapezoid or triangle with concave anterolateral sides (Fig. 10B). Paramedian band attaining or nearly attaining anterior margin of mesoscutum (Fig. 10B). Axilla with tip broadly rounded (Fig. 13A). Pseudopygidial area of female circular, with apical margin broadly convex (Fig. 10D) ..... *T. flavipennis* (Fries, 1916) (in part)
  - T1 with basal band (or pair of anterolateral patches) of yellow tomentum, on each side (or each) mesally concave, such that discal patch in dorsal view semicircular (Figs 2B, 11B). Paramedian band (if present) not attaining anterior margin of mesoscutum (Fig. 2B). Axilla with tip distinctly pointed (Fig. 13B). Pseudopygidial area of female triangular, with apical margin concave (Figs 2D, 11D) ..... 3
3. Mesoscutum with well-defined paramedian band of yellow tomentum (Fig. 2B) ..... *T. alvarengai* Moure, 1955 (in part)
  - Mesoscutum with large anteromedial ovate patch of yellow tomentum (Fig. 3B), which may be sparser medially such that patch suggestive of ill-defined paramedian band (Fig. 11B) ..... *T. nemoralis* (Holmberg, 1886)
4. T1 basal and apical transverse bands subparallel and joined on each side by distinct longitudinal band, such that discal patch in dorsal view transversely oblong (Figs 12B, 16B) ..... 5
  - T1 basal band arched and (except in *T. rufotegularis*) continuous with (and indistinguishable from) lateral longitudinal band, such that discal patch in dorsal view reniform, semicircular, trapezoidal, or triangular (Figs 3A, 5B, 6B, 7B, 8, 14B) ..... 6
5. Pro- and mesotrochanters not tuberculate (Fig. 15A). Axilla and mesoscutellum reddish brown and sparsely punctate (most  $i \geq 1d$ ) (Figs 12A–C, 13C). Pseudopygidial area of female circular, with apical margin broadly convex (Fig. 12D) ..... *T. osiriformis* (Schrottky, 1910)
  - Pro- and mesotrochanters distinctly tuberculate (Fig. 15B). Axilla and mesoscutellum black and densely punctate (most  $i < 1d$ ) (Figs 13D, 16A–C). Pseudopygidial area of female triangular, with apical margin concave (Fig. 16D) ..... *T. tuberculifer* Onuferko, Rightmyer & Roig-Alsina sp. nov.
6. Dorsum of mesosoma (at least anterolaterally) with dense, long ( $\geq \frac{1}{2}$  MOD), erect/suberect, minutely branched setae (Fig. 4A–B) ..... 7
  - Dorsum of mesosoma with only short ( $< \frac{1}{2}$  MOD), appressed, branched setae (Fig. 4C–D) ..... 8
7. Mesopleuron with dense, long ( $\geq \frac{1}{2}$  MOD), erect/suberect, minutely branched setae only in upper half, with sparse, erect, simple setae among short ( $< \frac{1}{4}$  MOD), appressed, branched setae in ventrolateral half (Fig. 4A). T1–T4 transverse bands all widely interrupted medially in both sexes (Fig. 5B) ..... *T. atoconganus* Moure, 1955
  - Mesopleuron with dense, long (clearly  $> \frac{1}{2}$  MOD), erect/suberect, minutely branched setae throughout (Fig. 4B). At least T3–T4 with apical transverse bands narrowed or narrowly interrupted medially (Figs 7B, 8) ..... *T. cecilyae* Packer, 2016
8. T2–T4 apical transverse bands complete (Fig. 3A) ..... 9
  - T2–T4 apical transverse bands all interrupted medially (Figs 6B, 14B) ..... 10

9. T1 basal band mesally concave, such that discal patch in dorsal view semicircular (Fig. 3A). Paramedian band not attaining anterior margin of mesoscutum (Fig. 3A). Axilla with tip distinctly pointed (Fig. 3A). Pseudopygidial area of female triangular, with apical margin concave (Fig. 2D) ..... *T. alvarengai* Moure, 1955 (in part)
  - T1 basal band on each side mesally convex, such that discal patch in dorsal view forming trapezoid or triangle with concave anterolateral sides (Fig. 10B). Paramedian band attaining or nearly attaining anterior margin of mesoscutum (Fig. 10B). Axilla with tip broadly rounded (Fig. 13A). Pseudopygidial area of female circular, with apical margin broadly convex (Fig. 10D) ..... *T. flavipennis* (Friese, 1916) (in part)
10. T2 apical transverse band with pair of lobe-like anterolateral extensions (Fig. 6A–C). Metasomal terga with bands of pale-yellow tomentum (Fig. 6) [Ecuador and Peru] ..... *T. buchwaldi* (Friese, 1908)
  - T2 apical transverse band without lobe-like anterolateral extensions (Fig. 14A–C). Metasomal terga with bands of white to off-white tomentum (Fig. 14) [Caribbean region] ..... *T. rufotegularis* (Ashmead, 1900)

## Discussion

In South America, a total of nine species of *Triepeolus* are confirmed, most of which are restricted to the northern and western parts of the continent. Colombia and Peru have the highest numbers of species, with eight recorded between the two countries. Whereas there is strong phylogenetic and biogeographic support for a South American (or at least Neotropical) origin for Epeolini and most of its constituent genera, *Triepeolus*, like the related genus *Epeolus*, likely originated in North America and subsequently dispersed to South America. This is suggested not only by the comparatively low levels of species richness of both genera in South America but also several other factors as follows.

Only two species groups are represented in South America—the *T. simplex* species group, which includes *T. alvarengai*, *T. nemoralis*, and *T. tuberculifer* sp. nov., and the *T. verbesinae* species group, which includes all the others—both of which exhibit their greatest diversity in North America (Rightmyer 2006). Although taxon sampling has been limited for molecular phylogenetic and phylogenomic analyses, phylogenies based on morphological (Rightmyer 2004), combined molecular and morphological (Onuferko *et al.* 2019), and phylogenomic (Sless *et al.* 2022) datasets have consistently placed the Palearctic species as sister to the rest of the genus, suggesting that *Triepeolus* originated somewhere in the Holarctic region. That *Triepeolus* is represented by only two species in the Palearctic (versus >100 in the Nearctic) further suggests a North American origin. However, it should be noted that none of the molecular phylogenies to date have included members of the *T. simplex* species group. A more recent arrival in South America would also explain the disparity in diversity there between *Triepeolus* and the tribe Eucerini (Hymenoptera: Apidae), which includes most of the known hosts of *Triepeolus* yet also exhibits higher generic diversity in South America than in North America (Rightmyer 2004; Michener 2007).

Similarly, almost all species of *Epeolus* in South America (*E. luteipennis* excepted) belong to a single species group, and only three (of the six) species in the genus represented on the continent are endemic (Onuferko 2019). The species in this group share several morphological peculiarities, and, as a result, they have at various times been regarded as belonging to a separate genus, *Trophocleptria* Holmberg, 1886. However, the most comprehensive phylogenetic and biogeographic study of *Epeolus* to date revealed a monophyletic *Trophocleptria* clade nested deeply within *Epeolus* and inferred a Nearctic origin for the species group (Onuferko *et al.* 2019).

A detailed morphological study by Rightmyer (2004) concluded that *Doeringiella*, *Pseudepeolus*, *Rhinepeolus*, *Thalestriina*, and *Triepeolus* form a natural group, and the five genera were thus placed in the same subtribe—Thalestriina. The first comprehensive molecular phylogenetic study of Apidae by Cardinal *et al.* (2010) recovered a monophyletic Thalestriina using Bayesian and maximum likelihood analyses (but not parsimony), although support for the clade was weak (PP = 0.68) in the Bayesian maximum clade credibility tree and negligible in the maximum likelihood tree (Percent bootstrap support = 37). Interestingly, the more recent respective phylogenetic and phylogenomic analyses of Onuferko *et al.* (2019) and Sless *et al.* (2022) rendered Thalestriina paraphyletic, and *Epeolus* and *Triepeolus* were recovered as sister genera with strong support (PP = 0.98 in Onuferko *et al.* 2019; SH-aLRT / ultrafast bootstrap values = 100 / 100 in Sless *et al.* 2022). Although this relationship was unexpected given the markedly different morphology of the female sixth sternum of *Epeolus*, it is sensible from a biogeographic perspective, as both genera appear to have originated outside the Neotropics. Still, a comprehensive phylogenetic analysis of *Triepeolus* based on molecular or combined molecular and morphological data is lacking and needed to better understand the evolutionary history of the genus.

Although the taxonomic understanding of *Triepeolus* in South America has improved through this study, the taxonomy of the *T. simplex* and *T. verbesinae* species groups remains problematic in part, with the North American species still in need of revision. It is hoped that the availability of new detailed images, updated taxon concepts, a fully illustrated identification key (available in English, Portuguese, and Spanish), and summarized known natural history information will increase the recognition of the treated species among naturalists as well as bee researchers (in South America and generally) and facilitate future studies thereof. Although most species of *Triepeolus* in South America were described many years ago (1886–1955), very little is known about their ecology in terms of habitat preferences, hosts, preferred floral rewards, and interactions with other organisms in their environment, which should be the subject of investigation in future studies. Given that two of the treated species were discovered in recent years, it is also important that additional representatives of this genus be collected, especially in the sparsely populated and traditionally understudied areas of the continent.

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**Supp. file 1.** A database of collection and observation records.

<https://doi.org/10.5852/ejt.2024.931.2505.11207>

**Supp. file 2.** Supplementary figures including images of the primary types and associated labels of all species of *Triepeolus* known from South America and their junior synonyms except that of *T. nemoralis*, which has been destroyed. <https://doi.org/10.5852/ejt.2024.931.2505.11209>

**Supp. file 3.** Portuguese and Spanish versions of the identification key.

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