Journal *of* Melittology
Bee Biology, Ecology, Evolution, & Systematics
No. 151, 1–13 22 September 2026

Trigonisca townsendi (Cockerell) from northwestern Peru: Taxonomic, biological, and ethnobiological notes (Hymenoptera: Apidae: Meliponini)

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Abstract. *Trigonisca townsendi* is a tiny stingless bee from the dry forests of northwestern Peru, where it plays a role in pollination and the traditional medicinal use of honey. *Trigonisca* has never been comprehensively revised, making species identification difficult. Accurate taxonomy requires information on male morphology, particularly the genitalia. Here, we provide a diagnosis of *T. townsendi* and high-resolution images of the male genitalia to aid future taxonomic work. We also summarize its distribution, nesting biology, and cultural significance.

INTRODUCTION

Tiny stingless bees with strongly reduced wing venation in South America are restricted to the genera *Trigonisca* Moure (38 spp.), *Celetrigona* Moure (4 spp.), *Leurotrigona* Moure (2 spp.), and *Exochotrigona* Engel (2 spp.). We exclude *Dolichotrigona* Moure from this list because recognizing it as a separate genus renders *Trigonisca* paraphyletic; it is now synonymized under *Trigonisca* (Rasmussen & Cameron, 2010; Engel *et al.*, 2023; Lepeco *et al.*, 2024). Alternatively, it could be treated as one of several subgenera of *Trigonisca* or as a species group within *Trigonisca*, or *Trigonisca* could be further divided following a rigorous taxonomic revision. In this treatment, we use *Dolichotrigona* as an informal name for a morphologically coherent and useful typological group of 10 species, despite the related phylogenetic issues. Species of *Dolichotrigona*, *Celetrigona*, *Leurotrigona*, and *Exochotrigona* are generally identifiable to species, and the biology of some *Leurotrigona* species is known (Sakagami & Zucchi, 1974; Moure *et al.*, 1988; Camargo & Pedro, 2005, 2009; Pedro & Camargo, 2009). Collectively, these four genera of tiny stingless bees—with *Dolichotrigona* included in *Trigonisca*—form the sister clade to the remaining Neotropical stingless bees.

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ISSN 2325-4467

Identification of South American *Trigonisca* species is challenging because identification keys are lacking and previously described species have been insufficiently assessed (listed in Camargo & Pedro, 2007). Albuquerque (1990) began revising the genus but was unable to examine enough material for a comprehensive treatment in her MSc thesis. She later described several new species in collaboration with Camargo (Albuquerque & Camargo, 2007). Species of *Dolichotrigona* and *Celetrigona* have been revised (Camargo & Pedro, 2005, 2009), as have species of *Leurotrigona* (Pedro & Camargo, 2009), two of which—*L. crispula* Pedro & Camargo and *L. pusilla* Moure & Camargo—have since been transferred to *Exochotrigona* (Engel *et al.*, 2019). These groups can be readily distinguished from the remaining taxa in the *Trigonisca* group by body sculpture, coloration, and proportions (Moure, 1950). In *Leurotrigona*, the mesoscutum, mesoscutellum, propodeum, and first terga are highly polished and nearly impunctate, with smooth, shiny integument. *Exochotrigona* closely resembles *Leurotrigona* in general sculpture but can be separated by its smaller size (head width <1.0 mm), shorter malar space (equal to the flagellar diameter), and slightly sinuate hind tibial margin with a produced distal angle. In contrast, all remaining taxa have a dull, microalveolate, or tessellate mesoscutum and mesoscutellum; a coarsely sculptured propodeum; a distinct preoccipital carina; and a convex mesoscutellum raised above the metanotum. Within this group, *Celetrigona* is recognizable by its bituberculate labrum, densely punctate integument, yellowish lower face, and very long antennae and legs; the scape surpasses the vertex, and the hind tibial setae exceed the tibial width. *Dolichotrigona* resembles *Celetrigona* but lacks labral tubercles and has uniformly dark, opaque integument without yellow markings, a short marginal cell with a strongly arched posterior margin, and very elongate, narrow hind tibiae and basitarsi, the latter about twice the tibial width; the scape reaches the level of the ocelli. Finally, *Trigonisca* (excluding *Dolichotrigona*) differs in having a simple labrum; legs and antennae shorter than those of *Celetrigona*; hind tibial setae that do not exceed the tibial width; a scape ending below the ocelli; and shorter, broader hind tibiae (less than three times as long as wide). Its mesoscutellum is distinctly convex anteroposteriorly, and its integument is finely reticulate. Beyond these efforts, taxonomic progress on *Trigonisca* has been limited to scattered descriptions of new species from Argentina (Álvarez & Lucia, 2018), Brazil (Moure, 1989), Colombia (Engel *et al.*, 2019), and Mexico (Ayala, 1999). In addition, a recent or subfossil species was described from Colombia (Penney *et al.*, 2013).

In *Trigonisca*, as in other groups of stingless bees, some species remain poorly defined and illustrated, making new specimens difficult to identify. Descriptions of new species and revisions of stingless bee species groups should include information on male genitalia because these structures can be critical for accurate species delimitation (*e.g.*, Sakagami, 1978). However, males are difficult to collect and, when collected away from a colony, can be difficult to associate with conspecific workers. Male genitalia have been illustrated for *Dolichotrigona* (1 sp.), *Celetrigona* (1 sp.), *Leurotrigona* (1 sp.), *Exochotrigona* (2 spp.), and *Trigonisca* (2 spp.) (Michener, 1990; Camargo & Pedro, 2005, 2009; Pedro & Camargo, 2009; Engel *et al.*, 2019). These structures clearly inform higher-level relationships; their utility for species-level circumscription remains poorly understood but appears informative (*e.g.*, *Exochotrigona*).

Stingless bees in Peru have a long cultural history (Rasmussen & Castillo Carrillo, 2003; Rasmussen *et al.*, 2024). Most scientific research has been conducted at a broader scale (Camargo & Moure, 1994, 1996; Pedro & Camargo, 2003), complemented by national surveys and studies (Baumgartner & Roubik, 1989; Rasmussen & Gonzalez, 2009; Rasmussen & Delgado Vásquez, 2019; Delgado *et al.*, 2020; Delgado Vásquez *et al.*, 2020; Marconi *et al.*, 2022; Delgado *et al.*, 2023).



Figures 1–6. *Trigonisca townsendi*. **1.** Habitat in the dry forest of northwestern Peru where the species occurs (Cerro Blanco, Tumbes, Peru; −3.659000, −80.356367). **2.** Traditional destructive harvesting of honey and pollen by cutting down a tree or the branch containing the nest in *Libidibia glabrata* (Fabaceae), shown here using an axe. **3.** Nest entrance on a branch. **4.** Close-up of the nest entrance showing protective propolis, vigilant guard bees, and intruding *Azteca* ants (Formicidae). **5.** Inside the opened nest cavity, showing brood cells in lighter, smaller clusters and provisions (honey and pollen) stored in larger, darker wax pots. **6.** Small quantity of honey shown in the honey hunter's palm.

The dry northwestern coast of Peru is ecologically similar to southwestern Ecuador. This region hosts endemic stingless bee species such as *Melipona mimetica* Friese, which is widely used in folk medicine and rural activities (Rasmussen & Castillo Carrillo, 2003; Elizalde Vilela *et al.*, 2006; Castillo Carrillo *et al.*, 2016). Approximately 21 species of stingless bees occur in this area (pers. obs.). We previously reported two species of *Trigonisca* from coastal Peru: the dark *Trigonisca townsendi* (Cockerell, 1911), known locally as "Papito negro" in dry forests, and the less common reddish *T.* cf. *atomaria* (Cockerell, 1917), known locally as "Papito Colorado" in tropical forests (Elizalde Vilela *et al.*, 2006).

Trigonisca townsendi belongs to the core *Trigonisca* group, a lineage for which improved taxonomic understanding remains critical. The species also exemplifies the problem of inadequate original species definitions and limited illustrations, particularly of males, which hampers revisionary work and the recognition of new species. In this contribution, we provide an expanded diagnosis of *T. townsendi*, including a description of the male and illustrations of the male terminalia, as well as information on the species' natural history and distribution.

MATERIAL AND METHODS

We collected individuals of this species on several occasions beginning in 2001 in the buffer zone surrounding Parque Nacional Cerros de Amotape, Department of Tumbes, Peru (Figs. 1–6). These collections include males collected from nests together with female workers. In addition, we conducted informal interviews with farmers and residents about the species on numerous occasions after our first collection. This information forms the basis of the present work.

Morphological terminology largely follows Michener (2007) and Albuquerque & Camargo (2007). We use the abbreviations S and T for metasomal sternum and tergum, respectively, and F for flagellar segment. To describe, photograph, and measure body features, we used Leica Enersight v1.2.0.56 software with a Leica Ivesta 3 stereomicroscope. Genitalia images were photographed with a Leica DM750 configurable microscope equipped with a Flexacam i5. Photomicrographs were prepared by stacking images captured with the microscopes, a Canon MP-E 65 mm 1–5× Macro Photo lens, and a Canon EF 100 mm f/2.8L Macro IS USM lens mounted with a Raynox DCR-250, using the Zerene Stacker software package.

The material examined is deposited in the Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru (MUSM); Claus Rasmussen Collection, Aarhus University, Denmark (CRC); and Smithsonian National Museum of Natural History, Washington, D.C., USA (USNM).

RESULTS AND DISCUSSION

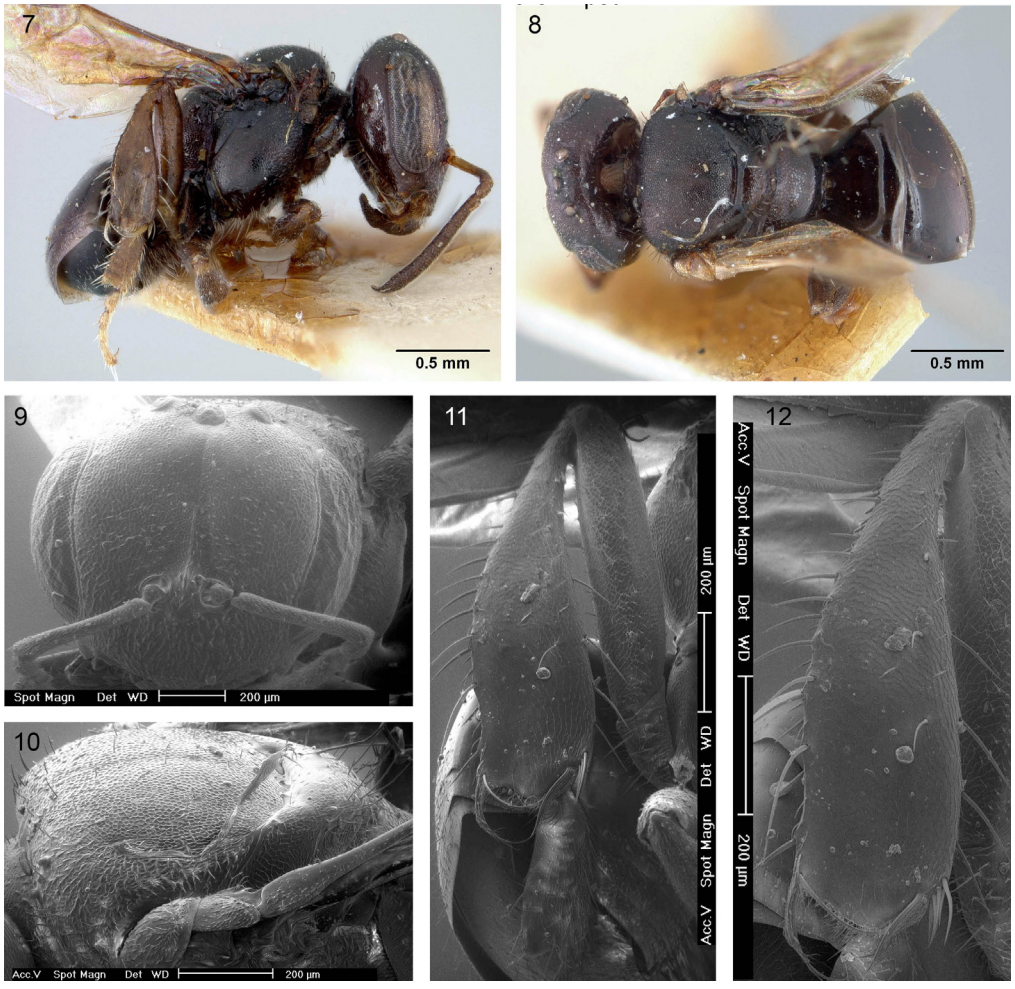
SYSTEMATICS

Family Apidae Latreille, 1802
Genus *Trigonisca* Moure, 1950
Trigonisca townsendi (Cockerell, 1911)
(Figs. 1–32)

TYPE MATERIAL

The species was described by T.D.A. Cockerell in August 1911 from a series of specimens sent to him by Charles Henry Tyler Townsend (5 December 1863–17 March 1944). In 1909, Townsend left the U.S. Department of Agriculture to travel to Peru at the invitation of then-president Augusto B. Leguía. Townsend worked as an expert

on insect-vectored human diseases and was based in Piura until he returned to the United States on 30 June 1914 (Anonymous, 1914). The specimen he collected bears the following labels: "Piura / Peru / (Towns)" [likely collected near the city of Piura, Peru, by C.H.T. Townsend]; "124 / Oct" [October 1909 or 1910, with field code 124]; "*Trigona* / *townsendi* / Ckll TYPE" [designated as the holotype; at that time, Cockerell used "type" for holotypes and "co-types" for paratypes]; "TypeNo. / 23250 / U.S.N.M." [red]; "HOLOTYPE / *Trigona townsendi* / Cockerell, 1911" [red; added by Claus Rasmussen in 2005]; "Examinated in / 27.07.2005 / Det. Camargo, 1999" [examined by Camargo and Rasmussen in 2005]; and "USNM ENT / 00534528." The holotype, housed at the USNM, is point-mounted and in very good condition (Figs. 7–12).



Figures 7–12. Holotype worker of *Trigonisca townsendi*. **7.** Lateral view. **8.** Dorsal view (photographs for Figs. 7–8 by the Smithsonian National Museum of Natural History). **9.** Frontal view. **10.** Dorsolateral view of the mesoscutum and mesoscutellum. **11.** Hind leg showing the tibia and metatarsus. **12.** Hind tibia showing the corbicula. Figs. 9–12 are Environmental scanning electron microscope (ESEM) images of the uncoated holotype.

DIAGNOSIS AND DESCRIPTIVE NOTES

DIAGNOSIS: In the worker-based key of Albuquerque & Camargo (2007), *T. townsendi* enters the branch beginning at couplet 5, rather than the group characterized by conspicuous pompon- or scale-like decumbent facial setae. Within this branch, it is distinguished from the species treated in the key by the combination of a strongly convex marginal cell, distinctly convex posterior margin of the hind tibia, short, fine, plumose decumbent microsetae on the face extending across the clypeus, and a shiny mesepisternum.

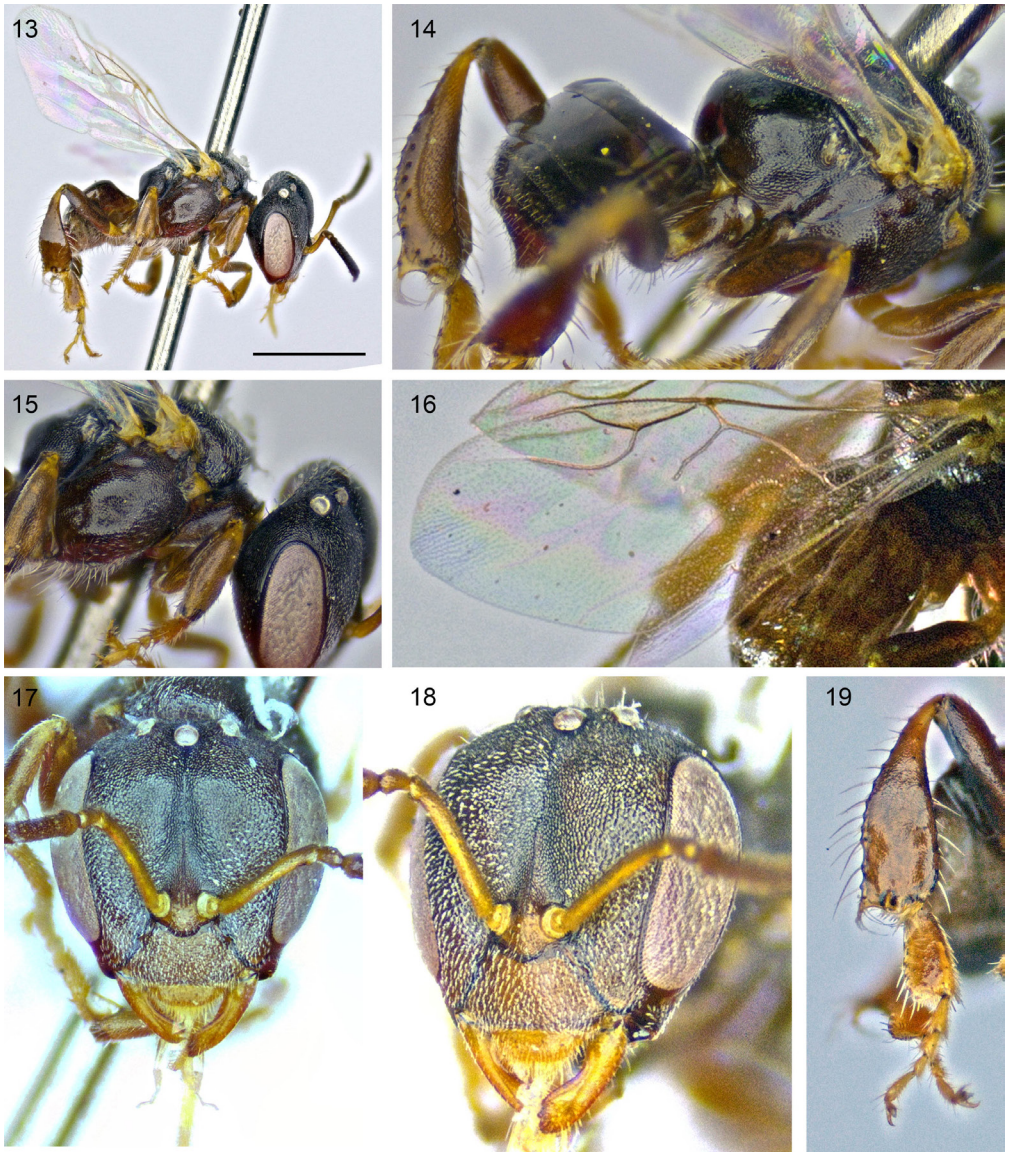
WORKER: Total length 2.48 mm; head width 1.06 mm; forewing length 2.41 mm; hind tibia 0.86 mm long and 0.28 mm wide. Mandible with two small teeth, inner corner tooth rounded. Short, plumose, non-scale-like and non-pompon-like decumbent microsetae on frons and clypeus; very short, decumbent setae on scape. Integument of frons and mesoscutum alveolate. Orbits converge slightly ventrally. Supraclypeal carina moderately distinct, forming well-marked line that extends to median ocellus beyond halfway point. Mesepisternum shiny. Posterior border of hind tibia notably convex. Marginal cell prominently convex (Fig. 16).

MALE: Total length approximately 2.57 mm; forewing length 2.56 mm; maximum head width 0.96 mm. Head 1.1× wider than long; malar area reduced and much shorter than flagellar length (worker malar space about equal to flagellar length). Clypeus 0.45× shorter than its maximum width; supraclypeal carina less distinct than worker but forming a line that extends to median ocellus. Antennal scape shorter than in worker (0.29 mm vs. 0.41 mm). Vestiture slightly finer and sparser on clypeus and frons compared to that of worker. Integument black except for following yellowish parts: antennal scape, pedicel, clypeus (lighter medially), apical part of hind tibia, and basitarsi. Integument alveolate on frons and mesoscutum; mesoscutellum 0.32× shorter than wide; mesepisternum shiny. Metasomal terga T1–T6 smooth and shiny, as in worker. Hind tibia slightly swollen, 0.83 mm long and 0.25 mm wide (3.3× longer than wide). Hind basitarsus 0.23 mm long and 0.13 mm wide (1.8× longer than wide and about half as wide as hind tibia).

ADDITIONAL WORKER CHARACTERS: Head. Frons with microsetae denser and directed anteriorly in antennal depressions and along supraclypeal area; setae higher on frons, anterior to ocelli and between ocelli and compound eyes, slightly longer and directed laterally. Paraocular area with sparser, longer, anteriorly directed setae, shortening toward malar area. Clypeal vestiture denser and longer along anterior margin, setae extending beyond margin, especially sublaterally. Labrum with semidecumbent setae denser and longer than clypeal setae; few long, erect setae present. Galea dorsally with several long, erect setae; ventrally with several very long setae curved toward apex. Mandible with sparse, variable setae, especially long along lower margin. Genal area nearly asetose, except long, erect setae along lower preoccipital ridge. Antenna with very short, semidecumbent setae, sparse on scape and denser on remaining antennal segments. Vertex posterior to ocelli with long, erect setae.

MESOSOMA: Mesoscutum with mostly decumbent setae interspersed with longer, erect setae. Mesoscutellum with very long setae, especially posteriorly. Mesepisternum laterally with very short, decumbent setae, becoming progressively longer ventrally; ventral surface with very long, semidecumbent setae.

INTEGUMENT AND ANTENNA: Malar area mostly smooth; alveolation of genal area elongate, nearly chagrined. Preoccipital ridge barely present. Antennal scape longer dorsally than ventrally, ending distoventrally in very small projection; pedicel dorsally convex and ventrally sigmoid, longer than F1; F1 triangularly divergent and distally broader than succeeding flagellomeres; terminal flagellomeres gradually broadened; F10 broadest in dorsal view, ventrally excavated, thin and curved in lateral view.

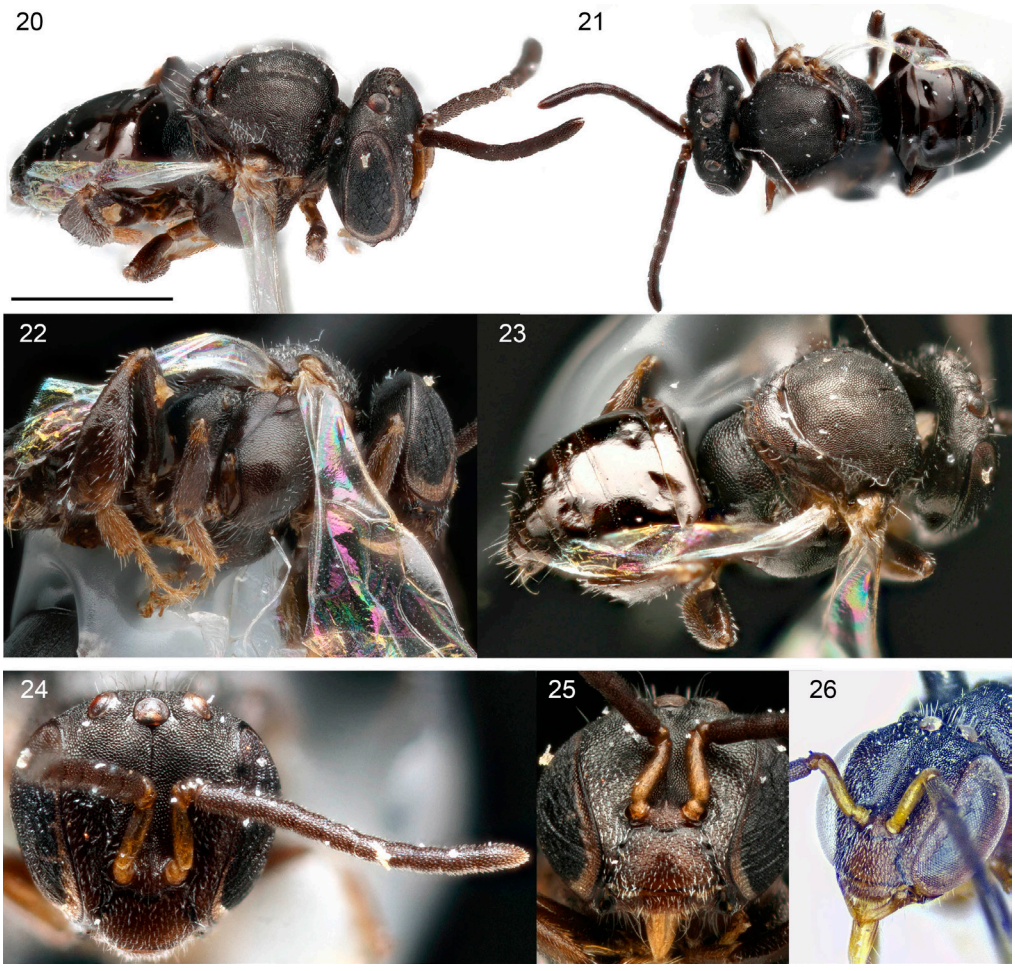


Figures 13–19. Worker of *Trigonisca townsendi*. **13.** Lateral view (scale bar: 1 mm). **14.** Posterolateral view of the propodeum, including the spiracle. **15.** Lateral view showing the mesosoma (including the mesopleuron) and head (including the gena). **16.** Forewing. **17.** Frontal view of the head. **18.** Anterolateral view of the head showing the labrum, mandible, and malar space. **19.** Hind leg.

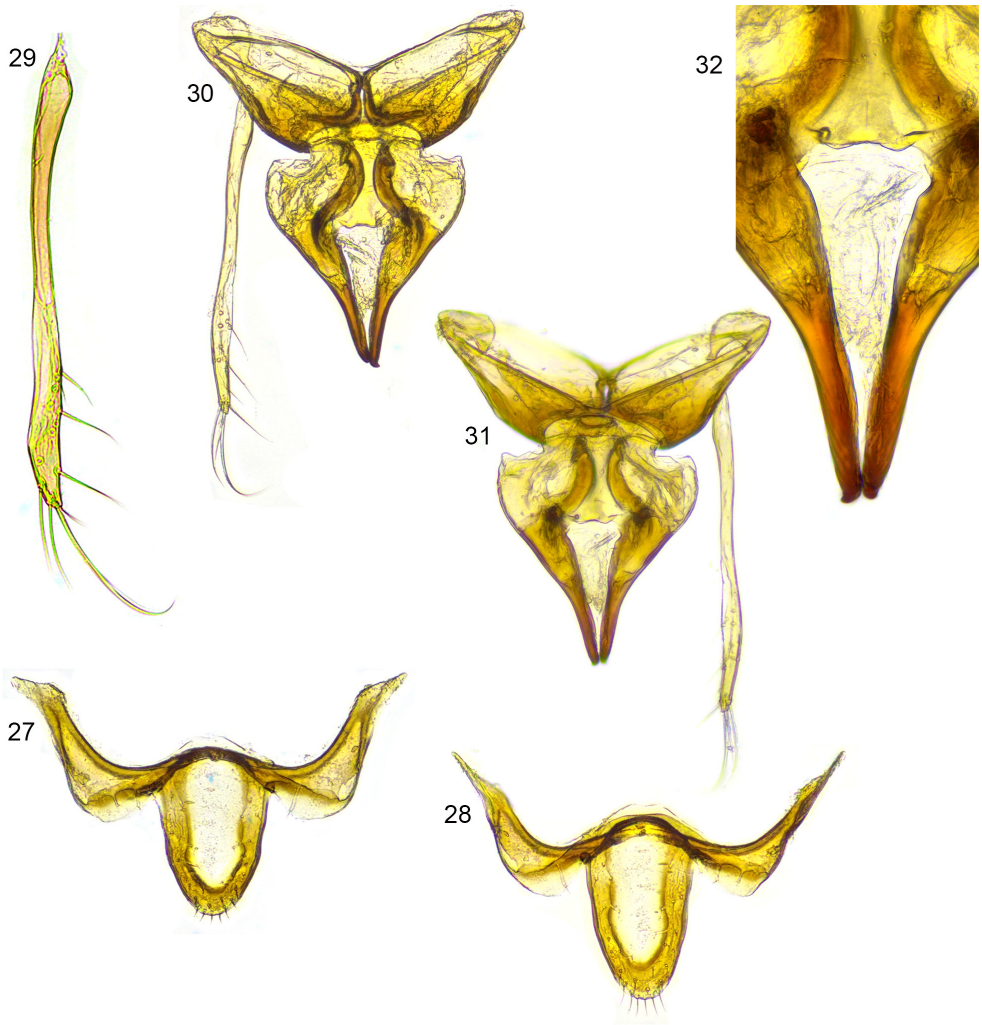
Comparisons of male terminalia: Genitalia and hidden sterna as shown in Figs. 27–32. Compared with the male genitalia of relatives (see illustrations in Michener, 1990; Camargo & Pedro, 2005; Camargo & Pedro, 2009; Pedro & Camargo, 2009; Engel *et al.*, 2019), the anterior margin of sternum VII is distinctly convex medially, and its posterior margin is broadly rounded and gently convex. This condition contrasts with the flat margin in *T. mepecheu* Engel & Gonzalez, the pointed margins of *Dolichotrigona tavaresi* Camargo & Pedro and *Exochotrigona pusilla*, the narrowly pointed form in *E. crispula*, and the bilobed condition in *Leurotrigona muelleri* (Friese). The gonostylus is

elongate and slender, slightly constricted medially, and terminates in a rounded apex; it differs from the broader apical form of *T. mepecheu* and the narrower apical portion of *T.* cf. *buyssoni* (Friese). Setae occur along the inner margin of the apical half and reach one-third the length of the gonostylus. They are longer than those in *T. mepecheu* and *T.* cf. *buyssoni* and approach the condition in *Dolichotrigona* and *Celetrigona*; only *L. muelleri* has relatively longer apical setae. The penis valve tapers broadly toward the apex rather than finely, as in *L. muelleri*. A broader survey of structural diversity in the concealed male genitalia of *Trigonisca* will likely underscore the taxonomic significance of these characters.

DISTRIBUTION: We are unaware of confirmed records outside Peru, but the species is expected to occur across the border in southwestern Ecuador, where one of us (REV) has observed but not collected it. The species appears to be closely associated with dry forest in this ecoregion, including Parque Nacional Cerros de Amotape. All recent observations and collections are from within this range, in the buffer zone around the park (Cafetería, Miraflores, and Bigotes in the San Juan de la Virgen District).



Figures 20–26. Male of *Trigonisca townsendi*. **20.** Dorsolateral view (scale bar: 1 mm). **21.** Dorsal view. **22.** Lateral view showing the hind leg and mesopleuron. **23.** Posterolateral view of the propodeum. **24.** Frontal view of the head with antennae. **25.** Frontal view of the head showing the clypeus. **26.** Anterolateral view of the head showing the labrum, mandible, and malar space.



Figures 27–32. Male of *Trigonisca townsendi*. **27.** Sternum VII, ventral view. **28.** Sternum VII, dorsal view. **29.** Gonostylus detached from the genitalia (see Fig. 30). **30.** Genitalia, ventral view. **31.** Genitalia, dorsal view. **32.** Close-up of the penis valve, dorsal view.

Reports of the species from Central America (Cockerell, 1913, 1920; Wheeler, 1913) are likely based on misidentified material. Specimens examined from Costa Rica and identified as *T. townsendi* are slightly larger (head width >1.20 mm) and have longer setae on the hind leg. They may represent a different species requiring further study. We document the male here and previously published molecular data for specimens from Tumbes: 16S large-subunit ribosomal RNA, arginine kinase, elongation factor 1α, long-wavelength rhodopsin, and 28S ribosomal RNA (Rasmussen & Cameron, 2010, voucher 383; GenBank accession numbers DQ790456, DQ813068, DQ813147, DQ813225, and FJ042105). These data should now be compared with those from additional material from the broader Chocó–Central America region (northwestern Peru to Mexico), as defined for stingless bees by Camargo & Pedro (2003).

Biology: In the Department of Tumbes in northwestern Peru, *T. townsendi* nests in cavities in tree trunks and branches (Figs. 1–2), being a very tiny flower visitor and pollinator, and that also gathers sweat from humans and animals. Their preferred

nesting tree is "Charán" (*Libidibia glabrata* (Kunth) C.Cast. & G.P.Lewis, Fabaceae); "Hualtaco" (*Loxopterygium huasango* Spruce ex Engl., Anacardiaceae) is used less frequently. Guard bees protect the nest entrance, which remains open at night. The bees are not defensive toward humans. The entrance is narrow, approximately 3.0 mm in diameter, and lined with black propolis (Figs. 3–4). The brood chambers (Fig. 5) consist of small brood cells in clusters (2.4 × 1.6 mm). Honey and pollen are stored in small pots (1.8 × 0.9 cm) (Figs. 5–6). One of us (REV) has observed the bees visiting flowers of "Charán" (*Libidibia glabrata*), "Almendro" (*Geoffroea spinosa* Jacq., Fabaceae), "Polo-polo" (*Cochlospermum vitifolium* (Willd.) Spreng., Bixaceae), "Hualtaco" (*Loxopterygium huasango*), "Algarrobo" (*Neltuma pallida* (Humb. & Bonpl. ex Willd.) C.E.Hughes & G.P.Lewis, Fabaceae), and "Añalque" (*Coccoloba ruiziana* Lindau, Polygonaceae). The species is traditionally valued and exploited for its honey, which is used to treat eye conditions such as cataracts, pterygium, cloudiness, inflammation, and trauma, as well as wound infections. However, the number of colonies has declined significantly over the past three decades (pers. obs.) because of unsustainable harvesting and the destruction of dry forest, particularly the cutting of tree species essential for nesting and foraging. We have received reports that some local communities historically used dried cucurbit fruits to rear colonies. Reported uses of bee products include honey for the purposes noted above and wax for waxing cords (Elizalde Vilela *et al.*, 2006).

CONCLUDING REMARKS: We provide sufficient diagnostic morphological detail to recognize *T. townsendi* and present detailed images of the male genitalia for comparison within *Trigonisca sensu lato*. We also provide previously unrecorded information on the life history and ecological interactions of *T. townsendi*, which can help address questions in integrative taxonomy and evolutionary biology. Finally, we share observations on the status of this narrowly distributed species.

ACKNOWLEDGEMENTS

We are grateful to local communities in Tumbes and Piura for sharing information about the use of these stingless bees over the last 25 years. We also thank Brian Harris, then curator at the Smithsonian National Museum of Natural History, for lending the type specimen to CR in 2005–2006. Comments by V.H. Gonzalez and anonymous reviewers improved the manuscript.

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The *Journal of Melittology* was established at the University of Kansas through the efforts of Michael S. Engel, Victor H. Gonzalez, Ismael A. Hinojosa-Díaz, and Charles D. Michener in 2013 and each article is published as its own number, with issues appearing online as soon as they are ready. Papers are composed using Microsoft Word® and Adobe InDesign® in Lawrence, Kansas, USA.

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ISSN 2325-4467