

New host record for the enigmatic Neotropical mantidfly genus *Anchieta* Navás, 1909 (Neuroptera, Mantispidae), a mimic of wasps and stingless bees

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Abstract. Species of Symphrasinae (Neuroptera: Mantispidae) are ectoparasitoids of larvae and pupae of holometabolous insects, primarily of Hymenoptera in their larval stages. Herein we present the third case of an association between the mantidfly genus *Anchieta* Navás, 1909 with the order Hymenoptera. The hymenopteran species attacked by the as of yet undescribed species of *Anchieta* is *Montezumia dimidiata* Saussure, 1852 (Vespidae: Eumeninae), a predacious wasp that constructs mud nests. The association was observed in Peruvian Amazonia (near Tarapoto, San Martín), after rearing the mantidflies from a wasp nest. The biology and mimicry pattern with stingless bees of the reared *Anchieta* species is discussed.

Keywords. Ectoparasitoids; Symphrasinae; Mimicry; Neotropics.

INTRODUCTION

The insect family Mantispidae (Neuroptera: Mantispoidea), commonly known as mantidflies are remarkable insects which have raptorial forelegs, a complex trait shared with the Rhachiberothidae, and the extinct Dipteromantispidae (Lambkin, 1986; Aspöck & Mansell, 1994; Ohl, 2007; Liu *et al.*, 2016; Engel *et al.*, 2018). Their general appearance superficially resembles that of praying mantises (Insecta: Mantodea), but such condition is evidently a product of evolutionary convergence (Aspöck & Aspöck, 2007). Despite the interesting morphology of the adults, the mimicry with toxic or poisonous insects exhibited by several genera, and the complex postembryonic development (hypermetamorphosis) (Brauer, 1852, 1869, 1887) – in which their larvae may be ectoparasitoids, parasites, and spider-egg predators –, many aspects of mantidflies biology and taxonomy still need research (Redborg & MacLeod, 1985; Eggleton & Belshaw, 1992; Redborg, 1998; Snyman *et al.*, 2020).

The Mantispidae species for which the biology is better known belong to the subfamily Mantispinae, whose larvae feed primarily on spi-

der eggs, yet sometimes can feed temporarily on spider hemolymph, when the eggs are unavailable (Redborg & MacLeod, 1985; Redborg, 1998). Of the remaining smaller subfamilies, the New World Symphrasinae, which is composed of three extant genera, *Anchieta* Navás, 1909, *Plega* Navás, 1928 and *Trichoscelia* Westwood, 1852 have been reported as ectoparasitoids of larval Hymenoptera, Lepidoptera, Coleoptera, and possibly Diptera (Redborg, 1998; Hook *et al.*, 2010; Maia-Silva *et al.*, 2013; Snyman *et al.*, 2020). Most of the hymenopteran records has been on *Polybia* Lepeletier, 1836 (Vespidae: White, 1841; Walker, 1853; Rogenhofer, 1862; Smith, 1863; Westwood, 1867; Hagen, 1877; Brauer, 1887; Berg, 1899; Parfin, 1958; Richards, 1978; Penny, 1982; Dejan & Canard, 1990), but also apoid wasps of the genus *Trypoxylon* Latreille, 1796 (Crabronidae: Parker & Stange, 1965; Buys, 2008), as well as various solitary bees, such as *Melitoma* Lepeletier & Serville, 1828 (Apidae: Linsley & MacSwain, 1955; Linsley *et al.*, 1980), *Hylaeus* Fabricius, 1793 (Colletidae: Hook *et al.*, 2010), and *Megachile* Latreille, 1802 (Megachilidae: Parker & Stange, 1965).

Both direct observation (Dejan & Canard, 1990) and circumstantial evidence (Linsley *et al.*, 1980;

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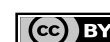
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Hook *et al.*, 2010) suggest that symphrasine females deposits their eggs near the host nest entrance, or near individual cells within the host nest. The newly hatched first instar mantispids then migrates into the cells while it is being provisioned, later the larva becomes attached to the surface of the host and remains attached until the host dies. The mantispid larvae feed on the host until completion of development when a mobile pupa chews its way out of the cocoon and emerges as a mobile pharate adult.

Anchieta is the smallest genus of Symphrasinae, including eight little-known species found from Panama to Southern Brazil, with most of the species distributed across the Amazon rainforest (Ardila-Camacho *et al.*, 2018; Oswald, 2020). The genus is remarkable among the symphrasine genera, as all of the species mimic different groups of Hymenoptera (*i.e.*, Apidae (Meliponini), Vespidae, and Braconidae), and is distinguished from other genera of the subfamily by having a prominent, blunt process on the fore trochanter, and a straight anterior radial cell of forewing (Ardila-Camacho *et al.*, 2018). The only previously reported host of *Anchieta* was the mud dauber *Trypoxylon* (*Trypargilum*) *aestivale* Richards, 1934 (Hymenoptera: Crabronidae) (Buys, 2008). From the mud nest of this wasp species, a single specimen of *A. fumosella* (Westwood, 1867) was reared out and presumably it had fed on the last instar larva or on the pupa of the wasp (Buys, 2008). Recently, further unspecified associations with wasps or bees were reported by Araújo *et al.* (2021).

Based on specimens of a new *Anchieta* species – referred here as *Anchieta* **sp. nov.** – which attacked mud nests of *M. dimidiata*, the purpose of the present paper is to provide the only second known and identified host record for the genus, as well as scattered observations on the biology and the mimicking of *Anchieta*.

MATERIAL AND METHODS

Irregular surveys for nests of Hymenoptera have been performed in San Martín since 2002 by the first author, including near “Urku Estudios Amazonicos” educational center close to the Boca Toma of Rio Shilcayo, Tarapoto, Peru (06.4595°S, 76.3512°W, 410 m a.s.l.). The locality is adjacent to the local water reservoir of Tarapoto, within 100 m of the Shilcayo river, and represents an interesting transition area between lowland rainforest and lower montane rain forest, or cloud forest, in Peru. The high precipitation associated with the abrupt elevational gradient in the region of the “Cordillera Escalera” result in great environmental heterogeneity and a unique biological diversity (*e.g.*, Rasmussen & Skov, 2006; Rasmussen, 2009; Rasmussen & Gonzalez, 2009). On this location a single adult female of the potter wasp *Montezumia dimidiata* Saussure, 1852 (Vespidae: Eumeninae) was observed resting on a mud nest plastered beneath a roof tile (Fig. 1A). The nest was collected the same day on July 10th, 2012 and left in a jar awaiting emergence (Figs. 1B, 1C). All observations

hereafter were made as insects emerged from the jar left at room temperature.

Species identification of the emerging *Anchieta* was made by dissecting and clearing the abdomen, following the standard procedures with 10% Potassium Hydroxide solution (KOH). The external morphology and genital sclerites were compared with the types of all known species of *Anchieta*. All these structures were examined using a Zeiss Discovery V8 stereomicroscope. Specimens were deposited at Museo de Historia Natural de Lima, Peru (MUSM) and Museum für Naturkunde, der Humboldt-Universität, Berlin, Germany (ZMB).

RESULTS AND DISCUSSION

Biology

The *M. dimidiata* nest was smaller but otherwise similar to two nests of the same species described from Colombia by Evans (1973), including the observation that individual cells were not obvious due to irregular plastering of mud covering the surface of the nest. The collected nest contained a total of five cells, three basal cells in parallel and adhered to the surface of the tile, followed by two additional cells in a second outer row. Of the three basal cells, the first was empty, possibly damaged during the collection of the nest, and the second cell was the only open and had a small 4 mm long turret at the entrance (Fig. 1B). No provision, egg, or larvae were observed in that cell, and it is possible that this cell was either ready for provisioning by the founding female wasp observed resting on the nest or, that the female outside was instead a recently emerged wasp from this very cell. However, the presence of a turret suggests that the female outside was the founding female, although it is unclear why the last cell to be provisioned would be the most basal cell in her construction. The last of the basal row cells is the one where all five mantispid cocoons were encountered together (Figs. 1C, 1E). The second row of cells both contained wasps, with one female *M. dimidiata* wasp later emerged while the wasp in the last cell was found dead. Cells measured internally about 9 by 24 mm. No provision for the wasps were encountered in this nest, but Evans (1973) reported microlepidoptera species as prey for *M. dimidiata*.

No egg chorions were found on the smooth inner walls of the cell and it is not clear when or where the eggs of the five mantispids were deposited, but the nest was collected on July 10th, 2012, and contained by then five cocoons with content. The adult mantispids emerged July 19th (female, Fig. 1D), July 22nd (male), July 28th (male, Fig. 2A), September 6th (male pupae, died), September 8th (male, Figs. 2C–2G). This is 9, 12, 18, 58, and 60 days after the encounter and collection of the nest. The emerging mantispids are identified as *Anchieta*, but does not correspond to any of the eight known species of the genus and will be described as a new species by Ardila-Camacho in a forthcoming taxonomic revision of the genus, so here we treat it as *Anchieta* **sp. nov.**

The mantispid cocoons (Fig. 2B) were only lightly attached to the cell wall and to each other, made of loosely woven silken threads, which upon maturing turned darker yellow until reaching the coloration of the pupae, including two dark spots presumably marking the eyes. The size of the cocoons were 6 by 3 mm (the four males) and a single larger, 8 by 4 mm (the single female), made from a darker (or older) thread.

Two of the emerging *Anchieta* **sp. nov.** were observed first actively moving around as exarate pupae or pharate adults (Fig. 2C-2E), but within hours of leaving the cocoon, shed the exuviae and then rested for hours (Fig. 2E) until the cuticle and wings had completely hardened and darkened (compare the coloration of the hind leg from the same individual in Figs. 2E and 2G). One of the exarate pupae did not survive and died be-



Figure 1. The potter wasp nest with the possible founding female *Montezumia dimidiata* (Hymenoptera: Vespidae), from which five specimens of *Anchieta* **sp. nov.** (Neuroptera: Mantispidae) were reared out (A). The *M. dimidiata* nest with a single open cell, with turret, shortly after the collection (B). The nest with three exposed cells (one damaged), including the left cell contained five pupae of *Anchieta* **sp. nov.** at different developmental stages. Five days later the specimen in the upper cocoon emerged (C). The first *Anchieta* **sp. nov.** (female) to emerge (D). The cell now contains four live pupae of *Anchieta* **sp. nov.** at different developmental stages (E).

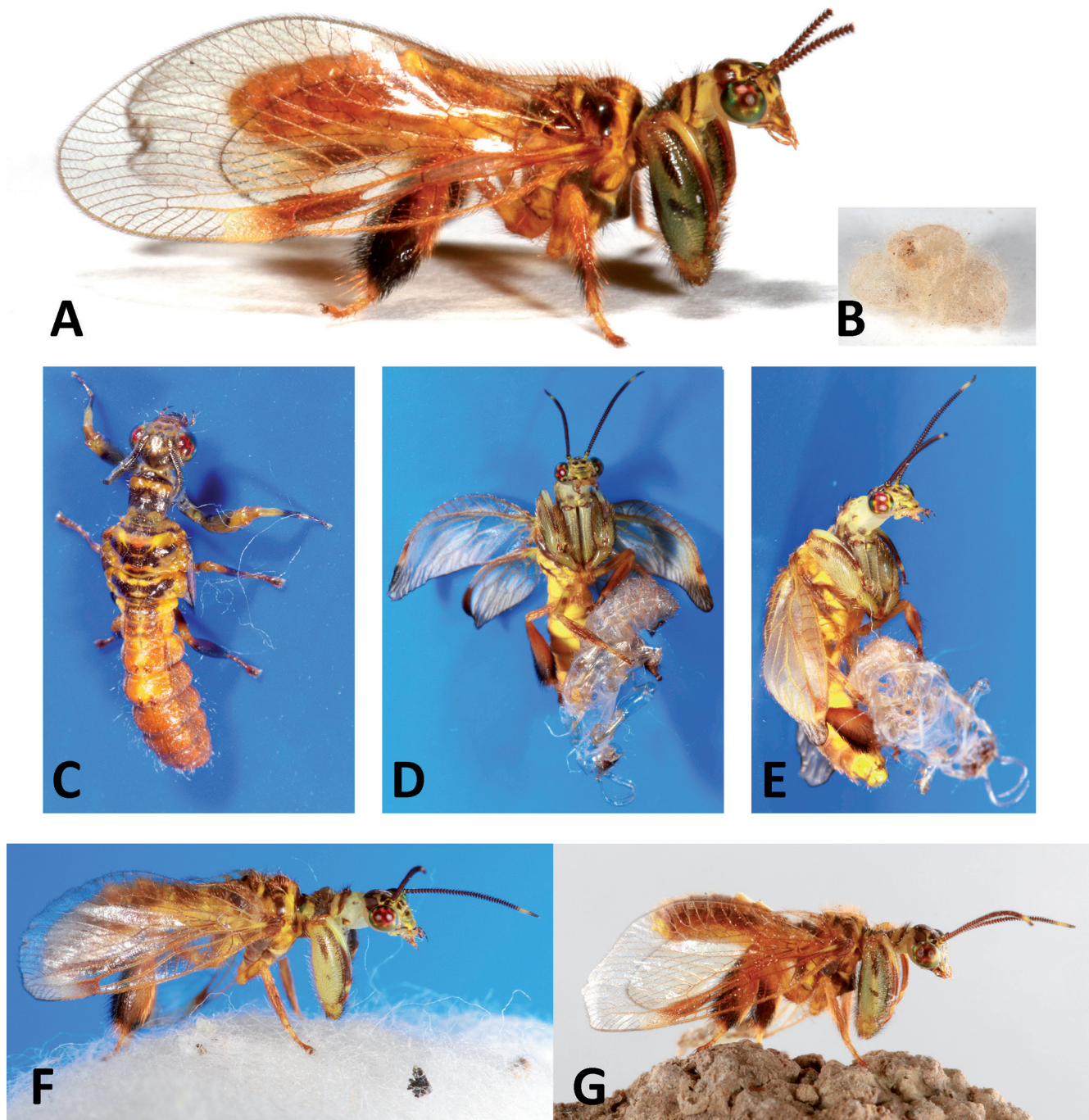


Figure 2. The third *Anchieta sp. nov.* (Neuroptera: Mantispidae), a male, to emerge from the nest of *Montezumia dimidiata* (Hymenoptera: Vespidae) (A). The empty cocoons from *Anchieta sp. nov.* (B). The last, and fifth, *Anchieta sp. nov.* to emerge, a male. This demonstrates that the pharate specimen is active and moving as a pupa (C). The specimen is removing the exuvia from the prepupa. Notice that the wings are still soft and bent (C and D). The same specimen is now waiting for the wings to strengthen few minutes after having shred the exuvia (F). The same specimen with hardened wing. Notice that the wing did not display perfectly (G).

fore molting, although it can be observed that a complete adult is trapped beneath the exuviae of the pupae. While active and moving exarate pupae were not observed for the specimens, the exuviae were always found away from the nest cell and the cocoon where they had emerged, suggesting that they would leave the pupae with the exuviae still attached. The actual shedding of the exuvia took less than ten minutes on the single instance when it was observed, that is from the individual began moving and until the exuvia was removed.

Mimicking

An interesting observation on this new species was the immediate confusion of its identity by the first author upon emergence. Having collected the nest of a known species of potter wasp and expecting the emergence of this wasp, the surprise was that the first emerging insect had a close resemblance to the social stingless bee, *Ptilotrigona lurida* (Smith, 1854), both with respect to size, coloration of wings and body, and down to the imitation of the expanded hind legs, resembling the pollen basket

of corbiculate bees (Engel & Rasmussen 2021). Dissected individuals are compared side by side in Figs. 3A-3B. The ovoid, light orange forefemur with black markings on the outer surface, plus the short and narrow hind wing resemble the compound eye and the overall shape of the hindwing of the bee, respectively. The first author has caught these bees commonly in the area, but only in forested parts, such as the type locality for *Anchieta* **sp. nov.** It has previously been reported that some species of *Anchieta* mimic stingless bees (Penny, 1982; Penny & Costa, 1984; Hogue, 1993), social wasps (e.g., *A. fumosella* in Buys, 2008) or braconids equipped with repugnant glands (e.g., *A. fasciatella* (Westwood, 1867) in Ardila-Camacho & García, 2015). Aggressive social paper wasps are common models for mantispids throughout the world (Batra, 1972; Boyden, 1983; Beck, 2005; Snyman *et al.*, 2020), and individual species have been shown to form distinct color morph mimics that traces the local wasp fauna through polymorphism (Batra, 1972; Opler, 1981). While a Vespidae wasp model is observed in a single species (*i.e.*, yellow and black morph of *A. fumosella*), most species of *Anchieta* appear to closely resemble either *Ptilotrigona* Moure, 1951 (e.g., *A. apiculasaeva* Thouvenot, 2009, *A. bella* (Westwood, 1867), *A. eurydella* (Westwood, 1867), *A. partheniella* (Westwood, 1867), *A. remipes* (Gerstaecker, 1888), and *Anchieta* **sp. nov.**) or *Trigona* Jurine, 1807 (e.g., dark morph of *A. fumosella*, and *A. notha* (Erichson, 1830)) stingless bees. For instance, *A. notha* co-occur with *Trigona spinipes* (Fabricius, 1793), while a Colombian specimen of *Anchieta eurydella* from Amacayacu (Amazonas, Colombia) was swept flying with a group of stingless bees, including *Trigona dallatorreana* Friese, 1900, *Plebeia* sp. and *Nogueirapis butteli* (Friese, 1900) with *T. dallatorreana* possibly the model in a protective Batesian mimicry system. These species of *Ptilotrigona* and *Trigona* form large nests and are amongst the most aggressive of all stingless bees, in part due to relatively large-sized and strong mandibles with pointed teeth (Kerr, 1951; Wille & Michener, 1973; Rasmussen & Camargo, 2008). The bees will attack in swarm near the nest but are unaggressive away from the nest. This is rather intriguing, as in order to provide an efficient model phenotype in a mimicry system, they also need to be noxious to predators away from the nest. However, stingless bees often carry sticky resins on the

legs, have distasteful and foul-smelling mandibular gland substances (Kerr, 1951; Smith & Roubik, 1983; Roubik, 1989), and plant-originated terpenes on the bees' cuticles (Lehmberg *et al.*, 2008; Leonhardt *et al.*, 2009) which makes them noxious and less prone to predation, as well as an efficient model for mimicry systems. In the case of *Anchieta*, the biological mimicry system is obviously Batesian, with the stingless bees being the model phenotype and *Anchieta* the mimic.

Several insect groups mimic in part stingless bees; this includes hover flies in South and Central America (Diptera: Syrphidae: *Ubristes* s.l. Walker, 1852, *Rhoga* Walker, 1857, *Copestylum* Macquart, 1846, *Ocyptamus* Macquart, 1834, a.o.) (Salt, 1929; Olesen, 1991; Cheng & Thompson, 2008; Reemer, 2010, 2012), horse flies (Tabanidae: *Lepiselaga* Macquart, 1938) (Brown *et al.*, 2009), long-horn beetles (Coleoptera: Cerambycidae: *Epimelitta* Bates, 1870, *Pseudophygopoda* Tavakilian & Peñaherrera-Leiva, 2007, *Epania* Pascoe, 1858, a.o.) (Wallace, 1867; Bates, 1870; Shelford, 1902; Schwarz, 1948; Linsley, 1959; Chemsak & Linsley, 1979), and maybe even parasitic wasps (Hymenoptera: Braconidae: *Hartemita* Cameron, 1910) (Long & Achterberg, 2011). A different strategy are found among certain predatory assassin bugs (Heteroptera: Reduviidae: *Apiomerus* Hahn, 1831, *Notocyrtus* Burmeister, 1835, *Pahabengkakia* Miller, 1941, a.o.) that resemble stingless bees (Kerr, 1951; Jackson, 1973; Johnson, 1983; Roubik, 1989; Gonzales-Bustamante, 1995; Silva & Gil-Santana, 2004; Wattanachaiyingcharoen & Jongjitvimol, 2007; Alvarez *et al.*, 2019). This is possibly in order to approach and prey on flower visiting insects.

While stingless bees are one possible model, other bees such as e.g., *Paratetrapedia* Moure, 1941 and *Tetrapedia* Klug, 1810 (Hymenoptera: Apidae) repeat the same coloration pattern (Kerr, 1951; Aguiar & Melo, 2011), and might form a mimicry complex, and a Müllerian mimicry model to the stingless bees. *Paratetrapedia* females have a sting and are able to defend themselves and their hind legs are expanded due to dense pubescence. However, suggestive of the stingless bees being the model phenotype for all mimics is the fact that stingless bees are the most abundant of the species. To provide a classical workable mimicry system imitators are always less numerous in individuals (Wallace,

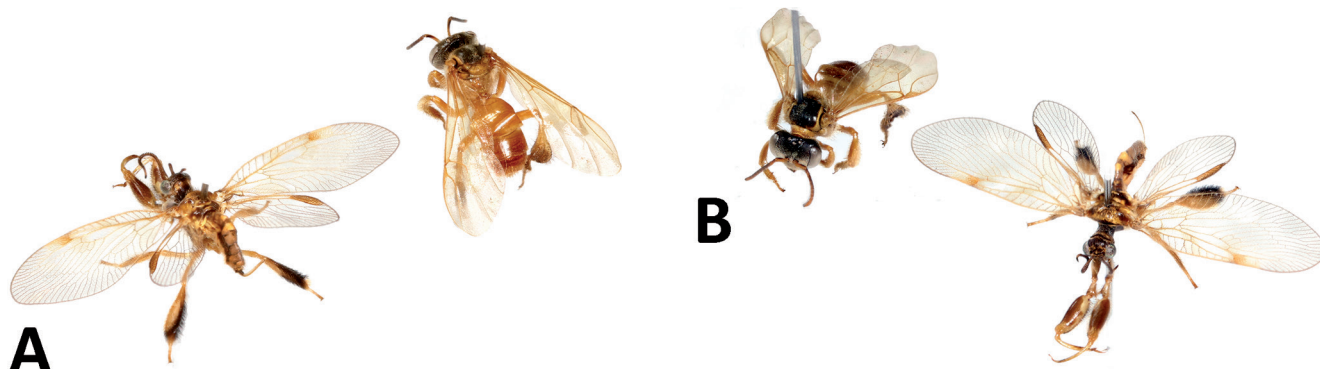


Figure 3. *Anchieta* **sp. nov.** and *Ptilotrigona lurida* (Smith, 1854) next to each other. The former with the abdomen inflated following the dried up condition (A and B).

1889; Poulton, 1890). Other bees mimicking stingless bees of the genus *Melipona* Illiger, 1806 are for example *Megachile* Latreille, 1802 and *Anthidium* Belavadi, 2017 (Megachilidae) (C. Rasmussen, pers. obs.).

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AUTHORS' CONTRIBUTIONS

C.R.: Fieldwork, Rearing, Methodology, Writing – original draft, Writing – review & editing. A.A.-C.: Identification, Methodology, Writing – review & editing. Both authors actively participated in the discussion of the results, they reviewed and approved the final version of the paper. Authors declare there are no conflicts of interest.

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